Lemurs

(Animal Diversity)

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Lemurs

Ring-tailed Lemur (*Lemur catta*)
Conservation status
CITES Appendix I (CITES)
Scientific classification
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Phylum: Chordata
Class: Mammalia
Order: Primates
Suborder: Strepsirrhini
Families
†Archaeolemuridae
Cheirogaleidae
Daubentoniidae
Indriidae
Lemuridae
Lepilemuridae
†Megaladapidae
†Palaeopropithecidae
Diversity

About 100 living species;

Range of all lemur species (green)

Lemurs are a clade of strepsirrhine primates endemic to the island of Madagascar. They are named after the *lemures* (ghosts or spirits) of Roman mythology due to the ghostly vocalizations, reflective eyes, and the nocturnal habits of some species. Although lemurs often are confused with ancestral primates, the anthropoid primates (monkeys, apes, and humans) did not evolve from them; instead, lemurs merely share morphological and behavioral traits with basal primates. Lemurs arrived in Madagascar around 62 to 65 mya by rafting on mats of vegetation at a time when ocean currents favored oceanic dispersal to the island. Since that time, lemurs have evolved to cope with an extremely seasonal environment and their adaptations give them a level of diversity that rivals that of all other primate groups. Until shortly after humans arrived on the island around 2,000 years ago, there were lemurs as large as a male gorilla. Today, there are nearly 100 species of lemurs, and most of those species have been discovered or promoted to full species status since the 1990s; however, lemur taxonomic classification is controversial and depends on which species concept is used. Even the higher-level taxonomy is disputed, with some experts preferring to place most lemurs within the infraorder **Lemuriformes**, while others prefer Lemuriformes to contain all living strepsirrhines, placing all lemurs in superfamily Lemuroidea and all lorises and galagos in superfamily Lorisoidea.

Ranging in size from 30 g (1.1 oz) to 9 kg (20 lb), lemurs share many common, basal primate traits, such as divergent digits on their hands and feet and nails instead of claws (in most species). However, their brain-to-body size ratio is smaller than that of anthropoid primates, and among many other traits they share with other strepsirrhine primates, they have a "wet nose" (rhinarium). Lemurs are generally the most social of the strepsirrhine primates and communicate more with scents and vocalizations than with visual signals. Many lemur adaptations are in response to Madagascar's highly seasonal environment. Lemurs have relatively low basal metabolic rates and may exhibit seasonal breeding, dormancy (such as hibernation or torpor), or female social dominance. Most eat a wide variety of fruits and leaves, while some are specialists. Although many share similar diets, different species of lemur share the same forests by differentiating niches.

Lemur research focused on taxonomy and specimen collection during the 18th and 19th centuries. Although field observations trickled in from early explorers, modern studies of lemur ecology and behavior did not begin in earnest until the 1950s and 1960s. Initially hindered by political instability and turmoil on Madagascar during the mid-1970s, field studies resumed in the 1980s and have greatly increased our understanding of these primates. Research facilities like the Duke Lemur Center have provided research opportunities under more controlled settings. Lemurs are important for research because their mix of primitive characteristics and traits shared with anthropoid primates can yield insights on primate and human evolution. However, many lemur species are threatened with extinction due to habitat loss and hunting. Although local traditions generally help protect lemurs and their forests, illegal logging, widespread poverty, and political instability hinder and undermine conservation efforts.

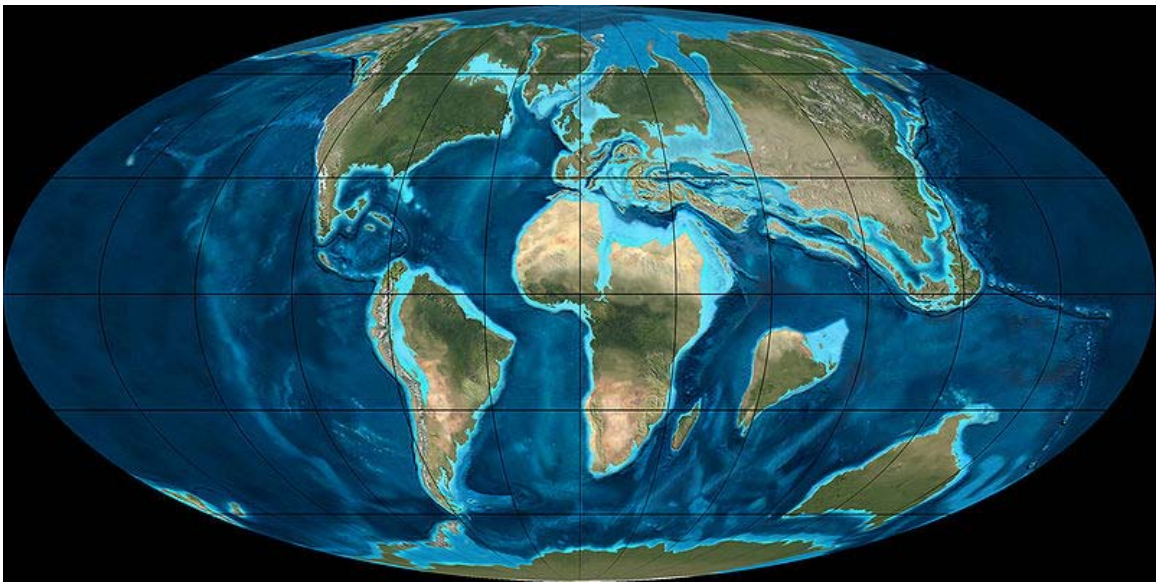
Etymology

Carl Linnaeus, the founder of modern binomial nomenclature, gave lemurs their name as early as 1754, when he used it in his catalog of the Museum of King Adolf Frederick to describe "*Lemur tardigradus*" (the Red Slender Loris, now known as *Loris tardigradus*). Four years later in *Systema Naturae*, Linnaeus put three species under the genus *Lemur*: *Lemur tardigradus*, *Lemur catta* (the Ring-tailed Lemur), and *Lemur volans* (the Philippine Colugo, now known as *Cynocephalus volans*). Although the term "lemur" was apparently at first used for lorises, it was soon limited to the endemic Malagasy primates, which have been known as "lemurs" ever since. The name derives from the Latin term *lemures*, which refers to specters or ghosts that were exorcised during the Lemuria festival. Linnaeus was familiar with the nocturnal habits and ghost-like appearance of lemurs and lorises, as well as their noiseless movements at night, reflective eyes, and ghostly cries. He may also have known that the some Malagasy people have held legends that lemurs are the souls of their ancestors. Being familiar with the works of Virgil and Ovid and seeing an analogy that fit with his naming scheme, Linnaeus adapted the term "lemur" for these nocturnal primates.

Evolutionary history

Lemurs are prosimian primates belonging to the suborder Strepsirrhini. Like other strepsirrhine primates, such as lorises, pottos, and galagos, they share ancestral (or plesiomorphic) traits with early primates. In this regard, lemurs are popularly confused with ancestral primates; however, lemurs did not give rise to monkeys and apes (simians). Instead, they evolved independently in isolation on Madagascar. All modern strepsirrhines including lemurs are traditionally thought to have evolved from primitive primates known as adapiforms during the Eocene (56 to 34 mya) or Paleocene (65 to 56 mya). Adapiforms, however, lack a specialized arrangement of teeth, known as a toothcomb, which nearly all living strepsirrhines possess. A more recent hypothesis is that lemurs descended from lorisiform (loris-like) primates. This is supported by comparative studies of the cytochrome b gene and the presence of the strepsirrhine toothcomb in both groups. Instead of being the direct ancestors of lemurs, the adapiforms may have given rise to both the lemurs and lorisiforms, a split that would be supported by

molecular phylogenetic studies. The later split between lemurs and lorises is thought to have occurred approximately 62 to 65 mya according to molecular studies, although other genetic tests and the fossil record in Africa suggest more conservative estimates of 50 to 55 mya for this divergence.



A reconstructed map of the Earth during the Early Paleocene, approximately 65 million years ago, around the time that lemurs first evolved and colonized Madagascar

Once part of the supercontinent Gondwana, the island of Madagascar has been isolated since it broke away from eastern Africa (~160 mya), Antarctica (~80–130 mya), and India (~80–90 mya). Since ancestral lemurs are thought to have originated in Africa around 62 to 65 mya, they would have had to have crossed the Mozambique Channel, a deep channel between Africa and Madagascar with a minimum width of about 560 km (350 mi). In 1915, paleontologist William Diller Matthew noted that the mammalian biodiversity on Madagascar (including lemurs) can only be accounted for by random rafting events, where very small populations rafted from nearby Africa on tangled mats of vegetation, which get flushed out to sea from major rivers. This form of biological dispersal can occur randomly over millions of years. In the 1940s, American paleontologist George Gaylord Simpson coined the term "sweepstakes hypothesis" for such random events. Rafting has since been the most accepted explanation for the lemur colonization of Madagascar, but until recently this trip was thought to be very unlikely because strong ocean currents flow away from the island. In January 2010, a report demonstrated that around 60 mya both Madagascar and Africa were 1,650 km (1,030 mi) south of their present-day positions, placing them in a different ocean gyre, producing currents that ran counter to what they are today. The ocean currents were shown to be even stronger than today, which would have pushed a raft along faster, shortening the trip to 30 days or less—short enough for a small mammal to survive easily. As the continental plates drifted northward, the currents gradually changed, and by 20 mya the window for oceanic dispersal had closed, effectively isolating the lemurs and the rest of the terrestrial Malagasy fauna from mainland Africa. Isolated on Madagascar with only a limited

number of mammalian competitors, the lemurs did not have to compete with other evolving arboreal mammalian groups, such as squirrels. They were also spared from having to compete with monkeys, which evolved later. The intelligence, aggression, and deceptiveness of monkeys gave them an advantage over other primates in exploiting the environment.

Distribution and diversity

A life restoration of *Babakotia radofilai*, a sloth lemur that became extinct less than two thousand years ago

Lemurs have adapted to fill many open ecological niches since making their way to Madagascar. Their diversity in both behavior and morphology (outward appearance)

rivals that of the monkeys and apes found elsewhere in the world. Ranging in size from the 30 g (1.1 oz) Madame Berthe's Mouse Lemur, the world's smallest primate, to the recently extinct 160–200 kg (350–440 lb) *Archaeoindris fontoynonti*, lemurs evolved diverse forms of locomotion, varying levels of social complexity, and unique adaptations to the local climate.

Lemurs lack any shared traits that make them stand out from all other primates. Different types of lemurs have evolved unique combinations of unusual traits to cope with Madagascar's harsh, seasonal climate. These traits can include seasonal fat storage, hypometabolism (including torpor and hibernation), small group sizes, low encephalization (relative brain size), cathemerality (activity both day and night), and strict breeding seasons. Extreme resource limitations and seasonal breeding are also thought to have given rise to three other relatively common lemur traits: female social dominance, sexual monomorphism, and male–male competition for mates involving low levels of agonism, such as sperm competition.

Before the arrival of humans roughly 1500 to 2000 years ago, lemurs were found all across the island. However, early settlers quickly converted the forests to rice paddies and grassland through slash-and-burn agriculture (known locally as *tavy*), restricting lemurs to approximately 10% of the island's area, ~60,000 km^2 (23,000 sq mi). Today, the diversity and complexity of lemur communities increases with floral diversity and precipitation and is highest in the rainforests of the east coast, where precipitation and floral diversity are also at their highest. Despite their adaptations for weathering extreme adversity, habitat destruction and hunting have resulted in lemur populations declining sharply, and their diversity has diminished, with the recent extinction of at least 17 species in eight genera, known collectively as the subfossil lemurs. Most of the approximately 100 species and subspecies of lemur are either threatened or endangered. Unless trends change, extinctions are likely to continue.

Until recently, giant lemurs existed on Madagascar. Now represented only by recent or subfossil remains, they were modern forms that were once part of the rich lemur diversity that has evolved in isolation. Some of their adaptations were unlike those seen in their living relatives.All 17 extinct lemurs were larger than the extant (living) forms, some weighing as much as 200 kg (440 lb), and are thought to have been active during the day. Not only were they unlike the living lemurs in both size and appearance, they also filled ecological niches that either no longer exist or are now left unoccupied. Large parts of Madagascar, which are now devoid of forests and lemurs, once hosted diverse primate communities that included more than 20 lemur species covering the full range of lemur sizes.

Taxonomic classification and phylogeny

From a taxonomic standpoint, the term "lemur" originally referred to the genus *Lemur*, which currently contains only the Ring-tailed Lemur. The term is now used in the colloquial sense in reference to all Malagasy primates.

Lemur taxonomy is controversial, and not all experts agree, particularly with the recent increase in the number of recognized species. According to Russell Mittermeier, the president of Conservation International (CI), taxonomist Colin Groves, and others, there are nearly 100 recognized species or subspecies of extant (or living) lemur, divided into five families and 15 genera. Because genetic data indicates that the recently extinct subfossil lemurs were closely related to living lemurs, an additional three families, eight genera, and 17 species can be included in the total. In contrast, other experts have labeled this as taxonomic inflation, instead preferring a total closer to 50 species.

The classification of lemurs within the suborder Strepsirrhini is equally controversial, although the most experts agree on the same phylogenetic tree. In one taxonomy published by Colin Groves, the Aye-aye was placed in its own infraorder, Chiromyiformes, while the rest of the lemurs were placed in Lemuriformes. In another taxonomy, Lemuriformes contains all living strepsirrhines in two superfamilies, Lemuroidea for all lemurs and Lorisoidea for lorises and galagos.

The Sahamalaza Sportive Lemur (*Lepilemur sahamalazensis*) was identified as a distinct species in 2006.

Lemur taxonomy has changed significantly since the first taxonomic classification of lemurs by Carl Linnaeus in 1758. One of the greatest challenges has been the classification of the Aye-aye, which has been a topic of debate up until very recently. Until Richard Owen published a definitive anatomical study in 1866, early naturalists were uncertain whether the Aye-aye (genus *Daubentonia*) was a primate, rodent, or marsupial. However, the placement of the Aye-aye within the order Primates remained problematic until very recently. Based on its anatomy, researchers have found support for classifying the genus *Daubentonia* as a specialized indriid, a sister group to all strepsirrhines, and as an indeterminate taxon within the order Primates. Molecular tests have now shown Daubentoniidae is basal to all Lemuriformes, and in 2008, Russell

Mittermeier, Colin Groves, and others ignored addressing higher-level taxonomy by defining lemurs as monophyletic and containing five living families, including Daubentoniidae.

Relationships among lemur families have also proven to be problematic and have yet to be definitively resolved. To further complicate the issue, several Paleogene fossil primates from outside Madagascar, such as *Bugtilemur*, have been classified as lemurs. However, scientific consensus does not accept these assignments based on genetic evidence, and therefore it is generally accepted that the Malagasy primates are monophyletic. Another area of contention is the relationship between the sportive lemurs and the extinct koala lemurs (Megaladapidae). Formerly grouped in the same family due to similarities in dentition, they are no longer considered to be closely related due to genetic studies.

More taxonomic changes have occurred at the genus level, although these revisions have proven more conclusive, often supported by genetic and molecular analysis. The most noticeable revisions included the gradual split of a broadly defined genus *Lemur* into separate genera for the Ring-tailed Lemur, ruffed lemurs, and brown lemurs due to a host of morphological differences.

Due to several taxonomic revisions by Russell Mittermeier, Colin Groves, and others, the number of recognized lemur species has grown from 33 species and subspecies in 1994 to approximately 100 in 2008. With continuing cytogenetic and molecular genetic research, as well as ongoing field studies, particularly with cryptic species such as mouse lemurs, the number of recognized lemur species is likely to keep growing. However, the rapid increase in the number of recognized species has had its critics among taxonomists and lemur researchers. Since classifications ultimately depend on the species concept used, conservationists often favor definitions that result in the splitting of genetically distinct populations into separate species to gain added environmental protection. Others favor a more thorough analysis.

Anatomy and physiology

Lemurs vary greatly in size. They include the smallest primates in the world and, until recently, also included some of the largest. They currently range in size from about 30 g (1.1 oz) for Madame Berthe's Mouse Lemur (*Microcebus berthae*) up to 7–9 kg (15–20 lb) for the Indri (*Indri indri*) and Diademed Sifaka (*Propithecus diadema*). When recently extinct species are considered, the size range extended up to that of a gorilla at 160–200 kg (350–440 lb) for *Archaeoindris fontoynonti*.

Close-up of a ruffed lemur's foot, showing the toilet-claw on the second toe and nails on all other toes

Like all primates, lemurs have five divergent digits with nails (in most cases) on their hands and feet. Most lemurs possess a laterally compressed, elongated nail, called a toilet-claw, on the second toe and use it for scratching and grooming. In addition to the toilet-claw, lemurs share a variety of other traits with other strepsirrhine primates, which include a rhinarium (or "wet nose"); a fully functional vomeronasal organ, which detects pheromones; a postorbital bar and the lack of postorbital closure (a wall of thin bone behind the eye); orbits (bony sockets that enclose the eye) that are not fully facing forward; left and right mandible (lower jaw) bones that are not fully fused; and a small brain-to-body mass ratio.

Additional traits shared with other prosimian primates (strepsirrhine primates and tarsiers) include a bicornuate (two-horned) uterus and epitheliochorial placentation. Because their thumbs are only pseudo-opposable, making their movement less independent of the other fingers, their hands are less than perfect at grasping and manipulating objects. On their feet, they have a widely abducted hallux (first toe) which

facilitates the grasping of tree limbs. A common misconception is that lemurs have a prehensile tail, a trait found only in New World monkeys, particularly atelids, among primates. Lemurs also rely heavily on their sense of smell, a trait shared with most other mammals and primitive primates, but not with the visually oriented higher primates.

Lemurs are a diverse group of primates in terms of morphology and physiology. Some lemurs, such as the sportive lemurs and indriids, have longer hind limbs than forelimbs, making them excellent leapers. Indriids also have a specialized digestive system for folivory, exhibiting enlarged salivary glands, a spacious stomach, and an elongated caecum (lower gut) that facilitates fermentation. The Hairy-eared Dwarf Lemur (*Allocebus trichotis*) reportedly has a very long tongue, allowing it to feed on nectar. Likewise, the Red-bellied Lemur (*Eulemur rubriventer*) has a feathery brush-shaped tongue, also uniquely adapted to feed on nectar and pollen. The Aye-aye has evolved some traits that are unique among primates, making it stand out among the lemurs. Such traits include continuously growing, rodent-like front teeth for gnawing through wood and hard seeds; a highly mobile, filiform (filament-shaped) middle finger for extracting food from tiny holes; large, bat-like ears for detecting hollow spaces within trees; and use of self-generated acoustical cues to forage.

Lemurs are unusual since they have great variability in their social structure, yet generally lack sexual dimorphism in size and canine tooth morphology. However, some species tend towards having larger females, and two species of true lemur (genus *Eulemur*), the Gray-headed Lemur (*E. albocollaris*) and the Red Lemur (*E. rufus*), exhibit size differences in canine teeth. True lemurs show sexual dichromatism (sexual differences in fur coloration), but the difference between the genders varies from strikingly obvious, as in the Black Lemur (*E. macaco*), to nearly imperceptible in the case of the Common Brown Lemur (*E. fulvus*).

Crypsis, or the inability of humans to visually distinguish between two or more distinct species, has recently been discovered among lemurs, particularly within the sportive lemurs (*Lepilemur*) and mouse lemurs (*Microcebus*). With sportive lemurs, subspecies were traditionally defined based on slight morphological differences, but new genetic evidence has supported giving full species status to these regional populations. In the case of mouse lemurs, the Gray Mouse Lemur (*M. murinus*), Golden-brown Mouse Lemur (*M. ravelobensis*), and Goodman's Mouse Lemur (*M. lehilahytsara*) were considered the same species until recently, when genetic tests identified them as cryptic species.

Dentition

Lemur deciduous and permanent dentitions

Family	Deciduous dental formula	Permanent dental formula
Cheirogaleidae, Lemuridae	$\frac{2.1.3}{2.1.3} \times 2 = 24$	$\frac{2.1.3.3}{2.1.3.3} \times 2 = 36$
Lepilemuridae	$\frac{2.1.3}{2.1.3} \times 2 = 24$	$\frac{0.1.3.3}{2.1.3.3} \times 2 = 32$

†Archaeolemuridae	$\frac{2.1.3}{2.0.3} \times 2 = 22$	$\frac{2.1.3.3}{1.1.3.3} \times 2 = 34$
†Megaladapidae	$\frac{1.1.3}{2.1.3} \times 2 = 22$	$\frac{0.1.3.3}{2.1.3.3} \times 2 = 32$
Indriidae, †Palaeopropithecidae	$\frac{2.1.2}{2.1.3} \times 2 = 22$	$\frac{2.1.2.3}{2.0.2.3} \times 2 = 30$
Daubentoniidae	$\frac{1.1.2}{1.1.2} \times 2 = 16$	$\frac{1.0.1.3}{1.0.0.3} \times 2 = 18$

The lemur dentition is heterodont (having multiple tooth morphologies) and derives from an ancestral primate permanent dentition of $\frac{2.1.3.3}{2.1.3.3}$. Indriids, sportive lemurs, the Aye-aye, and the extinct sloth lemurs, monkey lemurs, and koala lemurs have reduced dentitions, having lost incisors, canines, or premolars. The ancestral deciduous dentition is $\frac{2.1.3}{2.1.3}$, but young indriids, Aye-ayes, koala lemurs, sloth lemurs, and probably monkey lemurs have fewer deciduous teeth.

There are also noticeable differences in dental morphology and tooth topography between lemurs. Indri, for instance, have teeth that are perfectly adapted for shearing leaves and crushing seeds. In the toothcomb of most lemurs, the bottom incisors and canine teeth are procumbent (face forward rather than up) and finely spaced, thus providing a tool for either grooming or feeding. For instance, Indri use their toothcomb not only for grooming, but also to pry out the large seeds from the tough exocarp of *Beilschmiedia* fruits, while fork-marked lemurs use their relatively long toothcomb to cut through tree bark to induce the flow of tree sap. Only the Aye-aye, the extinct Giant Aye-aye, and the largest of the extinct giant sloth lemurs lack a functional strepsirrhine toothcomb. In the case of the Aye-aye, the morphology of the deciduous incisors, which are lost shortly after birth, indicate that its ancestors had a toothcomb. These milk teeth are lost shortly after birth and are replaced by open-rooted, continually growing (hypselodont) incisors.

A six-tooth version of the strepsirrhine toothcomb in a Ring-tailed Lemur, with canine-like premolars behind it

The toothcomb in lemurs normally consists of six teeth (four incisors and two canines), although indriids, monkey lemurs, and some sloth lemurs only have a four-tooth toothcomb due to the loss of either a canine or an incisor. Because the lower canine is either included in the toothcomb or lost, the lower dentition can be difficult to read, especially since the first premolar (P2) is often shaped like a canine (caniniform) to fill the canine's role. In folivorous (leaf-eating) lemurs, except for indriids, the upper incisors are greatly reduced or absent. Used together with the toothcomb on the mandible (lower jaw), this complex is reminiscent of an ungulate browsing pad.

Lemurs are unusual among primates for their rapid dental development, particularly among the largest species. For example, indriids have relatively slow body growth but extremely fast tooth formation and eruption. By contrast, anthropoid primates exhibit slower dental development with increased size and slower morphological development. Lemurs are also dentally precocious at birth, and have their full permanent dentition at weaning.

Lemurs generally have thin tooth enamel compared to anthropoid primates. This may result in extra wear and breakage to the anterior (front) teeth due to heavy use in grooming, feeding, and fighting. Little other dental health information is available for lemurs, except that wild Ring-tailed Lemurs at Berenty Private Reserve occasionally exhibit abscessed maxillary canines (seen as open wounds on the muzzle) and tooth decay, possibly due to the consumption of non-native foods.

Senses

The sense of smell, or olfaction, is highly important to lemurs and is frequently used in communication. Lemurs have long snouts (compared to the short snouts of haplorrhines) that are traditionally thought to position the nose for better sifting of smells, although long snouts do not necessarily translate into high olfactory acuity since its not the relative size of the nasal cavity that correlates with smell, but the density of olfactory receptors. Instead, the long snouts may facilitate better chewing.

Lemurs generally have a wet nose, or rhinarium, as well as a longer snout than anthropoid primates.

The wet nose, or rhinarium, is a trait shared with other strepsirrhines and many other mammals, but not with haplorrhine primates. Although it is claimed to enhance the sense of smell, it is actually a touch-based sense organ that connects with a well-developed

vomeronasal organ (VNO). Since pheromones are usually large, non-volatile molecules, the rhinarium is used to touch a scent-marked object and transfer the pheromone molecules down the philtrum (the nasal mid-line cleft) to the VNO via the nasopalatine ducts that travel through the incisive foramen of the hard palate.

To communicate with smell, which is useful at night, lemurs will scent mark with urine as well as scent glands located on the wrists, inside elbow, genital regions, or the neck. The scrotal skin of most male lemurs has scent glands. Ruffed lemurs (genus *Varecia*) and male sifakas have a gland at the base of their neck, while the Greater Bamboo Lemur (*Prolemur simus*) and the Ring-tailed Lemur have glands inside the upper arms near the axilla. Male Ring-tailed Lemurs also have scent glands on the inside of their forearms, adjacent to a thorn-like spur, which they use to gouge, and simultaneously, scent-mark tree branches. They will also wipe their tails between their forearms and then engage in "stink fights" by waving their tail as their opponents.

Lemurs (and strepsirrhines in general) are considered to be less visually oriented than the higher primates, since they rely so heavily on their sense of smell and pheromone detection. The fovea on the retina; which yields higher visual acuity, is not well-developed. The postorbital septum (or bony closure behind the eye) in haplorrhine primates is thought to stabilize the eye slightly, allowing for the evolution of the fovea. With only a postorbital bar, lemurs have been unable to develop a fovea. Therefore, regardless of their activity pattern (nocturnal, cathemeral, or diurnal), lemurs exhibit low visual acuity and high retinal summation. Lemurs can see a wider visual field, however, than anthropoid primates due to a slight difference in the angle between the eyes, as shown in the following table:

Optical angles and visual fields

	Angle between eyes	**Binocular field**	**Combined field (binocular + periphery)**
Lemurs	10–15°	114–130°	250–280°
Anthropoid primates	0°	140–160°	180–190°

Although they lack a fovea, some diurnal lemurs have a cone-rich, although less clustered, area centralis. This area centralis has a high rod-to-cone cell ratio in many diurnal species studied thus far, whereas diurnal anthropoids have no rod cells in their

fovea. Once again, this suggests lower visual acuity in lemurs than in anthropoids. Furthermore, the rod-to-cone cell ratio can be variable even among diurnal species. For instance, Verreaux's Sifaka (*Propithecus verreauxi*) and the Indri (*Indri indri*) have only a few large cones scattered along their predominantly rod-dominated retina. The eyes of the Ring-tailed Lemur contain one cone to five rods. Nocturnal lemurs such as mouse lemurs and dwarf lemurs, on the other hand, have retinas made up entirely of rod cells.

Since cone cells make color vision possible, the high prevalence of rod cells in lemur eyes suggest they have not evolved color vision. The most studied lemur, the Ring-tailed Lemur, has been shown to have blue-yellow vision, but lacks the ability to distinguish red and green hues. Due to polymorphism in opsin genes, which code for color receptivity, trichromatic vision may rarely occur in females of a few lemur species, such as Coquerel's Sifaka (*Propithecus coquereli*) and the Red Ruffed Lemur (*Varecia rubra*). Most lemurs, therefore, are either monochromats or dichromats.

Aye-ayes exhibit eyeshine because they have a reflective layer of tissue in the eye, called a tapetum lucidum.

Most lemurs have retained the tapetum lucidum, a reflective layer of tissue in the eye, which is found in many vertebrates. This trait is absent in haplorrhine primates, and its presence further limits the visual acuity in lemurs. The strepsirrhine choroidal tapetum is unique among mammals because it is made up of crystalline riboflavin, and the resulting optical scattering is what limits visual acuity. Although the tapetum is considered to be

ubiquitous in lemurs, there appear to be exceptions among true lemurs, such as the Black Lemur and the Common Brown Lemur, as well as the ruffed lemurs. Since the riboflavins in the tapetum have a tendency to dissolve and vanish when processed for histological investigation, however, the exceptions are still debatable.

Metabolism

Lemurs have low basal metabolic rates (BMR), which helps them to conserve energy during the dry season, when water and food are scarce. They can optimize their energy use by lowering their metabolic rate to 20% below the values predicted for mammals of similar body mass. The Red-tailed Sportive Lemur (*Lepilemur ruficaudatus*), for instance, reportedly has one of the lowest metabolic rates among mammals. Its low metabolic rate may be linked to its generally folivorous diet and relatively small body mass. Lemurs exhibit behavioral adaptations to complement this trait, including sunning behaviors, hunched sitting, group huddling, and nest sharing, in order to reduce heat loss and conserve energy. Dwarf lemurs and mouse lemurs exhibit seasonal cycles of dormancy to conserve energy. Before dry season, they will accumulate fat in white adipose tissue located at the base of the tail and hind legs, doubling their weight. At the end of the dry season, their body mass may fall to half of what it was prior to the dry season. Lemurs that do not experience states of dormancy are also able to shut down aspects of their metabolism for energy conservation.

Behavior

Lemur behavior is as variable as lemur morphology. Differences in diet, social systems, activity patterns, locomotion, communication, predator avoidance tactics, breeding systems, and intelligence levels help define lemur taxa and set individual species apart from the rest. Although trends frequently distinguish the smaller, nocturnal lemurs from the larger, diurnal lemurs, there are often exceptions that help exemplify the unique and diverse nature of these Malagasy primates.

Diet

Mouse lemurs primarily eat fruit, although their diet also includes insects

Lemur diets are highly variable and demonstrate a high degree of plasticity, although general trends suggest that the smallest species primarily consume fruit and insects (omnivory), while the larger species are more herbivorous, consuming mostly plant material. As with all primates, hungry lemurs might eat anything that is edible, whether or not the item is one of their preferred foods. For instance, the Ring-tailed Lemur eats insects and small vertebrates when necessary and as a result it is commonly viewed as an opportunistic omnivore. Coquerel's Giant Mouse Lemur (*Mirza coquereli*) is mostly frugivorous, but will consume insect secretions during the dry season.

A common assumption in mammalogy is that small mammals cannot subsist entirely on plant material and must have a high-calorie diet in order to survive. As a result, it was thought that the diet of tiny primates must be high in protein-containing insects (insectivory). Research has shown, however, that mouse lemurs, the smallest living primates, consume more fruit than insects, contradicting the popular hypothesis.

Plant material makes up the majority of most lemur diets. Members of at least 109 of all known plant families in Madagascar (55%) are exploited by lemurs. Since lemurs are primarily arboreal, most of these exploited species are woody plants, including trees, shrubs, or lianas. Only the Ring-tailed Lemur, the bamboo lemurs (genus *Hapalemur*), and the Black-and-white Ruffed Lemur (*Varecia variegata*) are known to consume herbs.

While Madagascar is rich in fern diversity, these plants are rarely eaten by lemurs. One possible reason for this is that ferns lack flowers, fruits, and seeds—common food items in lemur diets. They also occur close to the ground, while lemurs spend most of their time in the trees. Lastly, ferns have an unpleasant taste due to the high content of tannins in their fronds. Likewise, mangroves appear to be rarely exploited by lemurs due to their high tannin content. Some lemurs appear to have evolved responses against common plant defenses, however, such as tannins and alkaloids. The Golden Bamboo Lemur (*Hapalemur aureus*), for instance, eats giant bamboo (*Cathariostachys madagascariensis*), which contains high levels of cyanide. This lemur can consume twelve times the typically lethal dose for most mammals on a daily basis; the physiological mechanisms that protect it from cyanide poisoning are unknown. At the Duke Lemur Center (DLC) in the United States, lemurs that roam the outdoor enclosures have been observed eating poison ivy (*Taxicodendron radicans*), yet have shown no ill effects.

Up to 95% of the Greater Bamboo Lemur's diet consists of bamboo

Many of the larger lemur species consume leaves (folivory), particularly the indriids. However, some smaller lemurs such as sportive lemurs (genus *Lepilemur*) and woolly lemurs (genus *Avahi*) also primarily eat leaves, making them the smallest primates that do so. The smallest of the lemurs generally do not eat much leaf matter. Collectively, lemurs have been documented consuming leaves from at least 82 native plant families and 15 alien plant families. Lemurs tend to be selective in their consumption of the part of the leaf or shoot as well as its age. Often, young leaves are preferred over mature leaves.

Many lemurs that eat leaves tend to do so during times of fruit scarcity, sometimes suffering weight loss as a result. Most lemur species, including most of the smallest lemurs and excluding some of the indriids, predominantly eat fruit (frugivory) when available. Collectively, lemurs have been documented consuming fruit from at least 86 native plant families and 15 alien plant families. As with most tropical fruit eaters, the lemur diet is dominated by fruit from *Ficus* (fig) species. In many anthropoid primates, fruit is a primary source of vitamin C, but unlike anthropoid primates, lemurs (and all strepsirrhines) can synthesize their own vitamin C. Historically, captive lemur diets high in vitamin C-rich fruits have been thought to cause hemosiderosis, a type of iron overload disorder, since vitamin C increases iron absorption. Although lemurs in captivity have been shown to be prone to hemosiderosis, the frequency of the disease varies across institutions and may depend on the diet, husbandry protocols, and genetic stock. Assumptions about the problem need to be tested separately for each species. The Ring-tailed Lemur, for instance, seems to be less prone to the disorder than other lemur species.

Only eight species of lemur are known to be seed predators (granivores), but this may be under-reported since most observations only report fruit consumption and do not investigate whether the seeds are consumed as well. These lemurs include some indriids, such as the Diademed Sifaka (*Propithecus diadema*), the Golden-crowned Sifaka (*Propithecus tattersalli*), the Indri, and the Aye-aye. The Aye-aye, which specializes in structurally defended resources, can chew through *Canarium* seeds, which are harder than the seeds that New World monkeys are known to break open. At least 36 genera from 23 families of plants are targeted by lemur seed predators.

Inflorescences (clusters of flowers) of at least 60 plant families are eaten by lemurs ranging in size from the tiny mouse lemurs to the relatively large ruffed lemurs. If the flowers are not exploited, sometimes the nectar is consumed (nectarivory) along with the pollen (palynivory). At least 24 native species from 17 plant families are targeted for nectar or pollen consumption.

Bark and plant exudates such as tree sap are consumed by a few lemur species. The exploitation of exudates has been reported in 18 plant species and only in the dry regions in the south and west of Madagascar. Only the Masoala Fork-marked Lemur (*Phaner furcifer*) and Coquerel's Giant Mouse Lemur regularly consume tree sap. Bark has never been reported as an important food item in lemur diets, but at least four species eat it: the Aye-aye, the Red-tailed Sportive Lemur (*Lepilemur ruficaudatus*), the Common Brown Lemur (*Eulemur fulvus*), and Verreaux's Sifaka (*Propithecus verreauxi*). Most bark

feeding is directly linked to exudate feeding, except for the Aye-aye's bark feeding on *Afzelia bijuga* (genus *Afzelia*) at Nosy Mangabe in the northeast.

Soil consumption (geophagy) has also been reported and likely helps with digestion, provides minerals and salts, and helps absorb toxins. Sifakas have been observed eating soil from termite mounds, possibly adding beneficial intestinal flora to aid the digestion of cellulose from their folivorous diet.

Social systems

Lemurs are social and live in groups that usually include less than 15 individuals. Observed social organization patterns include "solitary but social", "fission-fusion", "pair bonds", and "multi-male group". Nocturnal lemurs are mostly solitary but social, foraging alone at night but often nesting in groups during the day. The degree of socialization varies by species, gender, location, and season. In many nocturnal species, for instance, the females, along with their young, will share nests with other females and possibly one male, whose larger home range happens to overlap one or more female nesting groups. In sportive lemurs and fork-marked lemurs, one or two females may share a home range, possibly with a male. In addition to sharing nests, they will also interact vocally or physically with their range-mate while they forage at night. Diurnal lemurs exhibit many of the social systems seen in monkeys and apes, living in relatively permanent and cohesive social groups. Multi-male groups are the most common, just as they are in most anthropoid primates. True lemurs utilize this social system, often living in groups of ten or less. Ruffed lemurs have been shown to live in fission-fusion societies, and Indri forms pair bonds.

Dwarf lemurs are solitary but social, foraging alone but often sleeping in groups.

Some lemurs exhibit female philopatry, where females stay within their natal range and the males migrate upon reaching maturity, and in other species both sexes will migrate. In some cases, female philopatry may help explain the evolution of female-bonded multi-male groups, such as those of the Ring-tailed Lemur, Milne-Edwards' Sifaka (*Propithecus edwardsi*), and the Verreaux's Sifaka. Their ancestors may have been more solitary, with females that lived in mother-daughter pairs (or dyads). Over time, these dyads may have allied themselves with other neighboring mother-daughter dyads in order to defend more distributed resources in a wide home range. If this is true, then multi-male groups in lemurs may differ fundamentally in their internal structure from those in catarrhine primates (Old World monkeys and apes).

The presence of female social dominance sets lemurs apart from most other primates and mammals; in most primate societies, males are dominant unless females band together to form coalitions that displace them. However, many *Eulemur* species are exceptions and the Greater Bamboo Lemur (*Prolemur simus*) does not exhibit female dominance. When

females are dominant within a group, the way they maintain dominance varies. Ring-tailed Lemur males act submissively with or without signs of female aggression. Male Crowned Lemurs (*Eulemur coronatus*), on the other hand, will only act submissively when females act aggressively towards them. Female aggression is often associated with, but not limited to, feeding.

There have been many hypotheses that have attempted to explain why lemurs exhibit female social dominance while other primates with similar social structures do not, but no consensus has been reached after decades of research. The dominant view in the literature states that female dominance is an advantageous trait given the high costs of reproduction and the scarcity of resources available. Indeed, female dominance has been shown to be linked to increased maternal investment. However, when reproductive costs and extreme seasonality of resources were compared across primates, other primates demonstrated male dominance under conditions that were similar to or more challenging than those faced by lemurs. In 2008, a new hypothesis revised this model using simple game theory. It was argued that when two individuals were equally matched in fighting capacity, the one with the most need would win the conflict since it would have the most to lose. Consequently, the female, with higher resource needs for pregnancy, lactation, and maternal care, was more likely to win in resource conflicts with equally sized males. This, however, assumed monomorphism between sexes. The following year, a new hypothesis was proposed to explain monomorphism, stating that because most female lemurs are only sexually receptive for a day or two each year, males can utilize a more passive form of mate guarding: copulatory plugs, which block the female reproductive tract, preventing other males from successfully mating with her, and thus reducing the need for aggression and the evolutionary drive for sexual dimorphism.

Social grooming serves many functions for social lemurs

In general, levels of agonism (or aggression) tend to correlate with relative canine height. The Ring-tailed Lemur has long, sharp upper canine teeth in both sexes, and it also exhibits high levels of agonism. The Indri, on the other hand, has smaller canines and exhibits lower levels of aggression. When neighboring groups of the same species defend their territories, the conflict can take the form of ritualized defense. In sifakas, these ritualized combats involve staring, growling, scent-marking, and leaping to occupy certain sections of the tree. The Indri defends its home range with ritualized "singing" battles.

Like other primates, lemurs groom socially (allogroom) to ease tensions and solidify relationships. They groom in greeting, when waking up, when settling in for sleep, between mother and infant, in juvenile relations, and for sexual advances. Unlike anthropoid primates, who part the fur with the hands and pick out particles with the fingers or mouth, lemurs groom with their tongue and scraping with their toothcomb. Despite the differences in technique, lemurs groom with the same frequency and for the same reasons as anthropoids.

Activity patterns

The biological rhythm can vary from nocturnal in smaller lemurs to diurnal in most larger lemurs. Diurnality is not seen in any other prosimian. Cathemerality, where an animal is active sporadically both day and night, occurs among some of the larger lemurs. Few if any other primates exhibit this sort of activity cycle, either regularly or irregularly under changing environmental conditions. The most heavily studied cathemeral lemurs are the true lemurs. Although the Mongoose Lemur (*E. mongoz*) is the best-documented example, every species in the genus studied has shown some degree of cathemeral behavior, although night activity is often restricted by light availability and moon periodicity. This type of behavior was first documented in the 1960s in true lemur species as well as other Lemuridae species, such as ruffed lemurs and bamboo lemurs. Initially described as "crepuscular" (active at dawn and dusk), anthropologist Ian Tattersall stimulated additional research and coined the new term "cathemeral", although many non-anthropologists prefer the terms "circadian" or "diel".

In order to conserve energy and water in their highly seasonal environment, mouse lemurs and dwarf lemurs exhibit seasonal behavioral cycles of dormancy where the metabolic rate and body temperature are lowered. They are the only primates known to do so. They accumulate fat reserves in their hind legs and the base of their tail before the dry winter season, when food and water are scarce, and can exhibit daily and prolonged torpor during the dry season. Daily torpor constitutes less than 24 hours of dormancy, whereas prolonged torpor averages two weeks in duration and signals hibernation. Mouse lemurs have been observed experiencing torpor that lasts for several consecutive days, but dwarf lemurs are known to hibernate for six to eight months every year, particularly on the west coast of Madagascar.

Dwarf lemurs are the only primates known to hibernate for extended periods. Unlike other hibernating mammals from temperate regions, which have to awaken regularly for a

few days, dwarf lemurs experience five months of continuous deep hibernation (May through September). Before and after this deep hibernation, there are two months (April and October) of transition, where they will forage on a limited basis to reduce demands on their fat reserves. Unlike any other hibernating mammal, the body temperature of hibernating dwarf lemurs will fluctuate with the ambient temperature rather than remaining low and stable.

Other lemurs that do not exhibit dormancy conserve energy by selecting thermoregulated microhabitats (such as tree holes), sharing nests, and reducing exposed body surfaces, such as by hunched sitting and group huddling. Also, the Ring-tailed Lemur, ruffed lemurs, and sifakas are commonly seen sunning, thus using solar radiation to warm their bodies instead of metabolic heat.

Locomotion

Sifakas are specially adapted to vertical clinging and leaping, so they must hop sideways to move on the ground.

Locomotor behavior in lemurs, both living and extinct, is highly varied and its diversity exceeds that of anthropoids. Locomotor postures and behaviors have included vertical clinging and leaping (including saltatory behavior), seen in indriids and bamboo lemurs; slow (loris-like) arboreal quadrupedal locomotion, once exhibited by *Mesopropithecus*; fast arboreal quadrupedal locomotion, seen in true lemurs and ruffed lemurs; partially terrestrial quadrupedal locomotion, seen in the Ring-tailed Lemur; highly terrestrial quadrupedal locomotion, once exhibited by monkey lemurs such as *Hadropithecus*; and sloth-like suspensory locomotion, once exhibited by many of the sloth lemurs, such as *Palaeopropithecus*. The Lac Alaotra Gentle Lemur (*Hapalemur alaotrensis*) has even been reported to be a good swimmer. Sometimes these locomotor types are lumped together into two main groups of lemurs, the vertical clingers and leapers and the arboreal (and occasionally terrestrial) quadrupeds.

The jumping prowess of the indriids have been well documented and are popular among ecotourists visiting Madagascar. Using their long, powerful back legs, they catapult themselves into the air and land in an upright posture on a nearby tree, with both hands and feet tightly gripping the trunk. Indriids can leap up to 10 m (33 ft) rapidly from tree trunk to tree trunk, an ability referred to as "ricochetal leaping". Verreaux's Sifaka (*Propithecus verreauxi*) manages to do this in the spiny forests of southern Madagascar. It is unknown how it avoids impaling its palms on the thorn-covered trunks of large plants such as *Alluaudia*. When distances between trees are too great, sifakas will descend to the ground and cross distances more than 100 m (330 ft) by standing upright and hopping sideways with the arms held to the side and waving up and down from chest to head height, presumably for balance. This is sometimes described as a "dance-hop".

Communication

Lemur communication can be transmitted through sound, sight, and smell (olfaction). The Ring-tailed Lemur, for instance, uses complex though highly stereotyped behaviors such as scent-marking and vocalizations. Visual signals are probably the least used by lemurs, since they lack many of the muscles used in common primate facial expressions. Given their poor vision, whole-body postures are probably more noticeable. However, the Ring-tailed Lemur has demonstrated distinct facial expressions including a threat stare, pulled back lips for submission, and pulled back ears along with flared nostrils during scent-marking. This species has also been observed using yawns as threats. Their ringed tails also communicate distance, warn off neighboring troops, and help locate troop members. Sifakas are known to exhibit an open-mouth play face as well as a submissive teeth-baring grimace used in agonistic interactions.

Lemurs communicate by scent-marking their territory

Olfaction is particularly important to lemurs, except for the Indri, which lacks most common lemur scent glands and has a greatly reduced olfactory region in the brain. Olfaction can communicate information about age, sex, reproductive status, as well as demarcate the boundaries of a territory. It is most useful for communication between animals that rarely encounter each other. Small, nocturnal lemurs mark their territories with urine, while the larger, diurnal species use scent glands located on various parts of their anatomy. The Ring-tailed Lemur engages in "stink fights" by rubbing its tail across scent glands on its wrists, and then flicking its tail at other male opponents. Some lemurs defecate in specific areas, otherwise known as latrine behavior. Although many animals exhibit this behavior, it is a rare trait among primates. Latrine behavior can represent territorial marking and aid in interspecies signaling.

Compared to other mammals, primates in general are very vocal, and lemurs are no exception. Some lemur species have extensive vocal repertoires, including the Ring-tailed Lemur and ruffed lemurs. Some of the most common calls among lemurs are predator alarm calls. Lemurs not only respond to alarm calls of their own species, but also alarm calls of other species and those of non-predatory birds. The Ring-tailed Lemur and a few other species have different calls and reactions to specific types of predators. With mating calls, it has been shown that mouse lemurs that cannot be discerned visually respond more strongly to the calls of their own species, particularly when exposed to the calls of other mouse lemurs that they would encounter normally within their home range. Lemur

calls can also be very loud and carry long distances. Ruffed lemurs use several loud calls that can be heard up to 1 km (0.62 mi) away on a clear, calm day. The loudest lemur is the Indri, whose calls can be heard up to 2 km (1.2 mi) or more and thus communicate more effectively the territorial boundaries over its 34 to 40 hectares (0.13 to 0.15 sq mi) home range. Both ruffed lemurs and the Indri exhibit contagious calling, where one individual or group starts a loud call and others within the area join in. The song of the Indri can last 45 seconds to more than 3 minutes and tends to coordinate to form a stable duet comparable to that of gibbons.

Tactile communication (touch) is mostly used by lemurs in the form of grooming, although the Ring-tailed Lemur also clumps together to sleep (in an order determined by rank), reaches out and touches adjacent members, and cuffs other members. Reaching out and touching another individual in this species has been shown to be a submissive behavior, done by younger or submissive animals towards older and more dominant members of the troop. Allogrooming, however, appears to occur more frequently between higher ranking individuals, a shared trait with other primate species. Unlike anthropoid primates, lemur grooming seems to be more intimate and mutual, often directly reciprocated. Anthropoids, on the other hand, use allogrooming to manage agonistic interactions. The Ring-tailed Lemur is known to be very tactile, spending between 5 and 11% of its time grooming.

Predator avoidance

All lemurs experience some predation pressure. Common defenses against predation include the use of alarm calls and predator mobbing, mostly among diurnal lemurs. The leaping abilities of lemurs may have evolved for predator avoidance rather than for travel, according to a study in kinematics. Nocturnal lemurs are difficult to see and track at night and decrease their visibility by foraging alone. They also try to avoid predators by using concealing sleeping locations, such as nests, tree holes, or dense vegetation, and alternating between multiple sleeping locations. Even torpor and hibernation states among cheirogaleids may be partly due to high levels of predation. Infants are protected while foraging by either leaving them in the nest or by stashing them in a hidden location, where the infant remains immobile in the absence of the parent.

Diurnal lemurs are visible during the day, so many live in groups, where the increased number of eyes and ears helps aid in predator detection. Diurnal lemurs use and respond to alarm calls, even those of other lemur species and non-predatory birds. The Ring-tailed Lemur has different calls and reactions to different classes of predators, such as predatory birds, mammals, or snakes. Some lemurs, such as the Indri, use crypsis to camouflage themselves. They are often heard but difficult to see in the trees due to the dappled light, earning them the reputation of being "ghosts of the forest".

Reproduction

Except for the Aye-aye and the Lac Alaotra Gentle Lemur, lemurs are seasonal breeders with very short mating and birth seasons influenced by the highly seasonal availability of

resources in their environment. Mating seasons usually last less than three weeks each year, with the female vagina opening up only during a few hours or days of her most receptive time of estrus. These narrow windows for reproduction and resource availability appear to relate to their short gestation periods, rapid maturation, and low basal metabolic rates, as well as the high energy costs of reproduction for females. This may also relate to the relatively high mortality rate among adult females and the higher proportion of adult males in some lemur populations—both unusual traits among primates. In both the Aye-aye and Lac Alaotra Gentle Lemur, birth (parturition) occurs over a six-month period.

Lemurs time their mating and birth seasons so that all weaning periods are synchronized to match the time of highest food availability. Weaning occurs either before or shortly after the eruption of the first permanent molars in lemurs. Mouse lemurs are able to fit their entire breeding cycle into the wet season, whereas larger lemurs, such as sifakas, must lactate for two months during the dry season. Infant survival in some species, such as Milne-Edwards' Sifaka, has been shown to be directly impacted by both environmental conditions and the rank, age, and health of the mother. The breeding season is also affected by geographical location. For example, mouse lemurs give birth between September and October in their native habitat in the southern hemisphere, but from May through June in the captive settings in the northern hemisphere.

Woolly lemurs are nocturnal and typically give birth to one offspring, which they carry with them while foraging.

Scent factors heavily into lemur reproduction. Scent-marking activity escalates during the mating season. Pheromones may coordinate reproductive timing for females coming into estrus. Mating can be either monogamous or promiscuous for both males and females, and mating can include individuals from outside the group. Monogamous lemurs include the Red-bellied Lemur (*Eulemur rubriventer*) and the Mongoose Lemur (*Eulemur mongoz*), although the Mongoose Lemur has been observed mating outside of its pair bond. Monogamy is most common among nocturnal species, although some exhibit scramble competition, sexual suppression of subordinates, or competitions between males that avoid direct fighting. In mouse lemurs, males utilize sperm plugs, developed enlarged testes during the mating season, and develop size dimorphism (likely due to the enlarged testes). These indicate a mating system known as scramble competition polygyny, where males cannot defend females or the resources that might attract them.

The gestation period varies within lemurs, ranging from 9 weeks in mouse lemurs and 9–10 weeks in dwarf lemurs to 18–24 weeks in other lemurs. The smaller, nocturnal lemurs, such as mouse lemurs, giant mouse lemurs, and dwarf lemurs, usually give birth to more than one infant, whereas the larger, nocturnal lemurs, such as fork-marked lemurs, sportive lemurs, and the Aye-aye usually have one offspring. Dwarf and mouse lemurs have up to four offspring, but both average only two. Ruffed lemurs are the only large, diurnal lemurs to consistently give birth to two or three offspring. All other lemurs have single births. Multiple births in lemurs are normally fraternal, and are known to occur in every five to six births in species such as the Ring-tailed Lemur and some *Eulemur*.

After the offspring are born, lemurs either carry them around or stash them while foraging. When transported, the infants either cling to the mother's fur or are carried in the mouth by the scruff. In some species, such as bamboo lemurs, infants are carried by mouth until they are able to cling to their mother's fur. Species that park their offspring include nocturnal species (e.g. mouse lemurs, sportive lemurs, and dwarf lemurs), bamboo lemurs, and ruffed lemurs. In the case of the ruffed lemurs, the young are altricial and the mothers build nests for them, much like the smaller, nocturnal lemur species. Woolly lemurs are unusual for nocturnal lemurs because they live in cohesive family groups and carry their single offspring with them rather than parking them. Alloparenting (multiple or group parenting) has been reported in all lemur families except the sportive lemurs and Aye-aye. Allonursing is also known to occur in several lemur groups. Even males have been observed caring for infants in species such as the Red-bellied Lemur, Mongoose Lemur, Eastern Lesser Bamboo Lemur, Silky Sifaka, Fat-tailed Dwarf Lemur, and ruffed lemurs.

Yet another trait that sets most lemurs apart from anthropoid primates is their long lifespan together with their high infant mortality. Many lemurs, including the Ring-tailed Lemur, have adapted to a highly seasonal environment, which has affected their birthrate, maturation, and twinning rate (r-selection). This helps them to recover rapidly from a population crash. In captivity, lemurs can live twice as long as they do in the wild, benefiting from consistent nutrition that meets their dietary requirements, medical advancements, and improved understanding of their housing requirements. In 1960, it was thought that lemurs could live between 23 and 25 years. We now know that the

larger species can live for more than 30 years without showing signs of aging (senescence) and still be capable of reproduction.

Cognitive abilities and tool use

Lemurs have traditionally been regarded as being less intelligent than anthropoid primates, with monkeys and apes often described as having more cunning, guile, and deceptiveness. Many lemur species, such as sifakas and the Ring-tailed Lemur, have scored lower on tests designed for monkeys while performing as well as monkeys on other tests. These comparisons may not be fair since lemurs prefer to manipulate objects with their mouths (rather than their hands) and only take interest in objects when in captivity. Tool use has not been witnessed by lemurs in the wild, although in captivity the Common Brown Lemur and the Ring-tailed Lemur have been demonstrated to be able to understand and use tools.

A few lemurs have been noted to have relatively large brains. The extinct *Hadropithecus* was as large as a large male baboon and had a comparably sized brain, giving it the largest brain size relative to body size among all prosimians. The Aye-aye also has a large brain-to-body ratio, which may indicate a higher level of intelligence. However, despite having a built-in tool in the form of its thin, elongated middle finger, which it uses to fish for insect grubs, the Aye-aye has tested poorly in the use of extraneous tools.

Ecology

Madagascar not only contains two radically different climatic zones, the rainforests of the east and the dry regions of the west, but also swings from extended drought to cyclone-generated floods. These climatic and geographical challenges, along with poor soils, low plant productivity, wide ranges of ecosystem complexity, and a lack of regularly fruiting trees (such as fig trees) have driven the evolution of lemurs' immense morphological and behavioral diversity. Their survival has required the ability to endure the persistent extremes, not yearly averages.

The Fossa (above) and the Madagascar Harrier-hawk (below) are predators of many lemur species.

Lemurs have either presently or formerly filled the ecological niches normally occupied by monkeys, squirrels, woodpeckers, and grazing ungulates. With the diversity of adaptations for specific ecological niches, habitat selections among lemur families and some genera are often very distinct, thus minimizing competition. In nocturnal lemurs from the more seasonal forests in the west, up to five species can coexist during the wet season due to high food abundance. However, to endure the extreme dry season, three of the five species utilize different dietary patterns and their underlying physiological traits to allow them to coexist: fork-marked lemurs feed on tree gum, sportive lemurs feed on leaves, and giant mouse lemurs sometimes feed on insect secretions. The other two species, the Gray Mouse Lemur and the Fat-tailed Dwarf Lemur (*Cheirogaleus medius*), avoid competition through reduced activity. The Gray Mouse Lemur uses bouts of torpor, while the Fat-tailed Dwarf Lemur hibernates completely. Similarly, on the east coast entire genera focus on specific food to avoid too much niche overlap. True lemurs and ruffed lemurs are frugivorous, indriids are folivorous, and bamboo lemurs specialize in bamboo and other grasses. Once again, seasonal dietary differences as well as subtle differences in substrate preferences, forest strata used, activity cycle, and social organization enable lemur species to coexist, although this time the species are more closely related and have similar niches. A classic example involves resource partitioning between three species of bamboo lemur that live in close proximity in small forested

areas: the Golden Bamboo Lemur, the Greater Bamboo Lemur, and the Eastern Lesser Bamboo Lemur (*Hapalemur griseus*). Each utilizes either different species of bamboo, different parts of the plant, or different layers in the forest. Nutrient and toxin content (such as cyanide) help regulate food selection, though seasonal food preferences are also known to play a role.

Dietary regimes of lemurs include folivory, frugivory, and omnivory, with some being highly adaptable while others specialize on foods such as plant exudates (tree gum) and bamboo. In some cases, lemur feeding patterns directly benefit the native plant life. When lemurs exploit nectar, they may act as pollinators as long as the functional parts of the flower are not damaged. In fact, several unrelated Malagasy flowering plants demonstrate lemur-specific pollination traits, and studies indicate that some diurnal species, such as the Red-bellied Lemur and the ruffed lemurs, act as major pollinators. Two examples of plant species that rely on lemurs for pollination include Traveller's Palm (*Ravenala madagascariensis*) and a species of legume-like liana, *Strongylodon cravieniae*. Seed dispersal is another service lemurs provide. After passing through the lemur gut, tree and vine seeds exhibit lower mortality and germinate faster. Latrine behavior exhibited by some lemurs may help improve soil quality and facilitate seed dispersal. Because of their importance in maintaining a healthy forest, frugivorous lemurs may qualify as keystone mutualists.

All lemurs, particularly the smaller species, are affected by predation and they are important prey items for predators. Humans are the most significant predator of diurnal lemurs, despite taboos that occasionally forbid the hunting and eating of certain lemur species. Other predators include native euplerids, such as the Fossa, feral cats, domestic dogs, snakes, diurnal birds of prey, owls, and crocodiles. Extinct giant eagles, including one or two species from the genus *Aquila* and the giant Malagasy Crowned Eagle (*Stephanoaetus mahery*), as well as the Giant Fossa (*Cryptoprocta spelea*), previously also preyed on lemurs, perhaps including the giant subfossil lemurs or their subadult offspring. The existence of these extinct giants suggests that predator-prey interactions involving lemurs were more complex than they are today. Today, predator size only restricts owls to the smaller lemurs, usually 100 g (3.5 oz) or less, while the larger lemurs fall victim to the larger diurnal birds of prey, such as the Madagascar Harrier-hawk (*Polyboroides radiatus*) and the Madagascar Buzzard (*Buteo brachypterus*).

Research

Similarities that lemurs share with anthropoid primates, such as diet and social organization, along with their own unique traits, have made lemurs the most heavily studied of all mammal groups on Madagascar. Research often focuses on the link between ecology and social organization, but also on their behavior and morphophysiology (the study of anatomy in relation to function). Studies of their life-history traits, behavior and ecology help understanding of primate evolution, since they are thought to share similarities with ancestral primates.

Lemurs have been the focus of monographic series, action plans, field guides, and classic works in ethology. However, few species have been thoroughly studied to date, and most research has been preliminary and restricted to a single locality. Only recently have numerous scientific papers been published to explain the basic aspects of behavior and ecology of poorly known species. Field studies have given insights on population dynamics and evolutionary ecology of most genera and many species. Long-term research focused on identified individuals is in its infancy and has only been started for a few populations. However, learning opportunities are dwindling as habitat destruction and other factors threaten the existence of lemur populations across the island.

Berenty Private Reserve in southern Madagascar is both a popular tourist destination and research location. Alison Jolly began her research here in 1962.

Lemurs are mentioned in sailors' voyage logs as far back as 1608 and in 1658 that at least seven lemur species were described in detail by the French merchant, Étienne de Flacourt, who may also have been the only westerner to see and chronicle the existence of a giant (now extinct) lemur, which he called the *tretretretre*. Around 1703 merchants and sailors began bringing lemurs back to Europe, at which time James Petiver, an apothecary in London, described and illustrated the Mongoose Lemur. Starting in 1751, the London illustrator George Edwards began describing and illustrating some lemur species, of which a few were included in various editions of *Systema Naturae* by Carl Linnaeus. In the 1760s and 1770s, French naturalists Georges-Louis Leclerc, Comte de Buffon and Louis-Jean-Marie Daubenton began describing the anatomy of several lemur species. The first traveling naturalist to comment on lemurs was Philibert Commerçon in 1771, although it was Pierre Sonnerat who recorded a greater variety of lemur species during his travels.

During the 19th century, there was an explosion of new lemur descriptions and names, which later took decades to sort out. During this time, professional collectors gathered specimens for museums, menageries, and cabinets. Some of the major collectors were Johannes Hildebrandt and Charles Immanuel Forsyth Major. From these collections, as well as increasing observations of lemurs in their natural habitats, museum systematists including Albert Günther and John Edward Gray continued to contribute new names for new lemur species. However, the most notable contributions from this century includes the work of Alfred Grandidier, a naturalist and explorer who devoted himself to the study of Madagascar's natural history and local people. With the help of Alphonse Milne-Edwards, most of the diurnal lemurs were illustrated at this time. However, lemur taxonomic nomenclature took its modern form in the 1920s and 1930s, being standardized by Ernst Schwarz in 1931.

Although lemur taxonomy had developed, it was not until the 1950s and 1960s that the in-situ (or on-site) study of lemur behavior and ecology began to blossom. Jean-Jacques Petter and Arlette Petter-Rousseaux toured Madagascar in 1956 and 1957, surveying many of its lemur species and making important observations about their social groupings and reproduction. In 1960, the year of Madagascar's independence, David Attenborough introduced lemurs to the West with a commercial film. Under the guidance of John Buettner-Janusch, who founded the Duke Lemur Center in 1966, Alison Jolly traveled to Madagascar in 1962 to study the diet and social behavior of the Ring-tailed Lemur and Verreaux's Sifaka at Berenty Private Reserve. The Petters and Jolly spawned a new era of interest in lemur ecology and behavior and were shortly followed by anthropologists such as Alison Richard, Robert Sussman, Ian Tattersall, and many others. Following the political turmoil of the mid-1970s and Madagascar's revolution, field studies resumed in the 1980s, thanks in part to the renewed involvement of the Duke Lemur Center under the direction of Elwyn Simons and the conservation efforts of Patricia Wright. In the decades that followed, huge strides have been made in lemur studies and many new species have been discovered.

Ex situ research (or off-site research) is also popular among researchers looking to answer questions that are difficult to test in the field. For example, efforts to sequence the genome of the Gray Mouse Lemur will help researchers understand which genetic traits set primates apart from other mammals and will ultimately help understand what genomic traits set humans apart from other primates. One of the foremost lemur research facilities is the Duke Lemur Center (DLC) in Durham, North Carolina. It maintains the largest captive lemur population outside of Madagascar, which it maintains for non-invasive research and captive breeding. Many important research projects have been carried out there, including studies of lemur vocalizations, basic locomotor research, the kinematics of bipedalism, the effects of social complexity transitive reasoning, and cognition studies involving a lemur's ability to organize and retrieve sequences from memory. Other facilities, such as the Lemur Conservation Foundation, located near Myakka City, Florida, have also hosted research projects, such as one that looked at lemurs' ability to preferentially select tools based on functional qualities.

Conservation status

Lemurs in the spiny forests of Madagascar are threatened by deforestation for the creation of farmland and pasture (above) as well as firewood and charcoal production (below) for cooking fuel.

Lemurs are threatened by a host of environmental problems, including deforestation, hunting for bushmeat, live capture for the exotic pet trade, and climate change. All species are listed by CITES on Appendix I, which prohibits trade of specimens or parts, except for scientific purposes. As of 2005, the International Union for Conservation of Nature (IUCN) listed 16% of all lemur species as Critically Endangered, 23% as Endangered, 25% as Vulnerable, 28% as "Data Deficient", and only 8% as Least Concern. Over the next five years, at least 28 species were newly identified, none of which have had their conservation status assessed. Many are likely to be considered threatened since the new lemur species that have been described recently are typically confined to small regions. Given the rate of continued habitat destruction, undiscovered species could go extinct before being identified. Since the arrival of humans on the island

approximately 2000 years ago, all endemic Malagasy vertebrates over 10 kg (22 lb) have disappeared, including 17 species, 8 genera, and 3 families of lemurs. The IUCN Species Survival Commission (IUCN/SSC), the International Primatological Society (IPS), and Conservation International (CI) have included as many as five lemurs in their biennial "Top 25 Most Endangered Primates". The 2008–2010 list includes the Greater Bamboo Lemur, Gray-headed Lemur (*Eulemur cinereiceps*), Blue-eyed Black Lemur (*Eulemur flavifrons*), Northern Sportive Lemur (*Lepilemur septentrionalis*), and Silky Sifaka.

Madagascar is one of the poorest countries in the world, with a high population growth rate of 2.5% per year and nearly 70% of the population living in poverty. The country is also burdened with high levels of debt and limited resources. These socioeconomic issues have complicated conservation efforts, even though the island of Madagascar has been recognized by IUCN/SSC as a critical primate region for over 20 years. Due to its relatively small land area—587,045 km^2 (226,659 sq mi)—compared to other high-priority biodiversity regions and its high levels of endemism, the country is considered one of the world's most important biodiversity hotspots, with lemur conservation being a high priority. Despite the added emphasis for conservation, there is no indication that the extinctions that began with the arrival of humans have come to an end.

Threats in the wild

The greatest concern facing lemur populations is habitat destruction and degradation. Deforestation takes the form of local subsistence use, such as slash and burn agriculture (referred to as *tavy* in Malagasy), the creation of pasture for cattle through burning, and legal and illegal gathering of wood for firewood or charcoal production; commercial mining; and the illegal logging of precious hardwoods for foreign markets. After centuries of unsustainable use, as well as rapidly escalating forest destruction since 1950, less than 60,000 km^2 (23,000 sq mi) or 10% of Madagascar's land area remains forested. Only 17,000 km^2 (6,600 sq mi) or 3% of the island's land area is protected and due to dire economic conditions and political instability, most of the protected areas are ineffectively managed and defended. Some protected areas were set aside because they were naturally protected by their remote, isolated location, often on steep cliffs. Other areas, such as the dry forests and spiny forests of the west and south, receive little protection and are in serious danger of being destroyed.

Some species may be in risk of extinction even without complete deforestation, such as ruffed lemurs, which are very sensitive to habitat disturbance. If large fruit trees are removed, the forest may sustain fewer individuals of a species and their reproductive success may be affected for years. Small populations may be able to persist in isolated forest fragments for 20 to 40 years due to long generation times, but in the long term, such populations may not be viable. Small, isolated populations also risk extirpation by natural disasters and disease outbreaks (epizootics). Two diseases that are lethal to lemurs and could severely impact isolated lemur populations are toxoplasmosis, which is spread by feral cats, and the herpes simplex virus carried by humans.

Lemurs, such as this White-fronted Brown Lemur, are killed for bushmeat in Madagascar

Climate change and weather-related natural disasters also threaten lemur survival. For the last 1000 years, western and highland regions have been growing significantly drier, but in the past few decades, severe drought has become much more frequent. There are indications that deforestation and forest fragmentation are accelerating this gradual desiccation. The effects of drought are even felt in the rainforests. As annual rainfall decreases, the larger trees that make up the high canopy suffer increased mortality, failure to fruit, and decreased production of new leaves, which folivorous lemurs prefer. Cyclones can defoliate an area, knock down canopy trees, and create landslides and flooding. This can leave lemur populations without fruit or leaves until the following spring, requiring them to subsist on crisis foods, such as epiphytes.

Lemurs are hunted for food by the local Malagasy, either for local subsistence or to supply a luxury meat market in the larger cities. Most rural Malagasy do not understand what "endangered" means, nor do they know that hunting lemurs is illegal or that lemurs are found only in Madagascar. Many Malagasy have taboo, or *fady*, about hunting and eating lemurs, but this does not prevent hunting in many regions. Even though hunting has been a threat to lemur populations in the past, it has recently become a more serious threat as socioeconomic conditions deteriorate. Economic hardships have caused people to move around the country in search of employment, leading local traditions to break down. Drought and famine can also relax the *fady* that protect lemurs. Larger species, such as sifakas and ruffed lemurs, are common targets, but smaller species are also hunted or accidentally caught in snares intended for larger prey. Experienced, organized hunting parties using firearms, slings and blowguns can kill as many as eight to twenty lemurs in one trip. Organized hunting parties and lemur traps can be found in both non-protected areas and remote corners of protected areas. National parks and other protected areas are not adequately protected by law enforcement agencies. Often, there are too few park rangers to cover a large area, and sometimes terrain within the park is too rugged to check regularly.

Although not as significant as deforestation and hunting, some lemurs, such as Crowned Lemurs and other species that have successfully been kept in captivity, are occasionally kept as exotic pets by Malagasy people. Bamboo lemurs are also kept as pets, although they only survive for up to two months. Live capture for the exotic pet trade in wealthier countries is not normally considered a threat due to strict regulations controlling their export.

Conservation efforts

Rosewood is logged illegally from national parks, such as Marojejy

Lemurs have drawn much attention to Madagascar and its endangered species. In this capacity, they act as flagship species, the most notable of which is the Ring-tailed Lemur, which is considered an icon of the country. The presence of lemurs in national parks helps drive ecotourism, which especially helps local communities living in the vicinity of the national parks, since it offers employment opportunities and the community receives half of the park entrance fees. In the case of Ranomafana National Park, job opportunities and other revenue from long-term research can rival that of ecotourism.

Starting in 1927, the Malagasy government has declared all lemurs as "protected" by establishing protected areas that are now classified under three categories: National Parks (Parcs Nationaux), Strict Nature Reserves (Réserves Naturelles Intégrales), and Special Reserves (Réserves Spéciales). There are currently 18 national parks, 5 strict nature reserves, and 22 special reserves, as well as several other small private reserves, such as Berenty Reserve and Sainte Luce Private Reserve, both near Fort Dauphin. All protected areas, excluding the private reserves, comprise approximately 3% of the land surface of Madagascar and are managed by Madagascar National Parks, formerly known as l'Association Nationale pour la Gestion des Aires Protégées (ANGAP), as well as other non-governmental organizations (NGOs), including Conservation International (CI), the Wildlife Conservation Society (WCS), and the World Wide Fund for Nature (WWF). Most lemur species are covered by this network of protected areas, and a few species can be found in multiple parks or reserves.

Conservation is also facilitated by the Madagascar Fauna Group (MFG), an association of nearly 40 zoos and related organizations, including the Duke Lemur Center, the Durrell Wildlife Conservation Trust, and the Saint Louis Zoological Park. This international NGO supports Madagascar's Parc Ivoloina, helps protect Betampona Reserve and other protected areas, and promotes field research, breeding programs, conservation planning, and education in zoos. One of their major projects involved the release of captive Black-and-white Ruffed Lemurs, designed to help restock the dwindling population within Betampona Reserve.

Rice paddies have gradually replaced lemur habitat, particularly in the central part of the island.

Habitat corridors are needed for linking these protected areas so that small populations are not isolated. In September 2003 in Durban, South Africa, Madagascar's former president Marc Ravalomanana promised to triple the size of the island's protected areas in five years. This became known as the "Durban Vision". In June 2007, the World Heritage Committee included a sizable portion of Madagascar's eastern rainforests as a new UNESCO World Heritage Site.

Debt relief may help Madagascar protect its biodiversity. With the political crisis in 2009, illegal logging has proliferated and now threatens rainforests in the northeast, including its lemur inhabitants and the ecotourism that the local communities rely upon.

Captive lemur populations are maintained outside of Madagascar in many zoos, although the diversity of species is limited. Sikafas, for instance, do not survive well in captivity, so few facilities have them. The largest captive lemur population can be found at the Duke Lemur Center (DLC), whose mission includes non-invasive research, conservation (e.g. captive breeding), and public education.

Chapter- 2

Evolutionary History of Lemurs

Mouse lemurs, the smallest primates in the world, evolved in isolation along with other lemurs on the island of Madagascar

The **evolutionary history of lemurs** occurred in isolation from other primates, on the island of Madagascar, for at least 40 million years. Lemurs are prosimian primates belonging to the suborder Strepsirrhini, which branched off from other primates less than 63 mya (million years ago). They share some traits with the most basal primates, and thus are often confused as being ancestral to modern monkeys, apes, and humans. Instead, they merely resemble ancestral primates.

Lemurs are thought to have evolved during the Eocene or earlier, sharing a closest common ancestor with lorises, pottos, and galagos (lorisiforms). Fossils from Africa and some tests of nuclear DNA suggest that lemurs made their way to Madagascar between 40 and 52 mya. Other mitochondrial and nuclear DNA sequence comparisons offer an alternative date range of 62 to 65 mya. An ancestral lemur population is thought to have inadvertently rafted to the island on a floating mat of vegetation, although hypotheses for land bridges and island hopping have also been proposed. The timing and number of hypothesized colonizations has traditionally hinged on the phylogenetic affinities of the Aye-aye, the most basal member of the lemur clade.

Having undergone their own independent evolution on Madagascar, lemurs have diversified to fill many niches normally filled by other types of mammals. They include the smallest primates in the world, and once included some of the largest. Since the arrival of humans approximately 2,000 years ago, lemurs are now restricted to 10% of the island, or approximately 60,000 square kilometres (23,000 sq mi), and many face extinction. For this reason, researchers have been trying to identify and assess every species. Over the last 10 to 20 years, there has been a steep increase in the number of recognized lemur species and subspecies both through the discovery of new species and the elevation of existing subspecies to full species status. Currently there are approximately 100 or more recognized species or subspecies of living lemur, which are divided into five families and 15 genera. If the extinct subfossil lemurs are included, an additional three families, eight genera, and 17 species would be included. The recent rise in species numbers is due to both improved genetic analysis and a push in conservation to encourage the protection of isolated and distinct lemur populations. Not everyone in the scientific community supports these taxonomic changes, with some preferring instead an estimate of 50 living species.

Evolutionary history

Lemurs are prosimian primates belonging to the suborder Strepsirrhini. Like other strepsirrhine primates, such as lorises, pottos, and galagos, they share ancestral traits with early primates. In this regard, lemurs are popularly confused with ancestral primates; however, lemurs did not give rise to monkeys and apes, but evolved independently on Madagascar.

Fossil evidence for the evolution of the toothcomb, a trait shared by lemurs with their closest relatives, the lorises, provides insight into both the evolutionary history of strepsirrhines and the lemur colonization of Madagascar.

Primates first evolved sometime between the Middle Cretaceous and the early Paleocene periods on either the supercontinent of Laurasia or in Africa. According to molecular clock studies, the last common ancestor of all primates dates to around 79.6 mya, although the earliest known fossil primates are only 54–55 million years old. The closest relatives of primates are the extinct plesiadapiforms, the modern colugos (commonly and inaccurately named "flying lemurs"), and treeshrews. Some of the earliest known true primates are represented by the fossil groups Omomyidae, Eosimiidae, and Adapiformes.

The relationship between known fossil primate families remains unclear. A conservative estimate for the divergence of haplorrhines (tarsiers, monkeys, apes, and humans) and strepsirrhines is 58 to 63 mya, and a consensus is emerging that places tarsiers close to omomyids, while eosimids gave rise to the simians (non-tarsier haplorrhines) and the adapiforms gave rise to modern strepsirrhines, including lemurs. In 2009, a highly publicized and scientifically criticized publication proclaimed that a 47 million-year-old adapiform fossil, *Darwinius masillae*, demonstrated both adapiform and simian traits,

making it a transitional form between the prosimian and simian lineages. Media sources inaccurately dubbed the fossil as a "missing link" between lemurs and humans.

Lemurs were traditionally thought to have evolved during the Eocene (55 to 37 mya) based on the fossil record, although molecular tests suggest the Paleocene (65 to 56 mya) or later. Until recently, they were thought to have descended directly from the diverse group of adapiforms due to several shared postcranial traits, as well as long snouts and small brains. Although adapiforms also had lemur-like auditory bullae, a prosimian characteristic, they had smaller brains and longer snouts than lemurs. There are also several other morphological differences. Most noticeably, adapiforms lack a key derived trait, the toothcomb, and possibly the toilet-claw, found not only in extant (living) strepsirrhines but also in tarsiers. Unlike lemurs, adapiforms exhibited a fused mandibular symphysis (a characteristic of simians) and also possessed four premolars, instead of three or two.

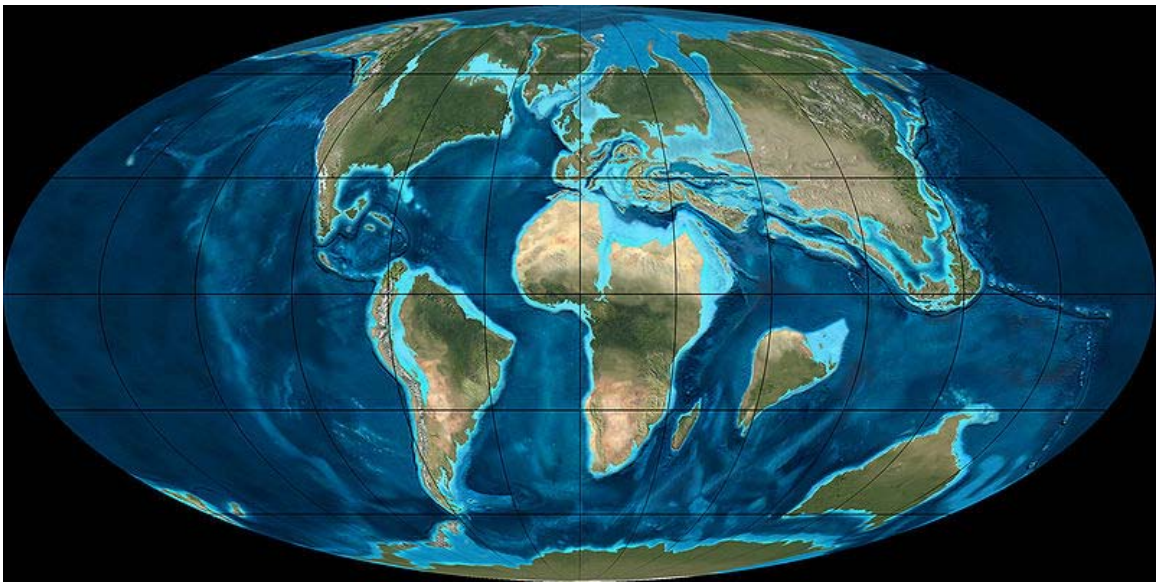
Comparative studies of the cytochrome *b* gene, which are frequently used to determine phylogenetic relationships among mammals—particularly within families and genera—have been used to show that lemurs share common ancestry with lorisiforms. This conclusion is also corroborated by the shared strepsirhine toothcomb, an unusual trait that is unlikely to have evolved twice. If adapiforms were the ancestors of the living strepsirrhines, then the last common ancestor of modern strepsirrhines would have to predate the early Eocene, a view supported by molecular phylogenetic studies by Anne D. Yoder and Ziheng Yang in 2004, which showed that lemurs split from lorises approximately 62 to 65 mya. These dates were confirmed by more extensive tests by Julie Horvath *et al*. in 2008. These molecular studies also showed that lemuriforms diversified before the modern lorisiforms. Using a more limited data set and only nuclear genes, another study in 2005 by Céline Poux *et al*. dated the split between lemurs and lorises at 60 mya, lemur diversification at 50 mya, and the lemur colonization of Madagascar somewhere between these two approximate dates. However, the 2003 discovery of fossil lorisiforms at the Fayum Depression in Egypt pushed the date of lorisiform divergence back to the Eocene, matching the divergence dates predicted by Yoder and Horvath.

The fossil record tells a different story. Although it cannot show the earliest possible date for the appearance of a taxonomic group, other concerns have arisen about these vastly earlier divergence dates predicted independently of the fossil record. First, palaeontologists have expressed concerns that if primates have been around for significantly more than 65 million years, then the first one-third of the primate fossil record is missing. Another problem is that some of these molecular dates have overestimated the divergence of other mammalian orders, such as Rodentia, suggesting primate divergence might also be overestimated. Currently the oldest known strepsirrhine, *Djebelemur*, dates from the early Eocene in northern Africa and lacks a fully differentiated toothcomb. Based on fossils and other genetic tests, a more conservative estimate dates the divergence between lemurs and lorises to around 50 to 55 mya.

To complicate the ancestry puzzle, no terrestrial Eocene or Paleocene fossils have been found on Madagascar, and the fossil record from both Africa and Asia around this time is not much better. Fossil sites in Madagascar are restricted to only five windows in time, which omit most of the Cenozoic, from 65 mya to ~26,000 years ago. What little fossil-bearing rock exists from this vast span of time is dominated by marine strata along the west coast. The oldest lemur fossils on Madagascar are actually subfossils dating to the Late Pleistocene.

Colonization of Madagascar

Once part of the supercontinent Gondwana, Madagascar broke away from eastern Africa, the likely source of the ancestral lemur population, about 160 mya and then from Antarctica between 80 and 130 mya. Initially, the island drifted south from where it split from Africa (around modern Somalia) until it reached its current position between 80 and 90 mya. Around that time, it split with India, leaving it isolated in the Indian Ocean and separated from nearby Africa by the Mozambique Channel, a deep channel with a minimum width of approximately 560 kilometers (350 mi). These separation dates and the estimated age of the primate lineage preclude any possibility that lemurs could have been on the island before Madagascar pulled away from Africa, an evolutionary process known as vicariance. In support of this, mammalian fossils on Madagascar from the Cretaceous include gondwanatheres and other mammalian groups that would not have been ancestral to lemurs or the other endemic mammals present on the island today.



A reconstructed map of the Earth during the Early Paleocene, approximately 65 million years ago, around the time that lemurs evolved and colonized Madagascar

With Madagascar already geographically isolated by the Paleocene and lemur diversification dating to the same time, an explanation was needed for how lemurs had made it to the island. In the 19th century, prior to the theory of continental drift, scientists including Philip Sclater, Étienne Geoffroy Saint-Hilaire, and Ernst Haeckel suggested

that Madagascar and India were once part of a southern continent—named Lemuria by Sclater—that has since disappeared under the Indian Ocean. By the early 20th century, oceanic dispersal emerged as the most popular explanation for how lemurs reached the island. The idea first took shape under the anti-plate tectonics movement of the early 1900s, when renowned paleontologist William Diller Matthew proposed the idea in his influential article "Climate and Evolution" in 1915. In the article, Matthew could only account for the presence of lemurs in Madagascar by "rafting". In the 1940s, American paleontologist George Gaylord Simpson coined the term "sweepstakes dispersal" for such unlikely events.

As plate tectonics theory took hold, oceanic dispersal fell out of favor and was even considered by many researchers to be "miraculous" if it occurred. Despite the low likelihood of its occurrence, oceanic dispersal remains the most accepted explanation for numerous vertebrate colonizations of Madagascar, including that of the lemurs. Although unlikely, over long periods of time terrestrial animals can occasionally raft to remote islands on floating mats of tangled vegetation, which get flushed out to sea from major rivers by floodwaters.

Any extended ocean voyage without fresh water or food would prove difficult for a large, warm-blooded (or "homeothermic") mammal, but today many small, nocturnal species of lemur exhibit heterothermy, which allows them to lower their metabolism and become dormant while living off fat reserves. Such a trait in a small, nocturnal lemur ancestor would have facilitated the ocean voyage and could have been passed on to its descendants. However, this trait has not been observed in the closely related lorisiforms studied to date, and could have evolved on Madagascar in response to the island's harsh environmental conditions.

Because only five terrestrial orders of mammals have made it to the island, each likely to have derived from a single colonization, and since these colonizations date to either the early Cenozoic or the early Miocene, the conditions for oceanic dispersal to Madagascar seem to have been better during two separate periods in the past. A report published in January 2010 supported this assumption by demonstrating that both Madagascar and Africa were 1,650 km (1,030 mi) south of their present-day positions around 60 mya, placing them in a different ocean gyre and reversing the strong current that presently flows away from Madagascar. The currents were even shown to be stronger than they are today, shortening the rafting time to approximately 30 days or less, making the crossing much easier for a small mammal. Over time, as the continental plates drifted northward, the currents gradually changed, and by 20 mya the window for oceanic dispersal had closed.

Since the 1970s, the rafting hypothesis has been called into question by claims that lemur family Cheirogaleidae might be more closely related to the other Afro-Asian strepsirrhines than to the rest of the lemurs. This idea was initially based on similarities in behavior and molar morphology, although it gained support with the 2001 discovery of 30 million-year-old *Bugtilemur* in Pakistan and the 2003 discovery of 40 million-year-old *Karanisia* in Egypt. *Karanisia* is the oldest fossil found that bears a toothcomb, whereas

Bugtilemur was thought to have a toothcomb, but also had even more similar molar morphology to *Cheirogaleus* (dwarf lemurs). If these relationships had been correct, the dates of these fossils would have had implications on the colonization of Madagascar, requiring two separate events. The most parsimonious explanation, given the genetic evidence and the absence of toothcombed primates in European fossil sites, is that stem strepsirrhines evolved on the Afro-Arabian landmass, dispersing to Madagascar and more recently from Africa to Asia. More recently, the structure and general presence of the toothcomb in *Bugtilemur* has been questioned, as well as many other dental features, suggesting it is most likely an adapiform.

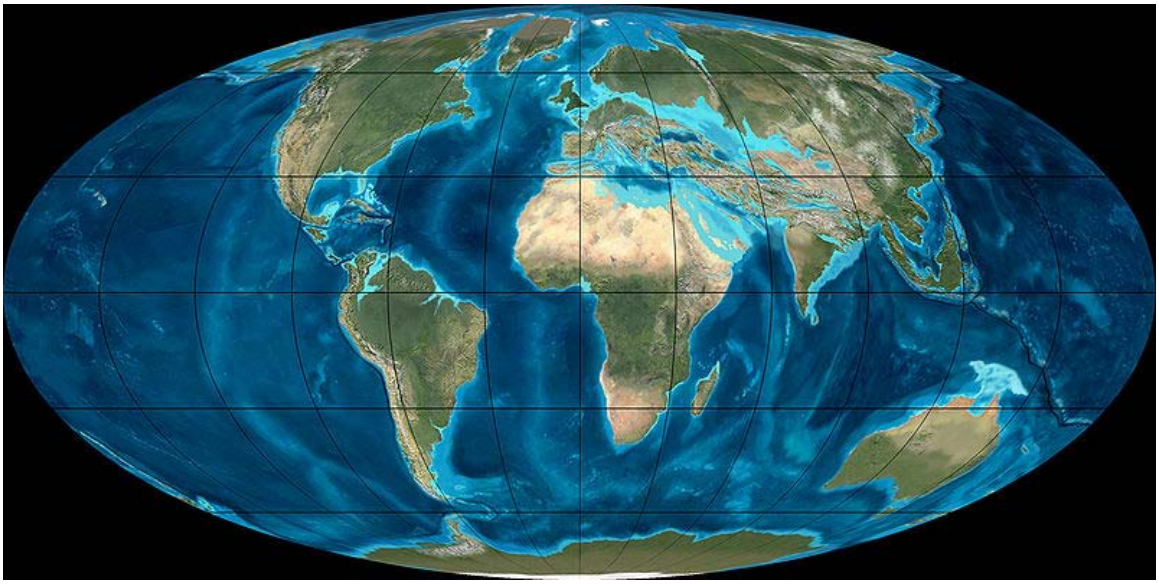
An alternative form of oceanic dispersal that had been considered was island hopping, where the lemur ancestors might have made it to Madagascar in small steps by colonizing exposed seamounts during times of low sea level. However, this is unlikely since the only seamounts found along the Davie Ridge would have been too small in a such a wide channel. Even though the Comoros Islands between Africa and Madagascar are significantly larger, they are too young, having been formed by volcanic activity only around 8 mya. A land bridge between Madagascar and Africa has also been proposed, but a land bridge would have facilitated the migration of a much greater sampling of Africa's mammalian fauna than is endemic to the island. Furthermore, deep trenches separate Madagascar from the mainland, and prior to the Oligocene, sea level was significantly higher than today.

A variant of the land bridge hypothesis has been proposed in an attempt to explain both how a land bridge could have formed, and why other mammalian orders failed to cross it. Geological studies have shown that following the collision of India and Asia, the Davie Fracture Zone had been pushed up by tectonic forces, possibly high enough to create a land bridge. Indeed, core samples along the Davie Fracture Zone suggest that at least parts of the Mozambique Channel were above sea level between 45 and 26 mya, or possibly as early as 55 mya. Following the Indian-Asian collision, the fault type changed from a strike-slip fault to a normal fault, and seafloor spreading created compression along the Davie Fracture Zone, causing it to rise. By the early Miocene, the East African Rift created tension along the fault, causing it to subside beneath the ocean. The divergence dates of many Malagasy mammalian orders formerly fell within this window. Old World monkeys, dogs, and cats did not diverge or arrive in Africa until later in the Miocene. However, more recent dating of divergence of the Malagasy mammalian clades falls outside of this land bridge window, and a much greater diversity of mammal groups would be expected on Madagascar had the land bridge been present during that stretch of time.

The dating of the lemur colonization is controversial for the same reasons as strepsirrhine evolution. Using both mitochondrial and nuclear DNA sequences, the colonization has been estimated at 62 to 65 mya based on the split between the Aye-aye and the rest of the lemurs. On the other hand, the sparse fossil record and some estimates based on other nuclear genes support a more recent estimate of 40 to 52 mya. Once safely established on Madagascar, with its limited mammalian population, the lemurs were protected from the increasing competition from evolving arboreal mammalian groups. Monkeys had evolved

by the Oligocene, and their intelligence, aggression, and deceptiveness may have given them the advantage in exploiting the environment over the diurnal adapiform primates in Africa and Asia, ultimately driving them to extinction and leaving only the nocturnal lorisiforms.

Diversification



A reconstructed map of the Earth during the Early Oligocene, approximately 35 million years ago, at a time when lemurs were diversifying

The ancestral lemur that colonized Madagascar is thought to have been small and nocturnal. More specifically, it is thought to have had adapiform-like cranial anatomy—particularly the cranial foramina and the middle ear—comparable to that of lemurids, while being similar to cheirogaleids in dentition and postcranial anatomy.

Nothing definitive is known about the island's biogeography at the time of the colonization, however, the paleoclimate (ancient weather patterns) may have have been affected by the Madagascar's location below the subtropical ridge at 30° S latitude and disruption of the weather patterns by India as it drifted northward. Both would have created a drying effect on Madagascar, and as a result, the arid spiny bush that is currently found in the south and southwest of Madagascar would have dominated the island. This would have placed strong selection pressure for drought tolerance on the inhabitants of the island between the Cretaceous and the Eocene. As Madagascar edged above the subtropical ridge and India moved closer to Asia, the climate became less dry and the arid spiny bush retreated to the south and southwest.

Lemurs have diversified greatly since first reaching Madagascar. The Aye-aye and its extinct relations are thought to have diverged first, shortly after colonization. According to molecular studies, there have since been two major episodes of diversification, from which all other known extant and extinct family lineages emerged. The remaining

families diverged in the first diversification episode, during a 10 to 12 million-year window between the Late Eocene (42 mya) and into the Oligocene (30 mya). The dates for this divergence window span the Eocene-Oligocene extinction event, during which time climate cooling took place and changes in ocean currents altered weather patterns. Outside of Madagascar, these dates also coincide with the divergence of the lorisiform primates and five major clades of squirrels, all occupying niches similar to those of lemurs. The dates do not suggest that increased predation drove family-level divergence since the first carnivores arrived on the island between 24 and 18 mya.

The second major episode of diversification occurred during the Late Miocene, approximately 8 to 12 mya, and included the true lemurs (*Eulemur*) and the mouse lemurs (*Microcebus*). This event coincided with the beginning of the Indian monsoons, the last major change in climate to affect Madagascar. The populations of both the true lemurs and mouse lemurs were thought to have diverged due to habitat fragmentation when humans arrived on the island roughly 2,000 years ago. Only recently has molecular research shown a more distant split in these genera. Most surprising were the mouse lemurs, a group which is now thought to contain cryptic species, meaning they are indistinguishable from each other based solely on appearance. In contrast, true lemurs are easier to distinguish and exhibit sexual dichromatism. Studies in karyology, molecular genetics, and biogeographic patterns have also assisted in understanding their phylogeny and diversification. Although the divergence estimates for these two genera are imprecise, they overlap with a change to a wetter climate in Madagascar, as new weather patterns generated monsoons and likely influenced the plant life.

This difference in evolutionary divergence between the two genera may be due to differences in their activity patterns. True lemurs are often diurnal, allowing potential mates to distinguish each other as well as other related species visually. Mouse lemurs, on the other hand, are nocturnal, reducing their ability to use visual signals for mate selection. Instead, they use olfactory and auditory signaling. For these reasons, true lemurs may have evolved sexual dichromatism while mouse lemurs evolved to be cryptic species.

Distribution and diversity

Since their arrival on Madagascar, lemurs have diversified both in behavior and morphology. Their diversity rivals that of the monkeys and apes found throughout the rest of the world, especially when the recently extinct subfossil lemurs are considered. Ranging in size from the 30 g (1.1 oz) Madame Berthe's Mouse Lemur, the world's smallest primate, to the extinct 160–200 kg (350–440 lb) *Archaeoindris fontoynonti*, lemurs evolved diverse forms of locomotion, varying levels of social complexity, and unique adaptations to the local climate. They went on to fill many niches normally occupied by monkeys, squirrels, woodpeckers, and large grazing ungulates. In addition to the incredible diversity between lemur families, there has also been great diversification among closely related lemurs. Yet despite separation by geographical barriers or by niche differentiation in sympatry, occasionally hybridization can occur. Lemur diversification has also created generalist species, such as the true lemurs of northern Madagascar,

which are very adaptable, mostly nondescript, and found throughout most of the island's forests.

The Diademed Sifaka (*Propithecus diadema*) is one of the largest of the living lemurs, comparable in size to the Indri. It lives in the rainforests of Madagascar and eats a varied diet of leaves and fruit.

Most of the 99 living lemur taxa are found only on Madagascar. Two species, the Common Brown Lemur (*Eulemur fulvus*) and the Mongoose Lemur (*Eulemur mongoz*), can also be found on the Comoro Islands, although it is assumed that both species were introduced to the islands from northwestern Madagascar by humans within the last few hundred years. Molecular studies on *Eulemur fulvus fulvus* (from the mainland) and *E. f. mayottensis* (from the Comoro Islands) and on Comoro and mainland Mongoose

Lemurs have supported this assumption by showing no genetic differences between the two populations. Because all lemurs, including these two brown lemur species, are only native to the island of Madagascar, they are considered to be endemic.

Historically, lemurs ranged across the entire island inhabiting a wide variety of habitats, including dry deciduous forests, lowland forests, spiny thickets, subhumid forests, montane forest, and mangrove. Today, their collective range is restricted to 10% of the island, or approximately 60,000 km^2 (23,000 sq mi). Most of the remaining forests and lemurs are found along the periphery of the island. The center of the island, the Hauts-Plateaux, was converted by early settlers to rice paddies and grassland through slash-and-burn agriculture, known locally as *tavy*. As erosion depleted the soil, the cyclical forest regrowth and burning ended as the forest gradually failed to return. Today, the level of floral diversity increases with precipitation, from the dry southern forests to the wetter norther forests to the rainforests along the east coast. Increased foliage corresponds to increased faunal diversity, including the diversity and complexity of lemur communities.

Having evolved in Madagascar's challenging environment, replete with poor soils, extreme shifts in poor, seasonal plant productivity, and devastating climatic events such as extended droughts and annual cyclones, lemurs have adopted unique combinations of unusual traits to survive, distinguishing them significantly from other primates. In response to limited, seasonal resources, lemurs may exhibit seasonal fat storage, hypometabolism (including torpor and hibernation in some cheirogaleids), small group sizes, low encephalization (relative brain size), cathemerality (activity both day and night), and/or strict breeding seasons. Secondarily, extreme resource limitations and seasonal breeding are thought to have resulted in three other relatively common lemur traits: female dominance, sexual monomorphism (lack of size differences between the sexes), and male-male competition for mates involving low levels of agonism (conflict), such as sperm competition.

The arrival of humans on the island 1,500 to 2,000 years ago has taken a significant toll, not only on the size of lemur populations, but also on their diversity. Due to habitat destruction and hunting, at least 17 species and 8 genera have gone extinct and the populations of all species have decreased. A couple of species once thought to have gone extinct have since been rediscovered. The Hairy-eared Dwarf Lemur (*Allocebus trichotis*) was only known from five museum specimens, most collected in the late 19th century and one in 1965. It was rediscovered in 1989 and has since been identified in five national parks, although it is very rare within its range. Likewise, the Greater Bamboo Lemur (*Prolemur simus*) was thought to be extinct as recently as the late 1970s, but a population was located near Ranomafana National Park in the late 1980s. Historically, it had a much wider geographic distribution, shown by subfossil remains, but today it remains one of the world's 25 most endangered primates. One distinctive morph (possibly a species or subspecies) of sifaka, has not been so fortunate, having been extirpated from all known localities. Unless trends change, extinctions are likely to continue.

A life restoration of *Palaeopropithecus ingens*, a giant sloth lemur that went extinct less than a thousand years ago.

Until recently, giant species of lemur existed on Madagascar. Now represented only by recent or subfossil remains, they were modern forms and are counted as part of the rich lemur diversity that evolved in isolation. Some of their adaptations were unlike those seen in lemurs today. All 17 extinct lemurs were larger than the extant forms, some weighing as much as 200 kg (440 lb), and are thought to have been active during the day. Not only were they unlike the living lemurs in both size and appearance, they also filled ecological niches that no longer exist or are now left unoccupied. Large parts of Madagascar, which are now devoid of forests and lemurs, once hosted diverse primate communities that included more than 20 species covering the full range of lemur sizes.

Taxonomic and phylogenetic classification

Lemur taxonomy is controversial, and not all experts agree, particularly with the recent increase in the number of recognized species. According to Russell Mittermeier, the president of Conservation International (CI), taxonomist Colin Groves, and others, there are currently 101 recognized species or subspecies of extant lemur, divided into five families and 15 genera. Conversely, other experts in the field label this as a possible example of taxonomic inflation, and prefer instead an estimate of at least 50 species. All sides generally agree that the recently extinct subfossil lemurs should be classified in three families, eight genera, and 17 species.

Since the first taxonomic classification of lemurs in 1758 by Carl Linnaeus, many changes have been made to lemur taxonomy. Within the order Primates, treeshrews (order Scandentia) were considered basal, prosimian primates—close relatives of lemurs—until the 1980s. Colugos, also incorrectly referred to as "flying lemurs", were once considered lemur-like primates, but were reclassified as close relatives of bats, and more recently as close relatives of primates within their own order, Dermoptera. Primates, together with their closest relatives, the treeshrews, colugos, and long-extinct plesiadapiforms, form the taxonomically unranked Euarchonta clade within the Euarchontoglires. Also, all lorisids originally placed in the genus *Lemur* by Carl Linnaeus have since been moved into either their own infraorder (Lorisiformes) or their own superfamily (Lorisoidea) within Lemuriformes.

For the Malagasy primate fauna, taxonomic nomenclature proliferated during the 1800s, with the aid of museum systematists, such as Albert Günther and John Edward Gray, as well as naturalists and explorers, such as Alfred Grandidier and Alphonse Milne-Edwards. The taxonomic nomenclature of lemurs was not sorted out until decades later, when Ernst Schwarz standardized it in 1931. It was not until the 1990s that this nomenclature started to see a new wave of taxonomic change.

Suprageneric classification

Since the 19th century, the classification of lemurs above the genus level has seen many changes. Early taxonomists proposed a variety of classifications for lemurs, but generally separated indriids from other lemurs and placed the Aye-aye in a major group of its own; some classified the dwarf and mouse lemurs with the galagos. In 1915, William King Gregory published a classification that remained generally accepted over the next decades. He placed all the lemurs together in a "series" Lemuriformes and recognized three families: Daubentoniidae, Indriidae, and Lemuridae (including the current Cheirogaleidae and Lepilemuridae). George Gaylord Simpson's influential 1945 classification of mammals placed the treeshrews and the fossil *Anagale* (both now classified outside Primates) inside Lemuriformes and classified the fossil families Plesiadapidae and Adapidae in a superfamily Lemuroidea with most of the lemurs.

Although treeshrews, plesiadapids, and the like are now no longer considered to be closely related to lemurs, disagreements persist over the classification of lemurs and

related groups, resulting in two competing arrangements of the infraorders and superfamilies within Strepsirrhini. Colin Groves, in the 2005 third edition of *Mammal Species of the World*, classifies living strepsirrhines under three infraorders and two superfamilies. This places the Aye-aye within its own infraorder, separate from both lemurs (divided into two superfamilies) and lorises. Since the publication of *Mammal Species of the World*, there has been little support in the academic literature for placing the Aye-aye in its own infraorder, and more recently Mittermeier, Groves, and other editors have ignored this taxonomic level. An alternative classification draws the lines for infraorders and superfamilies differently, though using the same general phylogenetic tree. It classifies all living strepsirrhines under one infraorder, with the lorises and lemurs in separate superfamilies.

The classification of several lemur taxa has elicited particular debate. Most significantly, the placement of the Aye-aye has been controversial since its introduction to Western science in 1782, and it has been a topic of debate up until very recently. Hinged upon morphological traits and molecular data, it has had profound implications on scientific theories. Arguing against Darwin's theory of natural selection, Richard Owen claimed in 1863 that the Aye-aye's distinct characteristics, including its ever-growing incisors and unique, highly flexible middle finger, are so perfectly adapted for their uses in extractive foraging that they could not have evolved gradually through natural selection. More recently, the Aye-aye's placement within the order Primates has posed problems for the rafting hypothesis for the primate colonization of Madagascar. If this species does not form a monophyletic group with the rest of the lemurs, then multiple colonization events would have had to occur to explain the present-day distribution of non-human primates on Madagascar.

The Aye-aye has traditionally been difficult to classify due to its unique physical traits

Until Richard Owen published a definitive anatomical study in 1866, early naturalists were uncertain whether the Aye-aye (genus *Daubentonia*) was a primate, rodent, or marsupial. In the late eighteenth century, for example, the Aye-aye was classified under the squirrel genus *Sciurus*. By emphasizing its primate features, such as its postorbital bar, stereoscopic vision, and opposable hallux, over its rodent-like teeth, Owen demonstrated its affinity with other primates. In 1996, Ankel-Simons demonstrated that the shape and arrangement of the Aye-aye's diminutive deciduous incisors indicate that this genus has a shared ancestry with the toothcombed primates. However, the placement of the Aye-aye within the order Primates remained problematic until very recently. The karyotype of the Aye-aye is noticeably different from that of its closest relatives, the lorises and the rest of the lemurs, with a diploid chromosome count of 2n=30. Based on its anatomy, researchers have found support for classifying the genus *Daubentonia* as a specialized indriid, a monotypic sister group to all strepsirrhines, and an indeterminate taxon within the order Primates. In 1931, Schwarz labeled the Aye-aye as an offshoot of Indriidae, claiming that all lemurs were monophyletic, whereas Reginald Innes Pocock had previously placed the Aye-aye outside of the lemurs. In that same year, Anthony and Coupin classified the Aye-aye under infraorder Chiromyiformes, a sister group to the other strepsirrhines. Colin Groves upheld this classification in 2005 because he was not entirely convinced the Aye-aye formed a clade with the rest of the Malagasy lemurs, despite molecular tests that had shown Daubentoniidae was basal to all Lemuriformes. In 2008, Russell Mittermeier, Colin Groves, and others ignored addressing higher-level taxonomy by defining lemurs as monophyletic and containing five living families, including Daubentoniidae.

Another interpretation of the Aye-aye's origins has once again called into question the single origins of the lemurs. Comparisons have been made between the Aye-aye and a fossil strepsirrhine primate from Africa, *Plesiopithecus*. Similarities in the shape of the skull and the morphology of the lower jaw have raised the question of whether or not this could be an Aye-aye ancestor. However, the placement of an Aye-aye ancestor in Africa would require multiple colonizations by strepsirrhine primates. Molecular tests may offer support since they show that the Aye-aye was the first to diverge in the lemur clade and that the other lemur families did not diverge until much later.

Often classified with the galagos by early students, the cheirogaleids were placed with the other lemurs from Gregory's 1915 classification until the early 1970s, when several anthropologists proposed that they are more closely related to lorisiforms, based on morphological data. However, relevant genetic studies nearly unanimously place cheirogaleids within the lemuriform clade and Groves, who had promoted the cheirogaleid-lorisiform relationship in a 1974 paper, by 2001 himself regarded the idea as refuted.

Classifications in the first half of the 20th century divided lemurs into three families—Daubentoniidae, Indriidae, and Lemuridae, with the latter including the current Cheirogaleidae and Lepilemuridae. Because of concerns that Lemuridae might not be monophyletic, the family was later split; in 1982, for example, Tattersall separated the Cheirogaleidae for the dwarf lemurs, mouse lemurs, and relatives and the Lepilemuridae

for the sportive lemurs and bamboo lemurs (including the Greater Bamboo Lemur). This classification is still used, except that the bamboo lemurs are placed in Lemuridae.

From the 1970s to the 1990s, there have been suggestions that the ruffed lemurs might be related to indriids or a sister group to Lemuridae and Indriidae and that the bamboo lemurs are related to the sportive lemurs, but neither view is supported by molecular phylogeny. The sportive lemurs and the extinct koala lemurs (Megaladapidae) both lack upper incisors in the permanent dentition, and in 1981, Groves placed both together in the family Megaladapidae, which he renamed Lepilemuridae in 2005 because that older name takes precedence. Genetic research does not support a close relationship between the sportive and koala lemurs and instead places the koala lemurs as a sister group to Lemuridae; therefore, the two are now placed in separate families (Lepilemuridae for the sportive lemurs and Megaladapidae for the koala lemurs). The sloth lemurs (Palaeopropithecidae) and monkey lemurs (Archaeolemuridae) were classified as subfamilies within Indriidae as late as 1982, but are now recognized as separate families.

The relationships among the families of lemurs have been problematic and have yet to be definitively resolved. Two competing phylogenies exist based on genetic and molecular data. One approach (Horvath *et al*.) looks at a larger number of genes, but among fewer species. This results in Lemuridae being a sister group to Lepilemuridae, Cheirogaleidae, and Indriidae. The other approach (Orlando *et al*.) looks at fewer genes, but more lemur species. Using this analysis, Lepilemuridae becomes the sister group to Lemuridae, Cheirogaleidae, and Indriidae. Both phylogenies agree that the Malagasy primates are monophyletic and that Daubentoniidae (the Aye-aye) is basal to the lemuriform clade, having split off significantly earlier than the other families. However, two problems create complications for both approaches. First, the four most closely related lemur families diverged within a narrow window of approximately 10 million years, making it much harder to distinguish the splits with molecular evidence. Second, the divergence occurred approximately 42 mya; such distant splits create a lot of noise for molecular techniques.

Genus-level classification

Early classifications of the genera of lemurs differed in a number of ways from current taxonomy. For example, the fork-marked lemurs were initially placed in the genus *Lemur* and then in *Microcebus* with the mouse lemurs before being placed in their own genus *Phaner*; and Charles Immanuel Forsyth Major split the *Cheirogaleus medius* species group of the dwarf lemurs into a separate genus *Opolemur*, but this was not accepted. Genus-level taxonomy was largely stabilized by Schwarz in 1931, but a number of changes have become accepted:

- The Ring-tailed Lemur, ruffed lemurs, and true lemurs were once grouped together in the genus *Lemur* due to a host of morphological similarities. For instance, the skeletons of the Ring-tailed Lemur and the true lemurs are nearly indistinguishable. However, ruffed lemurs were reassigned to the genus *Varecia* in 1962, and due to similarities between the Ring-tailed Lemur and the bamboo

lemurs, particularly in regards to molecular evidence and scent glands similarities, the true lemurs were moved to the genus *Eulemur* in 1988. The genus *Lemur* is now monotypic, containing only the Ring-tailed Lemur.

- In 2001, Colin Groves concluded that despite similarities, the Greater Bamboo Lemur was sufficiently distinct from the bamboo lemurs of the genus *Hapalemur* to merit its own monotypic genus, *Prolemur*. This follows Schwarz's 1931 opposition to Pocock's decision to separate *Prolemur* from *Hapalemur*.

- Originally placed in the genus *Microcebus* (mouse lemurs), the Giant Mouse Lemur was moved to its own genus, *Mirza*, in 1985 due to its larger size, morphological differences, dental characteristics, and behavior.

- The Hairy-eared Dwarf Lemur was first placed in the genus *Cheirogaleus* (dwarf lemurs) in 1875 and was later found to have closer affinities with *Microcebus*. However, its dentition and cranium structure were sufficiently distinct to merit elevation to its own genus, *Allocebus*.

Species-level classification

Over the past two decades, the number of recognized lemur species has more than doubled according to some experts. In 1994, 32 distinct species were named in the first edition of Conservation International's field guide, *Lemurs of Madagascar*, and 68 were described in the 2nd edition, published in 2006. In December 2008, Russell Mittermeier, Colin Groves, and other experts co-wrote an article in the *International Journal of Primatology* classifying 99 species and subspecies. In late 2010, the 3rd edition of *Lemurs of Madagascar* listed 101 taxa. The number of lemur species is likely to continue growing in the coming years, as field studies, cytogenetic and molecular genetic research continues, particularly on cryptic species, such as mouse lemurs, which cannot be distinguished visually.

The Sahamalaza Sportive Lemur (*Lepilemur sahamalazensis*) was identified as a distinct species as recently as 2006.

This threefold increase in nearly 15 years has not had universal support among taxonomists and lemur researchers. In many cases, classifications ultimately depends upon which species concept is used. Due to the critical condition that most Malagasy primate populations are in, taxonomists and conservationists sometimes favor splitting them into separate species to develop an effective strategy for the conservation of the full range of lemur diversity. Implicitly, this means that full species status will help grant genetically distinct populations added environmental protection.

The first large wave of new lemur species descriptions came in 2001 when Colin Groves elevated the Red Ruffed Lemur (*Varecia rubra*), five subspecies of brown lemur

(*Eulemur albifrons*, *E. albocollaris*, *E. collaris*, *E. rufus* and *E. sanfordi*), and four subspecies of sifaka (*Propithecus coquereli*, *P. deckenii*, *P. edwardsi*, and *P. perrieri*) to full species status. Additional elevations of all remaining subspecies within the *Eulemur* and *Propithecus* genera were made in the years that followed. These and subsequent changes in taxonomy were largely due to a shift to the phylogenetic species concept, yet are not universally endorsed.

By far the most explosive growth in species numbers has been in the genera *Microcebus* and *Lepilemur*. In 2006, 15 new species of *Lepilemur* were described, with three new species reported in February, one species in June, and 11 in September. Since then, two additional species have been described. Genetic and morphological differences seem to suggest that they are cryptic species, but there is still debate whether these merit full species status or should be regarded as subspecies of previously identified, "core" species.

In true lemurs and mouse lemurs, both groups were initially divided into a small number of species, either with no distinguishable subspecies (in the case of mouse lemurs) or with several distinguishable subspecies (in the case of true lemurs). With molecular research suggesting a more distant split in both genera, these subspecies or undistinguished populations have been promoted to species status.

In the case of mouse lemurs, the rise in species numbers has been only slightly less sudden and dramatic. Classified as one species by Ernst Schwarz in 1931 (excluding one, Coquerel's Giant Mouse Lemur, that is no longer classified in *Microcebus*), the genus was revised to contain two species, the Gray Mouse Lemur (*Microcebus murinus*) and the Brown Mouse Lemur (*M. rufus*), after an extensive field study in 1972 showed both living in sympatry in southeastern Madagascar. At the time, the Gray Mouse Lemur was known in the drier parts of the north, west, and south, while the Brown Mouse Lemur inhabited the humid rainforest regions of the east. However, we now know the species diversity and distribution to be significantly more complex. Revisions throughout the 1990s and 2000s identified numerous new species through genetic testing using mitochondrial DNA, demonstrating that the genus is represented by a multitude of cryptic species. Many, but not all of these defined species have been supported by nuclear DNA tests.

However, there are still concerns that species are being identified prematurely. Ian Tattersall, an anthropologist who recognized 42 species of lemur in 1982, has expressed concern that the geographically organized variety in lemur populations is being recognized with full species status while the number of subspecies in lemur genera has virtually disappeared. He has argued that taxonomists are confusing differentiation and speciation, two processes that are often unrelated, while denying the role of microevolution in evolutionary processes. Still, other researchers who emphasize the framework of the "general lineage concept of species" contend that lineage divergence or differentiation demarcates the beginning of a new species.

New species have been identified due to differences in morphology, karyotypes, cytochrome *b* sequences, and other genetic tests, as well as several combinations of these. When nuclear DNA (nDNA) was tested in conjunction with mitochondrial DNA (mtDNA) in mouse lemurs, a few species, such as Claire's Mouse Lemur (*Microcebus mamiratra*) were demonstrated to be indistinguishable from other closely related species. In such cases, nDNA did not vary, but the mtDNA that had been used to define it as a species was still distinct. Differences in results between nDNA, which is inherited from both parents, and mtDNA, which is inherited from the mother, was attributed to female philopatry, where females remain within or close to the home range into which they were born while males disperse. Since the isolated population known as Claire's Mouse Lemur has distinct mtDNA, but not nDNA, it is likely to contain a population descended from a related group of females, but which still disperses and interbreeds with nearby populations.

Traditionally, karyology has been considered when determining species status. From the lemurs studied so far, the diploid number of chromosomes in lemurs varies between 2n=20 and 2n=66. In the case of the true lemurs, the diploid number ranges from 2n=48 to 2n=60 while the individual chromosome sizes vary considerably.

Sometimes distinctions are made due to very slight differences in pelage coloration. For instance, three distinctly colored types of mouse lemur were discovered in a multi-year study in Beza Mahafaly Reserve in southern Madagascar, but rather than being separate species, DNA tests revealed that they all belonged to a single species, the Reddish-gray Mouse Lemur (*Microcebus griseorufus*). For this reason, further research is needed to confirm or deny the recent species splits. Only through detailed studies of morphology, ecology, behavior, and genetics can the true number of lemur species be determined.

Lemur species and subspecies count by year and genus

	1931 Schwarz		1982 Tattersall		1994 Mittermeier *et al.*		2005 Groves		2006 Mittermeier *et al.*		2010 Mittermeier *et al.*	
genus	**species**	**subspecies**	**species**	**subspecies**	**species**	**subspecies**	**species**	**subspecies**	**species**	**subspecies**	**species**	**subspecies**
Allocebus	–	–	1	0	1	0	1	0	1	0	1	0
Avahi	1	2	1	2	2	0	3	0	4	0	9	0
Cheirogaleus	3	4	2	0	2	0	7	0	7	0	5	0
Daubento	1	0	1	0	1	0	1	0	1	0	1	0

nia												
Eulemur	–	–	–	–	5	8	11	2	10	2	12	0
Hapalemur	2	2	2	3	3	3	4	2	5	0	5	3
Indri	1	0	1	0	1	0	1	2	1	0	1	0
Lemur	6	7	4	7	1	0	1	0	1	0	1	0
Lepilemur	2	0	1	6	7	0	8	0	8	0	26	0
Microcebus	2	2	2	0	3	0	8	0	12	0	18	0
Mirza	–	–	1	0	1	0	1	0	2	0	2	0
Phaner	1	0	1	0	1	4	4	0	4	0	4	0
Prolemur	–	–	–	–	–	–	1	0	1	0	1	0
Propithecus	2	9	2	9	3	8	7	4	9	0	9	0
Varecia	–	–	1	2	1	2	1	4	2	3	2	3
Totals	**21**	**26**	**20**	**29**	**32**	**25**	**59**	**14**	**68**	**5**	**97**	**6**
	38		**42**		**50**		**67**		**71**		**101**	

Chapter- 3

Cheirogaleidae and Aye-aye

Cheirogaleidae

Cheirogaleids

Eastern Fork-marked Lemur (*Phaner furcifer*)

Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	Primates
Suborder:	Strepsirrhini
Infraorder:	Lemuriformes
Family:	**Cheirogaleidae** Gray, 1873
Genera	

Cheirogaleus
Microcebus
Mirza
Allocebus
Phaner

Synonyms

- *Microcebina* Gray, 1870[a]
- *Cheirogalina* Gray, 1872

Cheirogaleidae is the family of strepsirrhine primates that contains the various dwarf and mouse lemurs. Like all other lemurs, **cheirogaleids** live exclusively on the island of Madagascar.

Characteristics

Cheirogaleids are smaller than the other lemurs and, in fact, they are the smallest primates. They have a soft, long fur colored grey-brown to reddish on top with a generally brighter underbelly. Typically they have small ears, large, close set eyes, and long hind legs. Like all strepsirrhines they have fine claws at the second toe of the hind legs. They grow to a size of only 13 to 28 cm, with a tail that is very long, sometimes up to one and a half times as long as the body. They weigh no more than 500 grams, with some species weighing as little as 60 grams.

Dwarf and mouse lemurs are nocturnal and arboreal. They are excellent climbers and can also jump far, using their long tail for balance. When on the ground (a rare occurrence) they move by hopping on their hind legs. They spend the day in tree hollows or leaf nests. Cheirogaleids are typically solitary but sometimes live together in pairs.

Their eyes possess a tapetum lucidum, a light-reflecting layer that improves their night vision. Some species, such as the Lesser Dwarf Lemur, store fat at the hind legs and the base of the tail and hibernate. Unlike lemurids, they have long upper incisors, although they do have the comb-like teeth typical of all strepsirhines. They have the dental formula: $\frac{2.1.3.3}{2.1.3.3}$

Cheirogaleids are omnivores, eating fruits, flowers and leaves (and sometimes nectar) as well as insects, spiders and small vertebrates.

The females usually have three pairs of nipples. After a meager 60 day gestation, they will bear two to four (usually two or three) young. After five to six weeks these are weaned and become fully mature near the end of their first year or sometime in their second year, depending on the species. In human care, they can live for up to 15 years, although their life expectancy in the wild is probably significantly shorter.

Classification

The five genera of cheirogaleids contain 32 species.

- Infraorder Lemuriformes
  - **Family Cheirogaleidae**
    - Genus *Cheirogaleus*: dwarf lemurs
      - *C. medius* group
        - Fat-tailed Dwarf Lemur, *Cheirogaleus medius*
        - Southern Fat-tailed Dwarf Lemur, *Cheirogaleus adipicaudatus*
      - *C. major* group
        - Greater Dwarf Lemur, *Cheirogaleus major*
        - Furry-eared Dwarf Lemur, *Cheirogaleus crossleyi*
        - Lesser Iron-gray Dwarf Lemur, *Cheirogaleus minusculus*
        - Greater Iron-gray Dwarf Lemur, *Cheirogaleus ravus*
        - Sibree's Dwarf Lemur, *Cheirogaleus sibreei*
    - Genus *Microcebus*: mouse lemurs
      - Gray Mouse Lemur, *Microcebus murinus*
      - Reddish-gray Mouse Lemur, *Microcebus griseorufus*
      - Golden-brown Mouse Lemur, *Microcebus ravelobensis*
      - Northern Rufous Mouse Lemur, *Microcebus tavaratra*
      - Sambirano Mouse Lemur, *Microcebus sambiranensis*
      - Simmons' Mouse Lemur, *Microcebus simmonsi*
      - Pygmy Mouse Lemur, *Microcebus myoxinus*
      - Brown Mouse Lemur, *Microcebus rufus*
      - Madame Berthe's Mouse Lemur, *Microcebus berthae*
      - Goodman's Mouse Lemur, *Microcebus lehilahytsara*
      - Jolly's Mouse Lemur, *Microcebus jollyae*
      - MacArthur's Mouse Lemur, *Microcebus macarthurii*
      - Mittermeier's Mouse Lemur, *Microcebus mittermeieri*
      - Claire's Mouse Lemur, *Microcebus mamiratra*
      - Bongolava Mouse Lemur, *Microcebus bongolavensis*
      - Danfoss' Mouse Lemur, *Microcebus danfossi*
      - Arnhold's Mouse Lemur, *Microcebus arnholdi*
      - Margot Marsh's Mouse Lemur, *Microcebus margotmarshae*
    - Genus *Mirza*: giant mouse lemurs
      - Coquerel's Giant Mouse Lemur or Coquerel's Dwarf Lemur, *Mirza coquereli*
      - Northern Giant Mouse Lemur, *Mirza zaza*
    - Genus *Allocebus*
      - Hairy-eared Dwarf Lemur, *Allocebus trichotis*
    - Genus *Phaner*: fork-crowned lemurs

- Masoala Fork-crowned Lemur, *Phaner furcifer*
- Pale Fork-crowned Lemur, *Phaner pallescens*
- Pariente's Fork-crowned Lemur, *Phaner parienti*
- Mt. d'Ambre Fork-crowned Lemur, *Phaner electromontis*

Aye-aye

Aye-aye

An aye-aye eating banana flowers

Conservation status

Near Threatened (IUCN 3.1)

Scientific classification [e]

Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	Primates
Family:	**Daubentoniidae** Gray, 1863
Genus:	***Daubentonia*** É. Geoffroy, 1795

Binomial name

Daubentonia madagascariensis
(Gmelin, 1788)

Species

D. madagascariensis
†D. robusta

Aye-aye range

Synonyms

Family:

- Cheiromyidae I. Geoffroy St. Hilaire, 1851
- Chiromyidae Bonaparte, 1850

Genus:

- *Aye-aye* Lacépède, 1799
- *Cheiromys* G. Cuvier, 1817
- *Cheyromys* É. Geoffroy, 1803
- *Chiromys* Illiger, 1811
- *Myslemur* Anon. [?de Blainville], 1846
- *Myspithecus* de Blainville, 1839
- *Psilodactylus* Oken, 1816
- *Scolecophagus* É. Geoffroy, 1795

Species:

- *daubentonii* Shaw, 1800
- *laniger* G. Grandidier, 1930
- *psilodactylus* Schreber, 1800

The **aye-aye** (*Daubentonia madagascariensis*) is a lemur, a strepsirrhine primate native to Madagascar that combines rodent-like teeth and a special thin middle finger to fill the same ecological niche as a woodpecker. It is the world's largest nocturnal primate, and is characterized by its unusual method of finding food; it taps on trees to find grubs, then gnaws holes in the wood and inserts its narrow middle finger to pull the grubs out. The only other animal species known to find food in this way is the striped possum. From an ecological point of view the Aye-aye fills the niche of a woodpecker as it is capable of penetrating wood to extract the invertebrates within.

The aye-aye is the only extant member of the genus *Daubentonia* and family Daubentoniidae (although it is currently classified as Near Threatened by the IUCN); a second species, *Daubentonia robusta*, appears to have become extinct at some point within the last 1000 years.

Etymology

Its binomial name honours the French naturalist Louis-Jean-Marie Daubenton and the island on which it is found, Madagascar. Among some Malagasy, the aye-aye is imitatively called "*hay-hay*" for a vocalization it is claimed to make. It is supposedly from the European acceptance of this name that its common name was derived. However, the aye-aye makes no such vocalization. The name was also hypothesized to be of European origin, with a European observer overhearing an exclamation of fear and surprise ("aiee!-aiee!") by Malagasy who encountered it. However, the name exists in remote villages, so it is unlikely to be of European origins. Another hypothesis is that it derives from "*heh heh*," which is Malagasy for, "I don't know." If correct, then the name might have originated from Malagasy people saying "*heh heh*" to Europeans to avoid saying the name of a feared, magical animal.

Classification

- Order Primates
  - Suborder Strepsirrhini: nontarsier prosimians
    - Family **Daubentoniidae**
      - Genus ***Daubentonia***
        - **Aye-aye (*Daubentonia madagascariensis*)**
        - †Giant aye-aye (*Daubentonia robusta*)
    - Family Cheirogaleidae
    - Family Lemuridae
    - Family Lepilemuridae
    - Family Indriidae

Due to its derived morphological features, the classification of the aye-aye has been debated since its discovery. The possession of continually growing incisors (front teeth) parallels those of rodents, leading early naturalists to mistakenly classify the aye-aye within mammalian order Rodentia.

The aye-aye's classification with the order Primates has been just as uncertain. It has been considered a highly derived member of the Indridae family, a basal branch of the strepsirrhine suborder, and of indeterminate relation to all living primates. In 1931, Anthony and Coupin classified the aye-aye under infraorder **Chiromyiformes**, a sister group to the other strepsirrhines. Colin Groves upheld this classification in 2005 because he was not entirely convinced the aye-aye formed a clade with the rest of the Malagasy lemurs, despite molecular tests that had shown Daubentoniidae was basal to all Lemuriformes, deriving from the same lemur ancestor that rafted to Madagascar during the Paleocene or Eocene. In 2008, Russell Mittermeier, Colin Groves, and others ignored addressing higher-level taxonomy by defining lemurs as monophyletic and containing five living families, including Daubentoniidae.

Habitat

The aye-aye lives primarily on the east coast of Madagascar. Its natural habitat is rainforest or deciduous forest, but many live in cultivated areas due to deforesting. Rainforest aye-ayes, the most common, dwell in canopy areas, and are usually sighted upwards of 700 meters altitude. They sleep during the day in nests built in the forks of trees.

Behavior

Social interaction

The aye-aye is classically considered 'solitary', but recent research suggests it is more social than once thought. It usually sticks to foraging in its own personal home range, or territory. The home ranges of males often overlap, and the males can be very social with each other. Female home ranges never overlap, though a male's home range often overlaps that of several females. The male aye-ayes live in large areas up to 80 acres (320,000 m^2), while females have smaller living spaces that goes up to 20 acres (81,000 m^2). Regular scent marking with their cheeks and neck is how aye-ayes let others know of their presence and repel intruders from their territory. Like many other prosimians, the female aye-aye is dominant to the male. They are not monogamous by any means, and often compete with each other for mates. Males are very aggressive in this regard, and sometimes even pull other males off a female during mating. Outside of mating, males and females interact only occasionally, usually while foraging.

The father will sometimes share food with the infant, but otherwise infants' primary source of social interaction is with their mothers. Mothers and infants often wrestle, chase, and play "peek-a-boo" for entertainment. After 13 weeks, infants are usually ready to interact with other young aye-ayes, usually by play-fighting.

Foraging

The aye-aye begins foraging anywhere between 30 minutes before and three hours after sunset. Up to 80% of the night is spent foraging in the canopy, separated by occasional rest periods. The monkey-like body of the aye-aye enables it to move vertically with ease. It climbs trees by making successive vertical leaps, much like a squirrel. Horizontal movement is more difficult, but the aye-aye rarely descends to jump to another tree, and can often cross up to 4 km (2.5 mi) a night.

Infants are fully dextrous within a month of birth. At first, they can only climb on a branch hanging upside down, but they gradually work their way up to the various acrobatic feats adults can perform. Curiously, walking and running on the ground are often hardest for an aye-aye to master.

Though foraging is mostly solitary, they will occasionally forage in groups. Individual movements within the group are coordinated using both sound (vocalisations) and scent signals.

Diet

Gnawed limb

The aye-aye commonly eats nuts, grubs, fruits, nectar, seeds, and fungi, classifying it as an omnivore. It picks fruit off trees as it moves through the canopy, often barely stopping to do so. An aye-aye not in its natural habitat will often steal coconuts, mangoes, sugar

cane, lychees and eggs from villages and plantations. Aye-ayes tap on the trunks and branches of the trees they visit up to eight times per second, and listen to the echo produced to find hollow chambers inside. Once a chamber is found, they chew a hole into the wood and get grubs out of that hole with their narrow and bony middle fingers.

History

The original meaning of the name aye-aye has been lost, as the originating language is extinct. The word "aye aye" is hypothesized to signify simply a cry of alarm to alert others to the presence of this animal, which many Malagasy consider an ill omen.

The aye-aye was thought to be extinct in 1933, but was rediscovered in 1957. Nine individuals were transported to Nosy Mangabe, an island near Maroantsetra off eastern Madagascar, in 1966. Recent research shows the aye-aye is more widespread than was previously thought, but is still categorized as Near Threatened.

Several aye-ayes are kept in zoos; the largest collection and most successful breeding program, with a current population of 22 individuals, is at the Duke Lemur Center at Duke University, Durham, North Carolina, US. Several also reside outside of the US at various locations.

Superstition and public controversy

Illustration of an aye-aye (*Daubentonia robusta*)

The aye-aye is a near threatened species not only because its habitat is being destroyed, but also due to native superstition. Besides being a general nuisance in villages, ancient Malagasy legend said the Aye-aye was a symbol of death. It is viewed as a good omen in some areas, but these areas are a minority.

Researchers in Madagascar report remarkable fearlessness in the aye-aye; some accounts tell of individual animals strolling nonchalantly in village streets or even walking right up to naturalists in the rainforest and sniffing their shoes.

However, public contempt goes beyond this. The aye-aye is often viewed as a harbinger of evil and killed on sight. Others believe, should one point its narrow middle finger at someone, they are condemned to death. Some say the appearance of an aye-aye in a village predicts the death of a villager, and the only way to prevent this is to kill it. The Sakalava people go so far as to claim aye-ayes sneak into houses through the thatched roofs and murder the sleeping occupants by using their middle finger to puncture the victim's aorta.

Incidents of aye-aye killings increase every year as its forest habitats are destroyed and it is forced to raid plantations and villages. Because of the superstition surrounding it, this often ends in death. On the other hand, the superstition can prevent people from hunting them for food.

Chapter- 4

Indriidae and Lemuridae

Indriidae

Indridae Temporal range: Pleistocene to Recent

Indri (*Indri indri*)
Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	Primates

Suborder:	Strepsirrhini
Infraorder:	Lemuriformes
Family:	**Indriidae** Burnett, 1828

Genera

Indri
Avahi
Propithecus

Synonyms

- Lichanotina Gray, 1825
- Indrisina Geoffroy Saint-Hilaire, 1851
- Indrisidae Alston, 1878
- Indrisinae Mivart, 1864
- Indriidae Hill, 1953
- Indriinae Hill, 1953
- Propitheci Winge, 1895
- Propithecinae Trouessart, 1897

The **Indriidae** (sometimes incorrectly spelled **Indridae**) are a family of strepsirrhine primates. They are medium to large sized lemurs with only four teeth in the toothcomb instead of the usual six. **Indriids**, like all lemurs, live exclusively on the island of Madagascar.

The group was once much larger, and, in addition to the thirteen species living today, also contains eleven extinct species in six genera. Most if not all were larger animals, called 'sloth lemurs'. These included the chimpanzee-sized *Palaeopropithecus* and the gorilla-sized *Archaeoindris*. Most went extinct within the last 1500 to 2000 years, after humans colonized Madagascar.

Characteristics

The ten extant indrid species vary considerably in size. Not counting the length of their tails, the avahis are only 30 centimetres (12 in) in length, while the Indri is the largest extant strepsirrhine. The tail of the Indri is only a stub, while avahi and the sifaka tails are as long as their bodies. Their fur is long and mostly from whitish over reddish up to grey. Their black faces, however, are always bald. The hind legs are longer than their fore limbs, their hands are long and thin, and their thumb cannot be opposed to the other fingers correctly.

All species are arboreal, though they do come to the ground occasionally. When on the ground, they stand upright and move with short hops forward, with their arms held high. In the trees, though, they can make extraordinary leaps and are extremely agile, able to change direction from tree to tree. Like most leaf eaters they adjust for the low nutrient content of their food by long rests. Often they can be seen lying stretched on trees

sunning themselves. Indrids live together in family federations from two to 15 animals, communicating with roars and also with facial expressions.

Indrids are strict vegetarians, eating mostly leaves, fruits and flowers. Like some other herbivores, they have a large cecum, containing bacteria that ferment cellulose, allowing for more efficient digestion of plant matter. They have fewer premolar teeth than other lemurs, with the dental formula of: $\frac{2.1.2.3}{2.1.2.3}$

Females and males usually mate monogamously for many years. Mostly at the end of the dry season, their four to five-month gestation ends with the birth of a single offspring, which lives in the family for a while after its weaning (at the age of five to six months).

Classification

There are 19 living species in the family, divided into 3 genera.

Family Indriidae

- Genus *Indri*
  - Indri, *Indri indri*
- Genus *Avahi*, woolly lemurs
  - Bemaraha Woolly Lemur, *Avahi cleesei*
  - Eastern Woolly Lemur, *Avahi laniger*
  - Moore's Woolly Lemur, *Avahi mooreorum*
  - Western Woolly Lemur, *Avahi occidentalis*
  - Sambirano Woolly Lemur, *Avahi unicolor*
  - Peyrieras' Woolly Lemur, *Avahi peyrierasi*
  - Southern Woolly Lemur, *Avahi meridionalis*
  - Ramanantsoavana's Woolly Lemur, *Avahi ramanantsoavani*
  - Betsileo Woolly Lemur, *Avahi betsileo*
- Genus *Propithecus*, sifakas
  - *Propithecus diadema* group
    - Diademed Sifaka, *Propithecus diadema*
    - Silky Sifaka, *Propithecus candidus*
    - Milne-Edwards' Sifaka, *Propithecus edwardsi*
    - Perrier's Sifaka, *Propithecus perrieri*
    - Golden-crowned Sifaka, *Propithecus tattersalli*
  - *Propithecus verreauxi* group
    - Verreaux's Sifaka, *Propithecus verreauxi*
    - Coquerel's Sifaka, *Propithecus coquereli*
    - Decken's Sifaka, *Propithecus deckenii*
    - Crowned Sifaka, *Propithecus coronatus*

Lemuridae

Lemuridae

Mongoose Lemur (*Eulemur mongoz*)

Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	Primates
Suborder:	Strepsirrhini
Infraorder:	Lemuriformes
Family:	**Lemuridae** Gray, 1821

Genera
Lemur
Eulemur
Hapalemur
Prolemur
Varecia

Lemuridae is a family of prosimian primates native to Madagascar, and one of five families commonly known as lemurs. These animals were thought to be the evolutionary predecessors of monkeys and apes, but this is no longer considered correct. The family gets its name from the Ancient Roman belief that the animals were ghosts or spirits ('lemures'), because many species are nocturnal.

Characteristics

Lemurids are medium-sized arboreal primates, ranging from 32 to 56 cm in length, excluding the tail, and weighing from 0.7 to 5 kg. They have long, bushy tails and soft, woolly fur of varying coloration. The hindlegs are slightly longer than the forelegs, although not enough to hamper fully quadrupedal movement (unlike the sportive lemurs). Most species are highly agile, and regularly leap several metres between trees. They have a good sense of smell and binocular vision. Unlike most other lemurs, all but one species

of lemurid (the Ring-tailed Lemur) lack a tapetum lucidum, a reflective layer in the eye that improves night vision.

Lemurids are herbivorous, eating fruit, leaves, and, in some cases, nectar. For the most part, they have the dental formula: $\frac{2.1.3.3}{2.1.3.3}$

With most lemurids, the mother gives birth to one or two young after a gestation period of between 120 and 140 days, depending on species. Though the ruffed lemur species are the only lemurids that have true litters, consisting of anywhere from 2 to 6 offspring. They are generally sociable animals, living in groups of up to thirty individuals in some species. In some cases, such as the Ring-tailed Lemur, the groups are long-lasting, with distinct dominance hierarchies, while in others, such as the Common Brown Lemur, the membership of the groups varies from day to day, and seems to have no clear social structure.

Classification

The family Lemuridae contains 5 extant genera, and 22 species.

FAMILY LEMURIDAE

- Genus *Lemur*
  - Ring-tailed Lemur, *Lemur catta*
- Genus *Eulemur*, true lemurs
  - Common Brown Lemur, *Eulemur fulvus*
  - Sanford's Brown Lemur, *Eulemur sanfordi*
  - White-headed Lemur, *Eulemur albifrons*
  - Red Lemur, *Eulemur rufus*
  - Red-fronted Lemur, *Eulemur rufifrons*
  - Collared Brown Lemur, *Eulemur collaris*
  - Gray-headed Lemur, *Eulemur cinereiceps*
  - Black Lemur, *Eulemur macaco*
  - Sclater's Lemur, *Eulemur flavifrons*
  - Crowned Lemur, *Eulemur coronatus*
  - Red-bellied Lemur, *Eulemur rubriventer*
  - Mongoose Lemur, *Eulemur mongoz*
- Genus *Varecia*, ruffed lemurs
  - Black-and-white Ruffed Lemur, *Varecia variegata*
  - Red Ruffed Lemur, *Varecia rubra*
- Genus *Hapalemur*, bamboo lemurs
  - Eastern Lesser Bamboo Lemur (Gray Gentle Bamboo Lemur), *Hapalemur griseus*
  - Gilbert's Bamboo Lemur, *Hapalemur gilberti*
  - Southern Lesser Bamboo Lemur, *Hapalemur meridionalis*
  - Western Lesser Bamboo Lemur, *Hapalemur occidentalis*
  - Lac Alaotra Gentle Lemur (Bandro), *Hapalemur alaotrensis*

    - Golden Bamboo Lemur, *Hapalemur aureus*
- Genus *Prolemur*
    - Greater Bamboo Lemur, *Prolemur simus*
- Genus †*Pachylemur*
    - *Pachylemur insignis* †
    - *Pachylemur jullyi* †

This family was once broken into two subfamilies, **Hapalemurinae** (bamboo lemurs and the Greater Bamboo Lemur) and **Lemurinae** (the rest of the family), but molecular evidence and scent glands similarities have since placed the Ring-tailed Lemur with the bamboo lemurs and the Greater Bamboo Lemur.

Lemur species in the *Eulemur* are known to interbreed, despite having dramatically different chromosome numbers. Red-fronted (2N=60) and Collared (2N=50–52) Brown Lemurs were found to hybridize at Berenty Reserve, Madagascar.

Chapter- 5

Sportive Lemur and Koala Lemur

Sportive lemur

Sportive lemurs

Sahamalaza Sportive Lemur
(*L. sahamalazensis*)

Scientific classification

Kingdom: Animalia

Phylum:	Chordata
Class:	Mammalia
Order:	Primates
Suborder:	Strepsirrhini
Infraorder:	Lemuriformes
Family:	**Lepilemuridae** Gray, 1870
Genus:	***Lepilemur*** I. Geoffroy, 1851

Type species

Lepilemur mustelinus I. Geoffroy

Species

Synonyms

Genus:

- *Galeocebus* Wagner, 1855
- *Lepidilemur* Giebel, 1859
- *Mixocebus* Peters, 1874

The **sportive lemurs** are the medium sized primates that make up the **Lepilemuridae** family. The family consists of only one extant genus, ***Lepilemur***, as well as the extinct genus *Megaladapis*. They are closely related to the other lemurs and exclusively live on the island of Madagascar. For a time, this family was named **Megaladapidae**, but the current name was given precedence.

Physical characteristics

Eyeshine

Their fur is grey brown or reddish colored on the top and whitish yellow underneath. They typically have a short head with large, round ears. They grow to a length of 30 to 35 cm (with a tail just about as long as their body) and weigh up to 0.9 kg. Their eyes have a tapetum lucidum behind the retina, hence they have eyeshine.

Behaviour and mating

Sportive lemurs are strictly nocturnal and predominantly arboreal, moving among the trees with long jumps powered by their strong hind legs. On the ground, they hop similarly as the kangaroos. During the day they hide in the leafy covering or tree hollows. Sportive lemurs are solitary but defend their territory vehemently against same sex intruders. The territories of males and females can overlap.

Diet

They are mainly herbivores and their diet consists predominantly of leaves.

Reproduction and lifespan

Birthing happens between September and December after a gestation of 120 to 150 days, and is usually of a single young which is often reared in a nest in a tree hollow. At about four months the juveniles are weaned but remain with their mother up to an age of one year. At about 18 months they are fully mature, and live to be about eight years old.

Classification

- **Order Primates**
  - **Suborder Strepsirrhini**: non-tarsier prosimians
    - **Infraorder Lemuriformes**
      - Family †Archaeolemuridae
      - Family Cheirogaleidae: dwarf and mouse lemurs
      - Family Daubentoniidae: Aye-aye
      - Family Indriidae: woolly lemurs and allies
      - Family Lemuridae: lemurs
      - **Family *Lepilemuridae***: sportive lemurs
        - **Genus *Lepilemur***
          - AEECL's Sportive Lemur (*Lepilemur aeeclis*) *
          - Ahmanson's Sportive Lemur (*Lepilemur ahmansonorum*) **
          - Ankarana Sportive Lemur, (*Lepilemur ankaranensis*)
          - Betsileo Sportive Lemur (*Lepilemur betsileo*) **
          - Gray-backed Sportive Lemur, (*Lepilemur dorsalis*)
          - Milne-Edwards' Sportive Lemur, (*Lepilemur edwardsi*)
          - Fleurete's Sportive Lemur (*Lepilemur fleuretae*) **
          - Grewcock's Sportive Lemur (*Lepilemur grewcockorum*) **
          - Holland's Sportive Lemur (*Lepilemur hollandorum*) *****
          - Hubbard's Sportive Lemur (*Lepilemur hubbardorum*) **
          - James' Sportive Lemur (*Lepilemur jamesorum*) **

        - White-footed Sportive Lemur, (*Lepilemur leucopus*)
        - Manasamody Sportive Lemur (*Lepilemur manasamody*) ***
        - Small-toothed Sportive Lemur, (*Lepilemur microdon*)
        - Daraina Sportive Lemur (*Lepilemur milanoii*) **
        - Weasel Sportive Lemur, (*Lepilemur mustelinus*)
        - Otto's Sportive Lemur (*Lepilemur otto*) ***
        - Petter's Sportive Lemur (*Lepilemur petteri*) **
        - Randrianasolo's Sportive Lemur (*Lepilemur randrianasoloi*) *
        - Red-tailed Sportive Lemur, (*Lepilemur ruficaudatus*)
        - Sahamalaza's Sportive Lemur (*Lepilemur sahamalazensis*) *
        - Scott's Sportive Lemur (*Lepilemur scottorum*)****
        - Seal's Sportive Lemur (*Lepilemur seali*) **
        - Northern Sportive Lemur, (*Lepilemur septentrionalis*)
        - Hawk's Sportive Lemur (*Lepilemur tymerlachsonorum*) **
        - Wright's Sportive Lemur (*Lepilemur wrightae*) **
    - Family †Megaladapidae
    - Family †Palaeopropithecidae
  - Infraorder Lorisiformes: lorises, pottos, galagos and allies
- Suborder Haplorrhini: tarsiers, monkeys and apes

* New species according to molecular analysis
** New species according to molecular analysis
*** New species according to molecular analysis
**** New species according to molecular analysis
***** New species according to molecular analysis

Koala lemur

Koala lemur

Megaladapis edwardsi
Conservation status
Extinct
Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	Primates
Suborder:	Strepsirrhini
Infraorder:	Lemuriformes
Family:	† **Megaladapidae**
Genus:	† ***Megaladapis*** Forsyth Major, 1894

Paleospecies

Subgenus *Peloriadapis*

- *M. edwardsi*

Subgenus *Megaladapis*

- *M. madagascariensis*
- *M. grandidieri*

Koala lemurs, genus ***Megaladapis***, belong to the family **Megaladapidae**, consisting of three extinct species of lemurs that once inhabited the island of Madagascar. The largest measured between 1.3 to 1.5 m (4 to 5 ft) in length.

Appearance and habits

Megaladapis was quite different from any living lemur. Its body was squat and built like that of the modern koala. Its long arms and fingers were specialized for grasping trees, while its legs were splayed for vertical climbing. Additionally, its head was unlike any other primate. *Megaladapis* had long canine teeth and a cow-like jaw, forming a tapering snout. Its jaw muscles were powerful for chewing through the tough native vegetation. Its body weight reached a total of 50 kilograms (110 lb). The shape of its skull was unique among all known primates, with a nasal region which showed similarities to those of rhinoceros, what was probably a feature combined with an enlarged upper lip for grasping leaves.

Its tree-grasping attributes probably made *Megaladapis* vulnerable to changes to the forests of Madagascar. Upon human arrival between 1,500 and 2,000 years ago, the forests of Madagascar were cleared to make farmland. Unable to adapt to these new environmental changes imposed by man and being a tempting target for hunters, *Megaladapis* became extinct approximately 500 years ago, around the time of European discovery of Madagascar.

Cultural references

It is often believed that Malagasy legends of the *tretretretre* or *tratratratra*, an extinct animal, refer to *Megaladapis*, but the details of these tales, notably the "human-like" face of the animal, match the related *Palaeopropithecus* much better. Bernard Heuvelmans proposed instead that *Megaladapis* was the basis for the ***tokandia***. Details such as a "hopping" motion while on the ground but usually being found in trees, a "non-human" face but "human-like" calls suggest that this identification may well be correct; at any rate, it agrees with *Megaladapis* far better than does the *tretretretre*.

Images of *Megaladapis*

Megaladapis edwardsi skeleton

Skull of *M. madagascariensis*

M. grandidieri skeleton

Chapter- 6

Subfossil Lemur

Palaeopropithecus ingens, an extinct subfossil lemur and a species of sloth lemur

Subfossil lemurs are lemurs from Madagascar that are represented by recent (subfossil) remains dating from nearly 26,000 years ago (during the late Pleistocene) to approximately 560 years ago. They include both living and extinct species, although the term more frequently refers to the extinct **giant lemurs**. The diversity of subfossil lemur communities was greater than that of present-day lemur communities, ranging from as high as 20 or more species per location, compared with 10 to 12 species today. Extinct species are estimated to have ranged in size from slightly over 10 kg (22 lb) to roughly 200 kg (440 lb). Even the subfossil remains of living species are larger and more robust than the skeletal remains of modern specimens. The subfossil sites found around most of the island demonstrate that most giant lemurs had wide distributions and that ranges of living species have contracted significantly since the arrival of humans.

Despite their size, the giant lemurs shared many features with living lemurs, including rapid development, poor day vision, relatively small brains, and lack of male dominance. They also had many distinct traits among lemurs, including a tendency to rely on terrestrial locomotion, slow climbing, and suspension instead of leaping, as well as a greater dependence on leaf-eating and seed predation. The giant lemurs likely filled ecological niches now left vacant, particularly seed dispersal for plants with large seeds. There were three distinct families of giant lemur, including the Palaeopropithecidae (sloth lemurs), Megaladapidae (koala lemurs), and Archaeolemuridae (monkey lemurs). Two other types were more closely related and similar in appearance to living lemurs: the Giant Aye-aye and *Pachylemur*, a genus of "giant ruffed lemurs".

Subfossil remains were first discovered on Madagascar in the 1860s, but giant lemur species were not formally described until the 1890s. The paleontological interest sparked by the initial discoveries resulted in an overabundance of new species names, the allocation of bones to the wrong species, and inaccurate reconstructions during the early 20th century. Discoveries waned during the mid-20th century, although paleontological work resumed in the 1980s and resulted in the discovery of new species and a new genus. Research has recently focused on diets, lifestyle, social behavior, and other aspects of biology. The remains of the subfossil lemurs are relatively recent, with all or most species dating within the last 2,000 years. Humans first arrived on Madagascar around that time and likely played a role in the demise of the lemurs and the other megafauna that once existed on the large island. Although hunting and habitat change have been investigated as the primary cause of their extinction, a mosaic of complex interactions between multiple factors is now seen as the ultimate cause of their disappearance. Yet oral traditions and recent sightings by Malagasy villagers are still reported, suggesting either lingering populations or very recent extinctions.

Diversity

Extinct giant lemurs

Until recently, giant lemurs existed on Madagascar. Although they are only represented by subfossil remains, they were modern forms, having adaptations unlike those seen in lemurs today, and are counted as part of the rich lemur diversity that has evolved in

isolation for up to 60 million years. All 17 extinct lemurs were larger than the extant forms, including the largest living lemurs, the Indri (*Indri indri*) and Diademed Sifaka (*Propithecus diadema*), which weigh up to 9.5 kg (21 lb). The estimated weights for the subfossil lemurs have varied. Techniques used for these weight estimations include the comparison of skull lengths, tooth size, the head diameter of the femur, and more recently, the area of cortical bone (hard bone) in long bones (such as the humerus). Despite the variations in the size estimates for some species, all subfossil lemurs were larger than living species, weighing 10 kg (22 lb) or more, and one species may have weighed as much as 200 kg (440 lb).

All but one species, the Giant Aye-aye, are thought to have been active during the day. Not only were they unlike the living lemurs in both size and appearance, they also filled ecological niches that no longer exist or are now left unoccupied. Their remains have been found in most parts of the island, except for the eastern rainforests and the Sambirano domain (seasonal moist forests in the northwest of the island), where no subfossil sites are known. Radiocarbon dates for subfossil lemur remains range from approximately 26,000 years BP (for *Megaladapis* in northern Madagascar at the Ankarana Massif) to around 500 years BP (for *Palaeopropithecus* in the southwest).

Characteristics

All of the extinct subfossil lemurs, including the smallest species (*Pachylemur*, *Mesopropithecus*, and the Giant Aye-aye), were larger than the lemur species alive today. The largest species were among the largest primates ever to have evolved. Due to their larger size, the extinct subfossil lemurs have been compared to large-bodied anthropoids (monkeys and apes), yet they more closely resemble the small-bodied lemurs. Like other lemurs, the subfossil lemurs did not exhibit appreciable differences in body or canine tooth size between males and females (sexual dimorphism). This suggests that they, too, either exhibited female social dominance or lacked male dominance, possibly exhibiting the same levels of agonism (aggressive competition) seen in extant lemurs. Like other lemurs, they had smaller brains than comparably sized anthropoids. Most species also had a unique strepsirrhine dental trait, called a toothcomb, which is used for grooming. Even tooth development and weaning was rapid compared to similarly sized anthropoids, suggesting faster sexual maturity of their offspring. Most subfossil lemurs also had high retinal summation (sensitivity to low light), resulting in poor day vision (low visual acuity) compared to anthropoids. This has been demonstrated by the ratio between their relatively small orbits (eye sockets) and the relative size of their optic canal, which is comparable to that of other lemurs, not diurnal anthropoids.

Although these traits are shared among both living and extinct lemurs, they are uncommon among primates in general. Two prevailing hypotheses to explain these unique adaptations are the *energy frugality hypothesis* by Patricia Wright (1999) and the *evolutionary disequilibrium hypothesis* by Carel van Schaik and Peter M. Kappeler (1996). The energy frugality hypothesis expanded on Alison Jolly's energy conservation hypotheses by claiming that most lemur traits not only help conserve energy, but also maximize the use of highly limited resources, enabling them to live in severely seasonal

environments with low productivity. The evolutionary disequilibrium hypothesis postulated that living lemurs are in the process of evolving to fill open ecological niches left by the recently extinct subfossil lemurs. For example, small nocturnal prosimians are typically nocturnal and monogamous, while the larger living lemurs are generally active both day and night (cathemeral) and live in small groups (gregarious). Cathemerality and increased gregariousness might indicate that the larger living lemurs are evolving to fill the role of the giant lemurs, which were thought to be diurnal (day-living) and more monkey-like in behavior. Since most giant subfossil lemurs have been shown to share many of the unique traits of their living counterparts, and not those of monkeys, Godfrey *et al*. (2003) argued that the energy frugality hypothesis seems to best explain both living and extinct lemur adaptations.

The skull and teeth of *Pachylemur insignis* suggest that it ate mostly fruit and some leaves.

Despite the similarities, subfossil lemurs had several distinct differences from their lemur relatives. In addition to being larger, the subfossil lemurs were more dependent on leaves and seeds in their diet, rather than fruit. They utilized slow climbing, hanging, and terrestrial quadrupedalism for locomotion, rather than vertical clinging and leaping and arboreal quadrupedalism. Also, all but one of them—the Giant Aye-aye—are assumed to have been diurnal (due to their body size and small orbits), whereas many small lemurs are nocturnal and medium-sized are cathemeral.

Their skeletons suggest that most subfossil lemurs were tree-dwellers, adapted for living in forests and possibly limited to such habitats. Unlike some of the living species, the subfossil lemurs lacked adaptations for leaping. Instead, suspension, used by some indriids and ruffed lemurs, was extensively used in some lineages. Although living

lemurs are known to visit the ground to varying extents, only the extinct archaeolemurids exhibit adaptations for semiterrestrial locomotion. Due to the size of the extinct subfossil lemurs, all were likely to travel on the ground between trees. They had shorter, more robust limbs, heavily built axial skeletons (trunks), and large heads and are thought to have shared the common lemur trait of low basal metabolic rates, making them slow-moving. Studies of their semicircular canals confirm this assumption, showing that koala lemurs moved slower than orangutans, monkey lemurs were less agile than Old World monkeys, and sloth lemurs exhibited slow movements like those of lorises and sloths.

Types

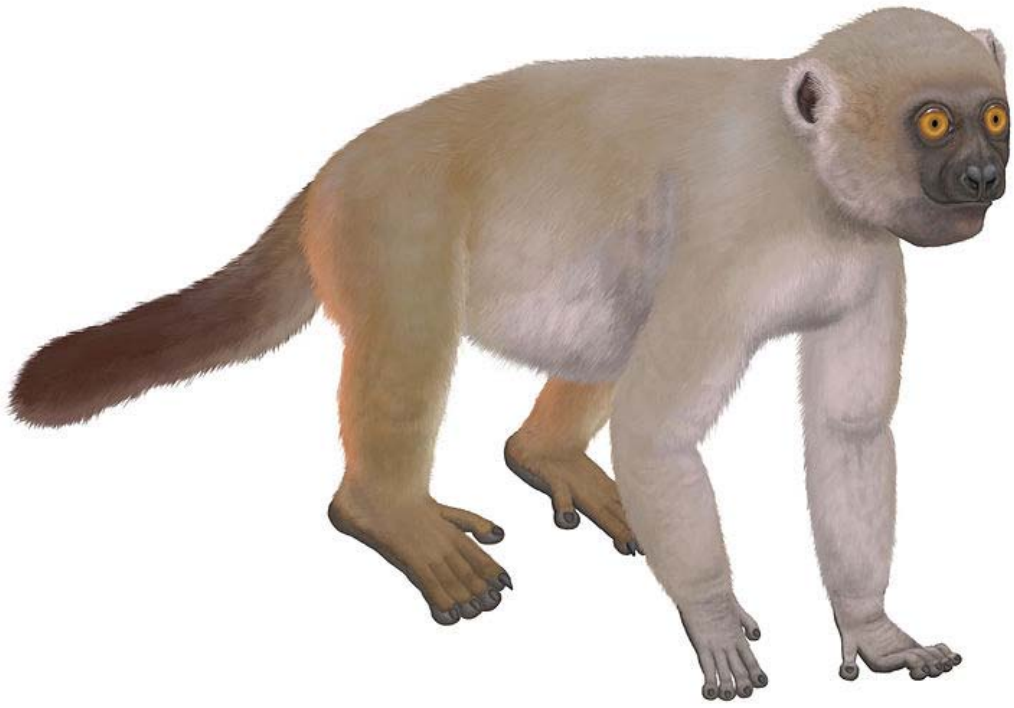
Archaeoindris was the largest of the sloth lemurs, and the largest known lemur. It weighed approximately 200 kg (440 lb).
Sloth lemurs

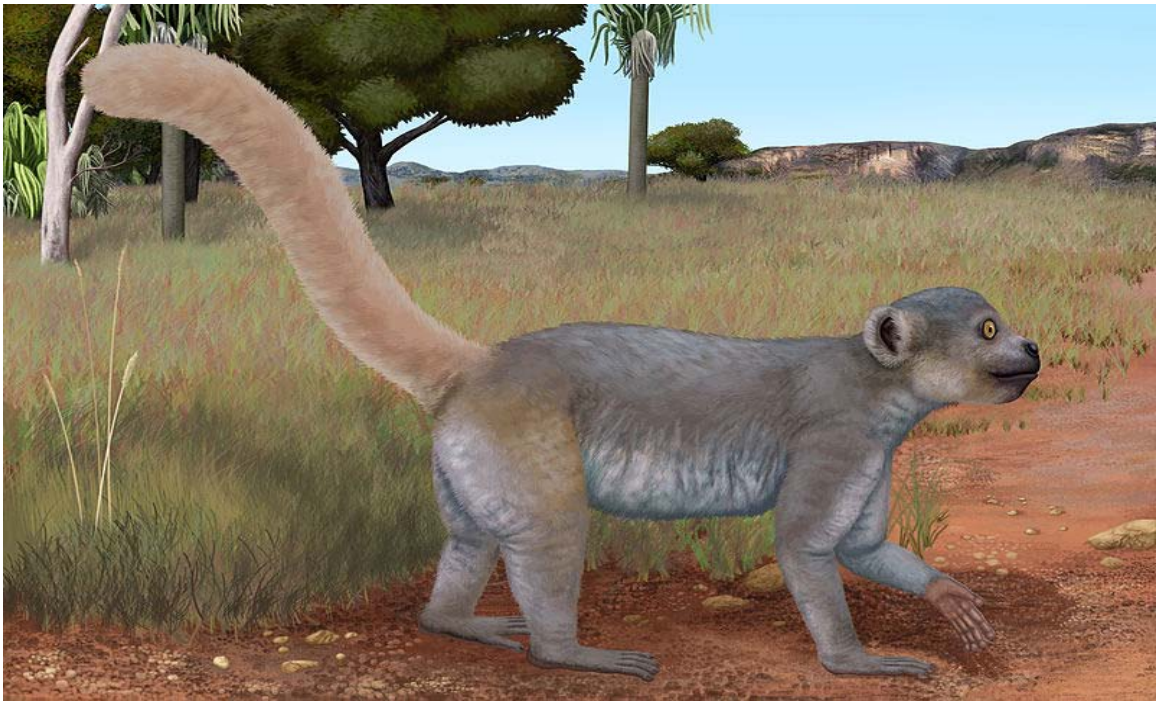
The sloth lemurs (family Palaeopropithecidae) were the most species-rich group of the subfossil lemurs, with four genera and eight species. The common name is due to strong similarities in morphology with arboreal sloths, or in the case of *Archaeoindris*, with

giant ground sloths. They ranged in size from some of the smallest of the subfossil lemurs, such as *Mesopropithecus*, weighing as little as 10 kg (22 lb), to the largest, *Archaeoindris*, weighing approximately 200 kg (440 lb). Their characteristic curved finger and toe bones (phalanges) suggest slow suspensory movement, similar to that of an orangutan or a loris, making them some of the most specialized mammals for suspension. Their day vision was very poor, and they had relatively small brains and short tails. Their diet consisted mostly of leaves, seeds, and fruit, although dental wear analysis suggests they were primarily folivorous seed-predators.

Koala lemurs

The koala lemurs of the family Megaladapidae most closely resemble marsupial koalas from Australia. According to genetic evidence they were most closely related to the family Lemuridae, although for many years they were paired with the sportive lemurs of the family Lepilemuridae due to similarities in their skulls and molar teeth. They were slow climbers and had long forelimbs and powerful grasping feet, possibly using them for suspension. Koala lemurs ranged in size from an estimated 45 to 85 kg (99 to 190 lb), making them as large as a male orangutan or a female gorilla. They had poor day vision, short tails, lacked permanent upper incisors, and had a reduced toothcomb. Their diet generally consisted of leaves, with some species being specialized folivores and others having a broader diet, possibly including tough seeds.





Monkey lemurs, such as *Hadropithecus stenognathus* (above) and *Archaeolemur edwardsi* (below), were the most terrestrial of the lemurs.

Monkey lemurs

Monkey lemurs, or baboon lemurs, share similarities with macaques, although they have also been compared to baboons. Members of the family Archaeolemuridae, they were the most terrestrial of the lemurs, with short, robust forelimbs and relatively flat digits. Although they spent a lot of time on the ground, they were only semi-terrestrial, spending time in trees to feed and sleep. They were heavy-bodied and ranged in size from approximately 13 to 35 kg (29 to 77 lb). They had relatively good day vision and large brains compared with other lemurs. Their robust jaws and specialized teeth suggest a diet of hard objects, such as nuts and seeds, yet other evidence, including fecal pellets, suggests they may have had a more varied diet, including leaves, fruit, and animal matter (omnivory). Dental wear analysis has shed some light on this dietary mystery, suggesting that monkey lemurs had a more eclectic diet, while using tough seeds as a fall-back food item. Within the family, the genus *Archaeolemur* was the most widespread in distribution, resulting in hundreds of subfossil specimens, and may have been one of the last subfossil lemurs to die out.

Giant Aye-aye

An extinct, giant relative of the living Aye-aye, the Giant Aye-aye shared at least two of the Aye-aye's bizarre traits: ever-growing central incisors and an elongated, skinny middle finger. These shared featured suggest a similar lifestyle and diet, focused on percussive foraging (tapping with the skinny digit and listening for reverberation from

hollow spots) of defended resources, such as hard nuts and invertebrate larvae concealed inside decaying wood. Weighing as much as 14 kg (31 lb), it was between two-and-half and five times the size of living Aye-aye. Alive when humans came to Madagascar, its teeth were collected and drilled to make necklaces.

Pachylemur

The only extinct member of the family Lemuridae, the genus *Pachylemur* contains two species that closely resembled living ruffed lemurs. Sometimes referred to as "giant ruffed lemurs", they were approximately three times larger than ruffed lemurs, weighing between 10 and 13 kg (22 and 29 lb). Despite their size, they were arboreal quadrupeds, possibly utilizing more suspensory behavior and cautious climbing than their sister taxon. Their skull and teeth were similar to those of ruffed lemurs, suggesting a diet high in fruit and possibly some leaves. The rest of its skeleton (postcrania) was much more robust and their vertebrae had distinctly different features.

Living species

Subfossil remains of the Indri (*Indri indri*) suggest a recent and significant reduction in its geographic range.

Subfossil sites in Madagascar have yielded the remains of more than just extinct lemurs. Extant lemur remains have also been found, and radiocarbon dating has demonstrated that both types of lemur lived at the same time. Furthermore, in some cases living species are locally extinct for the area in which their subfossil remains were found. Because subfossil sites are found across most of the island, with the most notable exception being the eastern rainforest, both paleocommunity composition and paleodistributions can be determined. Geographic ranges have contracted for numerous species, including the Indri, Greater Bamboo Lemur, and ruffed lemurs. For instance, subfossil remains of the Indri have been found in marsh deposits near Ampasambazimba in the Central Highlands and in other deposits in both central and northern Madagascar, demonstrating a much larger range than the small region on the east coast that it currently occupies. Even the Greater Bamboo Lemur, a critically endangered species restricted to a small portion of the south-central eastern rainforest, has undergone significant range contraction since the mid-Holocene, with subfossil remains from Ankarana Massif in the far north of Madagascar dating to 2565 BCE ± 70 years. Combined with finds from other subfossil sites, data suggests that it used to range across the northern, northwestern, central, and eastern parts of the island. It is unclear whether these locations were wetter in the past or whether distinct subpopulations or subspecies occupied the drier forests, much like modern diversity of sifakas.

In addition to previously having expanded geographic ranges, extant subfossil lemurs exhibited significant variation in size. Researchers have noted that subfossil bones of living species are more robust and generally larger than their present-day counterparts. The relative size of living species may be related to regional ecological factors, such as resource seasonality, a trend that is still observable today, where individuals from the spiny forests are, on average, smaller than individuals from the southwestern succulent woodlands or the dry deciduous forests.

Ecology

As a group, the lemurs of Madagascar are extremely diverse, having evolved in isolation and radiated over the past 40 to 60 million years to fill many ecological niches normally occupied by other primates. In the recent past, their diversity was significantly greater, with 17 extinct species sharing body proportions and specializations with lorises and various non-primates, such as tree sloths, giant ground sloths, koalas, and striped possums (genus *Dactylopsila*). Although the diversity of lemur communities today can be as high as 10 to 12 species per region, communities of 20 or more lemur species existed as recently as 1,000 years ago in areas that now have no lemurs at all. Just like living species, many of the extinct species shared overlapping ranges with closely related species (sympatry) through niche differentiation (resource partitioning). Among all the late Quaternary assemblages of megafauna, only Madagascar was dominated by large primates.

Sloth lemurs, such as *Babakotia radofilai*, were highly arboreal

Although anatomical evidence suggests that even the large, extinct species were adapted to tree-climbing, some habitats, including gallery forests and the spiny forests of southern Madagascar, in which they occurred would not have allowed them to be strictly arboreal. Even today, most lemur species will visit the ground to cross open areas, suggesting that the extinct species did the same. Monkey lemurs (family Archaeolemuridae), including *Archaeolemur majori* and *Hadropithecus stenognathus*, have been reconstructed as being primarily terrestrial. In contrast, the sloth lemurs (family Palaeopropithecidae) were highly arboreal despite the large size of some species.

Species of both extinct and living (extant) lemur vary in size based on habitat conditions, despite their differences in niche preference. Within related groups, larger species tend to

inhabit wetter, more productive habitats, while smaller sister taxa are found in drier, less productive habitats. This pattern suggests that populations of both living and extinct lemur species had become geographically isolated by differences in habitat and evolved in isolation due to varying primary production within different ecosystems. Thermoregulation may also have played a role in the evolution of their increased body size. Yet despite this pressure to specialize and differentiate, some of the extinct subfossil lemurs, such as *Archaeolemur*, may have had island-wide distributions during the Holocene, unlike the living lemurs. If this is the case, it may suggest that some larger lemurs might have been more tolerant to regional differences in ecology than living lemurs.

Diet

Research on subfossil lemur diets, particularly in southern and southwestern Madagascar, has indicated that ecological communities have been significantly affected by their recent extinction. Many extinct subfossil lemurs were large-bodied leaf-eaters (folivores), seed predators, or both. Today, leaf-eating along with seed predation is only seen in mid-sized lemurs, and is far less common than it was in the past. Strict folivory is also less common, now found primarily in small lemurs. In certain cases, subfossil lemurs, such as the sloth lemurs and koala lemurs, may have used leaves as an important fallback food, whereas other species, such as the monkey lemurs and the Giant Aye-aye, specialized on structurally defended resources, such as hard seeds and wood-boring insect larvae. Last, *Pachylemur* was primarily a fruit eater (frugivorous). Subfossil lemur diets have been reconstructed using analytical tools, including techniques to compare tooth anatomy, structure, and wear; biogeochemistry (analysis of isotope levels, like carbon-13); and the dissection of fecal pellets associated with subfossil remains.

The diets of most subfossil lemurs, most notably *Palaeopropithecus* and *Megaladapis*, consisted primarily of C_3 plants, which use a form of photosynthesis that results in higher water loss through transpiration. Other subfossil lemurs, such as *Hadropithecus* and *Mesopropithecus*, fed on CAM and C_4 plants, which use more water-efficient forms of photosynthesis. Fruit and animal matter was more common in the diets of subfossil lemurs including *Pachylemur*, *Archaeolemur*, and the Giant Aye-aye. In southern and southwestern Madagascar, the subfossil lemurs of the spiny forests generally favored the C_3 plants over the more abundant CAM plants, although closely related sympatric species may have fed upon the two types of plants in different ratios, allowing each to divide resources and coexist. Since plants produce defenses against leaf-eating animals, the extensive use of spines by plants in the spiny forests suggest that they evolved to cope with leaf-eating lemurs, large and small.

Seed dispersal

Giant subfossil lemurs are thought to have also played a significant role in seed dispersal, possibly targeting species that did not attract the seed dispersal services of the extinct elephant birds. Biogeochemistry studies have shown that they may have been the primary seed dispersers for the endemic and native C_3 trees in the spiny forests. Terrestrial species

may even have dispersed seeds for small bushes in addition to tall trees. Seed dispersal can involve passing seeds through the gut (endozoochory) or attaching the seeds to the animal's body (epizoochory), and both processes probably occurred with subfossil lemurs. Seeds from *Uncarina* species embed themselves in lemur fur, and likely did the same with subfossil lemurs. Seed dispersal biology is known for very few species in the spiny forest, including genera of plants suspected of depending on giant lemurs, such as *Adansonia*, *Cedrelopsis*, *Commiphora*, *Delonix*, *Diospyros*, *Grewia*, *Pachypodium*, *Salvadora*, *Strychnos*, and *Tamarindus*. For example, *Delonix* has edible pods that are rich in protein, and *Adansonia* fruits have a nutritious pulp and large seeds that may have been dispersed by *Archaeolemur majori* or *Pachylemur insignis*.

Seed size may be a limiting factor for some plant species, since their seeds are too large for living (extant) lemurs. The Common Brown Lemur (*Eulemur fulvus*) can swallow seeds 20 mm (0.79 in) in diameter, while the Black-and-white Ruffed Lemur (*Varecia variegata*) is capable of swallowing seeds up to 30 mm (1.2 in) in diameter. A large lemur, such as *Pachylemur*, which was more than twice the size of today's ruffed lemurs, could probably swallow even larger seeds. Seed dispersal limitations tied to megafaunal extinction are exhibited by *Commiphora guillaminii*. At present, this tree species has a short dispersal distance, but its genetics indicate higher levels of regional gene flow in the past, based on comparisons with a closely related species in Africa that still has its seeds dispersed by large animals.

Discovery and research

The writings of French colonial governor Étienne de Flacourt in the mid-17th century introduced the existence of giant Malagasy mammals to Western science with recorded eye-witness accounts from the local people of dangerous animals, hornless "water cows", and an large lemur-like creature referred to locally as the *tretretretre* or *tratratratra*. Today, the latter is thought to have been a species of *Palaeopropithecus* or possibly *Megaladapis*. Flacourt described it as:

An animal as big as a two-year-old calf, with a round head and a human face: the front feet are monkeylike, and the rear ones as well. It has frizzy hair, a short tail, and humanlike ears. One has been seen near Lake Lipomami, around which it lives. It is a very solitary animal; the local people fear it greatly and flee from it as it does from them.
—Étienne de Flacourt, *Histoire de la Grande Isle Madagascar, 1658*

Early depictions of subfossil lemurs, such as this one of *Megaladapis madagascariensis* (top) from 1902, were based on inaccurate reconstructions due to confused pairing of skeletal remains. Modern recostructions, such as this one of *M. edwardsi* (bottom), are much more accurate.

Local tales of a *song'aomby* (Malagasy for "cow that is not a cow"), or pygmy hippopotamus, led French naturalist Alfred Grandidier to follow a village headman to a marsh in southwestern Madagascar, a site called Ambolisatra, which became the first known subfossil site in Madagascar. In 1868, Grandidier uncovered the first subfossil remains of lemurs—a humerus from *Palaeopropithecus* and a tibia of a sifaka. The *Palaeopropithecus* remains were not described for several decades, and it took decades more for the remains to be correctly paired with other sloth lemur remains. It was not until 1893 that giant lemur species were formally described, when Charles Immanuel

Forsyth Major discovered and described a long, narrow skull of *Megaladapis madagascariensis* in a marsh. His discoveries in various marshes of central and southwestern Madagascar sparked paleontological interest, resulting in an overabundance of taxonomic names and confused assemblages of bones from numerous species, including non-primates. Specimens were distributed between European museums and Madagascar, often resulting in the loss of field data that went with the specimens, if the data had been recorded at all.

In 1905, Alfred Grandidier's son, Guillaume Grandidier, reviewed subfossil lemur taxonomy and determined that too many names had been created. His review established most of the presently known family and genera names for the extinct lemurs. Despite the taxonomic clarification, subfossil postcrania from different genera, particularly *Megaladapis*, *Palaeopropithecus* and *Hadropithecus*, continued to be incorrectly paired and sometimes assigned to non-primates. Since subfossil remains were often dredged from marshes one by one, pairing skulls with other bones was often guesswork based on size-matching, and was not very accurate as a consequence. Even as late as the 1950s, bones of non-primates were attributed to subfossil lemurs. One reconstruction of the confounded subfossil remains by paleontologist Herbert F. Standing depicted *Palaeopropithecus* as an aquatic animal that swam near the surface, keeping its eyes, ears, and nostrils slightly above water. Postcranial remains of *Palaeopropithecus* had previously been paired with *Megaladapis* by Guillaume Grandidier, who viewed it as a giant tree sloth, which he named *Bradytherium*. Standing's aquatic theory was supported by Italian paleontologist Guiseppe Sera, who reconstructed *Palaeopropithecus* as an "arboreal-aquatic acrobat" that not only swam in water but climbed trees and dove from there into the water. Sera took the aquatic theory further in 1938 by including other extinct lemurs, including *Megaladapis*, which he viewed as a thin ray-like swimmer that fed on mollusks and crustaceans while concealed underwater. It was primarily the paleontologist Charles Lamberton who correctly paired many of the confused subfossils, although others had also helped address problems of association and taxonomic synonyms. Lamberton also refuted Guillaume Grandidier's sloth theory for *Megaladapis*, as well as the aquatic lemur theory of Standing and Sera.

Excavations during the early 20th century by researchers like Lamberton failed to unearth any new extinct lemur genera. Fourteen of the approximately seventeen known species had previously been identified from field work in southern, western, and central Madagascar. When paleontological field work resumed in the early 1980s, new finds provided associated skeletal remains, including rare bones such as carpal bones (wrist bones), phalanges (finger and toe bones), and bacula (penile bone). In some cases, nearly complete hands and feet were found. Enough remains have been found for some groups to demonstrate the physical development of juveniles. Standard long-bone indices have been calculated in order to determine the intermembral index (a ratio that compares limb proportions), and body mass estimates have been made based on long-bone circumference measurements. Even preserved fecal pellets from *Archaeolemur* have been found, allowing researchers to learn about its diet. More recently, electron microscopy has allowed researchers to study behavioral patterns, and DNA amplification has helped

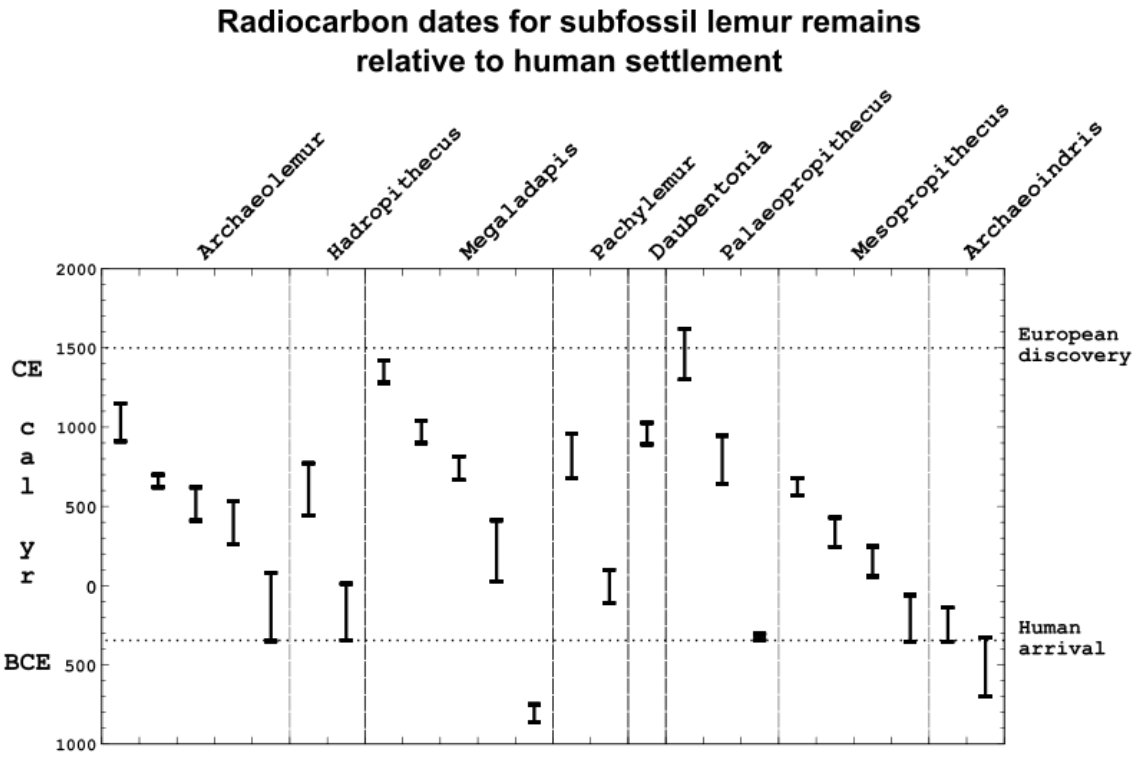
with genetic tests that determine the phylogenetic relationships between the extinct and living lemurs.

A new genus of sloth lemur, *Babakotia*, was discovered in 1986 by a team led by Elwyn Simons of Duke University in karst caves on the Ankarana Massif in northern Madagascar. Along with *Babakotia*, a new species of *Mesopropithecus*, *M. dolichobrachion*, was also discovered, but not formally described until 1995. The same team has also helped promote new ideas about sloth lemur adaptations and the relationships among the four genera. They have also provided evidence that living species, such as the Indri and the Greater Bamboo Lemur, have lost much of their original range. In 2009, a new species of large sloth lemur, called *Palaeopropithecus kelyus*, was described from northwestern Madagascar by a Franco-Madagascan team. The new species was found to be smaller than the two previously known species from the genus, and its diet reportedly consisted of more hard-textured food. The resurgence in subfossil lemur work has also sparked new interest in Madagascar's small mammals, which have also been found at the subfossil sites. This has led to new ideas about the origins, diversity, and distribution of these animals.

The number of Malagasy subfossil sites containing subfossil lemurs has increased significantly since the mid-20th century. At that time, subfossil lemurs had only been found in the center, south, and southwest of the island. Since then, only the eastern rainforests have not been represented, and paleodistributions are now known for both extinct and living species around most of the island. Large quantities of subfossil lemur remains have been found in caves, marshes, and streambank sites in drier regions. The subfossil sites are clustered together geographically and are recent in age, mostly dating between 2,500 and 1,000 years old, with a few spanning back into the last glaciation, which ended approximately 10,000 years ago.

Extinction

At least 17 species of giant subfossil lemur vanished during the Holocene, with all or most extinctions happening after the colonization of Madagascar by humans around 2,000 years ago. Madagascar's megafauna included not only giant lemurs, but also elephant birds, giant tortoises, several species of Malagasy hippopotamuses, *Cryptoprocta spelea* (a "giant Fossa"), large crocodiles (*Voay robustus*), and *Plesiorycteropus*, a unique digging mammal, all of which died out during the same period. Madagascar's megafaunal extinctions were among the most severe for any continent or large island, with all endemic wildlife over 10 kg (22 lb) disappearing, totaling approximately 25 species. The most severely impacted lemurs were generally large and diurnal, particularly the clade containing the living indriids and extinct sloth lemurs. Although only the indriids are alive today and represent only a small percentage of the living lemur species, this clade collectively contained the majority of the extinct giant lemur species.



Radiocarbon dating of multiple subfossil specimens shows that the giant subfossil lemurs were present on the island until after human arrival.

By region, the Central Highlands lost the greatest number of lemur species. Although it has lost nearly all of its woodland habitat, some lemur species still survive in isolated forest patches. Lemur diversity is tightly linked with plant diversity, which in turn decreases with increased forest fragmentation. In extreme cases, treeless sites such as the town of Ampasambazimba from the central region no longer support any of the lemur species represented in their subfossil record. However, other locations no longer have giant subfossil lemurs, yet they still maintain forested habitat that could support them. Even though the giant lemurs have disappeared from these locations, while the smaller species survive in the forest patches that remain, the subfossil remains indicate that the living species used to be more widespread and coexisted with the extinct species. Although the Central Highlands saw the greatest species loss, it was not the only region or habitat type to witness extinctions. However, the least-understood region is the eastern rainforests, which have not yielded subfossil lemur remains. Consequently, it is impossible to know what percentage of lemur taxa were recently lost there, although studies of Malagasy customs (ethnohistory) along with archaeological evidence suggests the eastern rainforests were more ecologically disturbed in the past than they are today. Hunting and trapping by humans may have severely impacted large lemurs in this region as well.

Comparisons of species counts from subfossil deposits and remnant populations in neighboring Special Reserves has further demonstrated decreased diversity in lemur

communities and contracted geographic ranges. At Ampasambazimba in central Madagascar, 20 species of subfossil lemur have been found. At nearby Ambohitantely Reserve, only 20% of those species still survive. Only six of 13 species found at Ankilitelo and Ankomaka Caves in the southwest still survive at Beza Mahafaly Reserve. In the extreme north, the caves of Ankarana have yielded 19 species, yet only nine remain in the surrounding forests. In the northwest, 10 or 11 subfossil species have been found at Anjohibe, whereas only six species remain at nearby Ankarafantsika National Park.

As with the extinctions that occurred on other land masses during the late Pleistocene and Holocene (known as the Quaternary extinction event), the disappearance of Madagascar's megafauna is tightly linked with the arrival of humans, with nearly all extinctions dating to around the same time of the earliest evidence of human activity on the island or significantly later. The exact date of human arrival is unknown, although a radius (arm bone) of a *Palaeopropithecus ingens* with distinct cut marks from the removal of flesh with sharp objects dates to approximately 2325 ± 43 BP (2366–2315 cal yr BP). Based on this evidence from Taolambiby in the southwest interior, as well as other dates for human-modified dwarf hippo bones and introduced plant pollen from other parts of the island, the arrival of humans is conservatively estimated at approximately 350 cal yr BCE. Measurements of stratigraphic charcoal and the appearance of exotic plant pollen dated from Holocene core samples confirm these approximated dates for human arrival in the southwestern corner of the island and further suggest that the central and northern parts of the island did not experience significant human impact until 700 to 1,500 years later. The humid forests of the lower interior of the island were the last to be settled (as shown by the presence of charcoal particles), possibly due to the prevalence of human diseases, such as plague, malaria, and dysentery. The entire island was not fully colonized by humans until the beginning of the second millennium CE.

The extinction of Madagascar's megafauna, including the giant lemurs, was one of the most recent in history, with large lemur species like *Palaeopropithecus ingens* surviving until approximately 500 years ago and one bone of the extinct *Hippopotamus laloumena* radiocarbon dated to about 100 years BP An even wider extinction window for the subfossil lemurs, ranging up until the 20th century, may be possible if reports of unidentified animals are true. As recently as the early 17th century, dwindling populations of subfossil lemurs may have persisted in coastal regions where tree-cutting and uncontrolled fires had less of an impact. By that date, the Central Highlands' forests were mostly gone, with the exception of scattered forest fragments and strips. Along the northwest coast, forms such as *Archaeolemur* may have survived for more than a millennium after the arrival of humans. This is supported by radiocarbon dates for *Archaeolemur* from the Ankarana Massif dating to 975 ± 50 CE as well as archaeological data that show there was little human activity in the area until a few centuries ago, with low human population density along the northwest coast until nearly 1500 CE.

Hypotheses

In the 20th century, six hypotheses for explaining the extinction of the giant subfossil lemurs have been proposed and tested. They are known as the "Great Fire", "Great Drought", "Blitzkrieg", "Biological Invasion", "Hypervirulent Disease", and "Synergy" hypotheses. The first was proposed in 1927 when Henri Humbert and other botanists working in Madagascar suspected that human-introduced fire and uncontrolled burning intended to create pasture and fields for crops transformed the habits quickly across the island. In 1972, Mahé and Sourdat proposed that the arid south had become progressively drier, slowly killing off lemur fauna as the climate changed. Paul S. Martin applied his overkill hypothesis or "blitzkrieg" model to explain the loss of the Malagasy megafauna in 1984, predicting a rapid die-off as humans spread in a wave across the island, hunting the large species to extinction. That same year, Robert Dewar speculated that introduced livestock outcompeted the endemic wildlife in a moderately fast series of multiple waves across the island. In 1997, MacPhee and Marx speculated that a rapid spread of hypervirulent disease might explain the die-offs that occurred after the appearance of humans worldwide, including Madagascar. Finally, in 1999, David Burney proposed that the complete set of human impacts worked together, in some cases along with natural climate change, and very slowly brought about the demise of the giant subfossil lemurs and other recently extinct endemic wildlife.

Since all extinct lemurs were larger than the ones that currently survive, and the remaining large forests still support large populations of smaller lemurs, large size appears to have conveyed some distinct disadvantages. Large-bodied animals require larger habitats in order to maintain viable populations, and are most strongly impacted by habitat loss and fragmentation. Large folivores typically have slower reproductive rates, live in smaller groups, and have low dispersal rates (vagility), making them especially vulnerable to habitat loss, hunting pressure, and possibly disease. Large, slow-moving animals are often easier to hunt and provide a larger amount of food than smaller prey. Furthermore, leaf-eating, large-bodied slow climbers, and semiterrestrial seed predators and omnivores disappeared completely, suggesting an extinction pattern based on habitat use.

Since the subfossil bones of extinct lemurs have been found alongside the remains of highly arboreal living lemur species, we know that much of Madagascar had been covered in forest prior to the arrival of humans; however, the forest coverage of the high plateau region has been debated. Humbert and other botanists suggested that the central plateau had once been blanketed in forest, later to be destroyed by fire for use by humans. However, recent paleoenvironmental studies by Burney have shown that the grasslands of that region have fluctuated over the course of millennia and were not entirely created by humans. Similarly, the role humans played in the aridification of the south and southwest has been questioned, since natural drying of the climate started before human arrival. The marshes of the region (in which subfossil remains have been found) have dried up, subfossil sites have yielded a host of arboreal lemurs, and site names, such as Ankilitelo ("place of three *kily* or tamarind trees") suggest a recent wetter past. Pollen studies have shown that the aridification process began nearly 3,000 years ago, and peaked

1,000 years prior to the time of the extinctions. However, no extinctions occurred prior to the arrival of humans, and the recent climatic changes have not been as severe as those prior to human arrival, suggesting that humans and their effect on the vegetation did play a role in the extinctions. The central plateau lost more species than the dry south and southwest, suggesting that degraded habitats were more affected than arid habitats.

Over-hunting by humans has been one of the most widely accepted hypotheses for the ultimate demise of the subfossil lemurs. The extinctions and human hunting pressure are associated due to the synchronicity of human arrival and species decline, as well as the suspected naïveté of the Malagasy wildlife during the early encounters with human hunters. Despite the assumptions, evidence of butchery has been minimal until recently, although folk memories of rituals associated with the killing of megafauna have been reported. Archeological evidence for butchery of giant subfossil lemurs, including *Palaeopropithecus ingens* and *Pachylemur insignis*, was found on specimens from two sites in southwestern Madagascar, Taolambiby and Tsirave. Although the bones had been collected in the early 20th century and lacked stratigraphic records, one of the bones with tool marks had been dated to the time of the first arrival of humans. Tool-induced bone alterations, in the form of cuts and chop marks near joints and other characteristic cuts and fractures, indicated the early human settlers skinned, disarticulated, and filleted giant lemurs. Prior to these finds, only modified bones of dwarf hippos and elephant birds, as well as Giant Aye-aye teeth, had been found.

Although there is evidence that habitat loss, hunting, and other factors played a role in the demise of the subfossil lemurs, prior to the synergy hypothesis, each had its own discrepancies. Humans may have hunted the giant lemurs for food, but no signs of game-dependent butchery have been found. In fact, Madagascar was colonized by Iron-age pastoralists, horticulturalists, and fishermen, not big-game hunters. Additionally, the blitzkrieg hypothesis predicts extinction within 100 and 1,000 years as humans sweep across the island, yet humans lived alongside the giant lemurs for more than 1,500 years. Alternatively, habitat loss and deforestation have been argued against because many giant lemurs were thought to be terrestrial, they are missing from undisturbed forested habitats, and their environment was not fully forested prior to the arrival of humans. Anthropologist Laurie Godfrey defended the effects of habitat loss by pointing out that most of the extinct lemurs have been shown to have been at least partly arboreal and dependent upon leaves and seeds for food, and also that these large-bodied specialists would be most vulnerable to habitat disturbance and fragmentation due to their low reproductive resilience and their need for large, undisturbed habitats. Still, much of the island remained covered in forest, even into the 20th century.

Linking human colonization to a specific cause for extinction has been difficult since human activities have varied from region to region. Although no single human activity can account for the extinction of the giant subfossil lemurs, the humans are still regarded as being primarily responsible. Each of the contributing human-caused factors played a role (having a synergistic effect) in varying degrees. Even the most widespread and adaptable species, such as *Archaeolemur*, were able to survive despite hunting pressure

and human-caused habitat change until human population growth and other factors reached a tipping point, cumulatively resulting in their extinction.

Extinction timeline and the primary trigger

While it is generally agreed that both human and natural factors contributed to the subfossil lemur extinction, studies of sediment cores have helped to clarify the general timeline and initial sequence of events. Spores of the coprophilous fungus, *Sporormiella*, found in sediment cores experienced a dramatic decline shortly after the arrival of humans. Since this fungus cannot complete its life cycle without dung from large animals, its decline also indicates a sharp decline in giant subfossil lemur populations, as well as other large herbivores, starting around 230–410 cal yr CE. Following the decline of megafauna, the presence of charcoal particles increased significantly, starting in the southwest corner of the island, gradually spreading to the other coasts and the island's interior over the next 1,000 years. The first evidence for the introduction of cattle to the island dates to 1,000 years after the initial decline of coprophilous fungal spores.

The loss of grazers and browsers might have resulted in the accumulation of excessive plant material and litter, promoting more frequent and destructive wildfires, which would explain the rise in charcoal particles following the decline in coprophilous fungus spores. This in turn resulted in ecological restructuring through the elimination of the wooded savannas and preferred arboreal habits on which the giant subfossil lemurs depended. This left their populations at unsustainably low levels, and factors such as their slow reproduction, continued habitat degradation, increased competition with introduced species, and continued hunting (although at lower levels, depending on the region) prevented them from recovering and gradually resulted in their extinction.

Hunting is thought to have caused the initial rapid decline, referred to as the primary trigger, although other explanations may be plausible. In theory, habitat loss should affect frugivores more than folivores, since leaves are more widely available. However, both large-bodied frugivores and large-bodied folivores disappeared simultaneously, while smaller species remained. Furthermore, other large non-primate grazers also disappeared around the same time. Consequently, large body size has been shown to have the strongest link to the extinctions—more so than activity patterns or diet. Since large animals are more attractive as prey, fungal spores associated with their dung declined rapidly with the arrival of humans, and butchery marks have been found on giant subfossil lemur remains, hunting appears to be a plausible explanation for the initial decline of the megafauna.

By region, studies have revealed specific details that have helped outline the series of events that led to the extinction of the local megafauna. In the Central Highlands, dense forests existed until 1600 CE, with lingering patches persisting until the 19th and 20th centuries. Today, small fragments stand isolated among vast expanses of human-created savanna, despite an average annual rainfall that is sufficient to sustain the evergreen forests once found there. Deliberately set fires were the cause of the deforestation, and forest regrowth is restricted by soil erosion and the presence of fire-resistant, exotic

grasses. In the southeast, an extended drought dating to 950 cal yr BP led to fires and transition of open grasslands. The drought may also have pushed humans populations to rely more heavily on bushmeat. Had humans not been present, the subfossil lemur populations might have adjusted to the new conditions and recovered. Had the drought not reduced the population of the subfossil lemurs, the pressure from the small number of people living in the region at the time might not have been enough to cause the extinctions. As in the past, all of the factors that have played a role in past extinctions are still present and active today. As a result, the extinction event that claimed Madagascar's giant subfossil lemurs has not fully concluded.

Lingering populations and oral tradition

Recent radiocarbon dates from accelerator mass spectrometry ^{14}C dating, such as 630 ± 50 BP for *Megaladapis* remains and 510 ± 80 BP for *Palaeopropithecus* remains, indicate that the giant lemurs survived into modern times. Moreover, it is likely that memories of these creatures persist in the oral traditions of some Malagasy cultural groups. Some recent stories from around Belo sur Mer in southwestern Madagascar might even suggest that some of the giant subfossil lemurs still survive in remote forests.

Flacourt's 1658 description of the *tretretretre* or *tratratratra* was the first mention of the now extinct giant lemurs in Western culture, although it is unclear whether he saw it. The creature Flacourt described has traditionally been interpreted as a species of *Megaladapis*. However, the size may have been exaggerated, and the "round head and a human face" would not match *Megaladapis*, which had an enlarged snout and eyes that did not face entirely forward. In fact, *Megaladapis* had the least forward-facing eyes of all primates. The facial description, along with the mention of a short tail, solitary habits, and other traits better match the most recent interpretation—*Palaeopropithecus*. Likewise, Malagasy tales recorded by the 19th-century folklorist Gabriel Ferrand describing a large animal with a flat, human-like face that was unable to negotiate smooth, rock outcrops best match *Palaeopropithecus*, which would also have had difficulty on flat, smooth surfaces.

In 1995, a research team led by David Burney and Ramilisonina performed interviews in and around Belo sur Mer, including Ambararata and Antsira, in order to locate subfossil megafaunal sites used early in the century by other paleontologists. During carefully controlled interviews, the team recorded stories of recent sightings of dwarf hippos (called *kilopilopitsofy*) and of a large, lemur-like creature known as *kidoky*; a report of the interviews was published in 1998 with encouragement from primatologist Alison Jolly and anthropologist Laurie Godfrey. In one interview, an 85-year-old man named Jean Noelson Pascou recounted seeing the rare *kidoky* up close in 1952. Pascou said that the animal looks similar to a sifaka, but had a human-like face, and was "the size of a seven-year-old girl." It had dark fur and a discernible white spot both on the forehead and below the mouth. According to Pascou, it was a shy animal that fled on the ground instead of in the trees. Burney interpreted the old man as saying that it moved in "a series of leaps", but Godfrey later claimed that "a series of bounds" was a better translation—a description that would closely match the foot anatomy of monkey lemurs, such as *Hadropithecus* and

Archaeolemur. Pascou was also able to imitate its call, a long single "whoop", and said that *kidoky* would come closer and continue calling if he imitated the call correctly. The call Pascou imitated was comparable to that of a short call for an Indri, from the other side of the island. When shown a picture of an Indri, Pascou said *kidoky* did not look like that, and that it had a rounder face, more similar to a sifaka. Pascou also speculated that *kidoky* could stand on two legs and that it was a solitary animal.

Another interviewee, François, a middle-aged woodcutter who spent time in the forests inland (east) from the main road between Morondava and Belo sur Mer, along with five of his friends, reported seeing *kidoky* recently. Their description of the animal and François's imitation of its long call were virtually identical to Pascou's. One of the young men insisted that its fur had a lot of white in it, but the other men could not confirm that. François and his friends reported that it had never climbed a tree in their presence, and that it flees on the ground in short leaps or bounds. When Burney imitated the sideways leaping of a sifaka moving on the ground, one of the men corrected him, pointing out that he was imitating a sifaka. The man's imitation of the gallop *kidoky* used was very baboon-like. The men also reported that imitating its call can draw the animal closer and cause it to continue calling.

Burney and Ramilisonina admitted that the most parsimonious explanation for the sightings was that *kidoky* was a misidentified sifaka or other larger living lemur species. However, the authors did not feel comfortable with such a dismissal because of their careful quizzing and use of unlabeled color plates during the interviews and because of the competence demonstrated by the interviewees in regards to local wildlife and lemur habits. The possibility of a wild, introduced baboon surviving in the forests could not be dismissed. However, the descriptions of *kidoky*, with its terrestrial, baboon-like gait, make *Hadropithecus* and *Archaeolemur* the most plausible candidates among the giant subfossil lemurs. At the very least, the stories support a wider extinction window for the giant subfossil lemurs, suggesting that their extinction was recent enough for such vivid stories to still survive in the oral traditions of the Malagasy people.

Chapter- 7

Ring-Tailed Lemur

Ring-tailed Lemur

Conservation status

Near Threatened (IUCN 3.1)

CITES Appendix I (CITES)

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	Primates
Family:	Lemuridae
Genus:	***Lemur*** Linnaeus, 1758
Species:	***L. catta***

Binomial name

Lemur catta
Linnaeus, 1758

Distribution of *Lemur catta*

Synonyms

Genus:

- *Prosimia* Brisson, 1762
- *Procebus* Storr, 1780
- *Catta* Link, 1806
- *Maki* Muirhead, 1819
- *Mococo* Trouessart, 1878
- *Odorlemur* Bolwig, 1960

Species:

- *Maki mococo* Muirhead, 1819

The **Ring-tailed Lemur** (*Lemur catta*) is a large strepsirrhine primate and the most recognized lemur due to its long, black and white ringed tail. It belongs to Lemuridae, one of four lemur families. It is the only member of the ***Lemur*** genus. Like all lemurs it is endemic to the island of Madagascar. Known locally in Malagasy as *hira* or *maky* (spelled *maki* in French), it inhabits gallery forests to spiny scrub in the southern regions of the island. It is omnivorous and the most terrestrial of lemurs. The animal is diurnal, being active exclusively in daylight hours.

The Ring-tailed Lemur is highly social, living in groups of up to 30 individuals. It is also female dominant, a trait common among lemurs. To keep warm and reaffirm social bonds, groups will huddle together forming a *lemur ball*. The Ring-tailed Lemur will also sunbathe, sitting upright facing its underside, with its thinner white fur towards the sun. Like other lemurs, this species relies strongly on its sense of smell and marks its territory with scent glands. The males perform a unique scent marking behavior called *spur*

marking and will participate in *stink fights* by impregnating their tail with their scent and wafting it at opponents.

As one of the most vocal primates, the Ring-tailed Lemur utilizes numerous vocalizations including group cohesion and alarm calls. Experiments have shown that the Ring-tailed Lemur, despite the lack of a large brain (relative to simiiform primates), can organize sequences, understand basic arithmetic operations and preferentially select tools based on functional qualities.

Despite being listed as Near Threatened by the IUCN Red List and suffering from habitat destruction, the Ring-tailed Lemur reproduces readily in captivity and is the most populous lemur in zoos worldwide, numbering more than 2000 individuals. It typically lives 16 to 19 years in the wild and 27 years in captivity.

Etymology

The genus name *Lemur* was created by Carl Linnaeus, the founder of modern binomial nomenclature, to describe only three species, but the word eventually became the collective name used for all primates endemic to Madagascar. Linnaeus was familiar with the historical works of Virgil and Ovid and their references to the festival of Lemuria, during which specters or ghosts—referred to as lemures—were exorcised. As an analogy to these ghosts from Roman mythology, he created the name "*Lemur*" to include these prosimian primates due to their nocturnal habits and ghost-like appearance. Their noiseless movements at night, reflective eyes, and ghostly cries may also have been a factor. It is even possible that Linnaeus knew that some Malagasy people have held legends that lemurs are the souls of their ancestors.

The species name, *catta*, refers to the Ring-tailed Lemur's cat-like appearance. Its purring vocalization is similar to that of the Domestic Cat.

Evolutionary history

All mammalian fossils from Madagascar come from recent times. Thus, little is known about the evolution of the Ring-tailed Lemur, let alone the rest of the lemur clade, which comprises the entire endemic primate population of the island. However, chromosomal and molecular evidence suggest that lemurs are more closely related to each other than to other Strepsirrhine primates. For this to have happened, it is thought that a very small ancestral population came to Madagascar via a single rafting event between 50 and 80 million years ago. Subsequent evolutionary radiation and speciation has created the diversity of Malagasy lemurs seen today.

According to analysis of amino acid sequences, the branching of the family Lemuridae has been dated to 26.1 ±3.3 mya while rRNA sequences of mtDNA place the split at 24.9 ±3.6 mya. The ruffed lemurs are the first genus to split away (most basal) in the family, a view that is further supported by analysis of DNA sequences and karyotypes. Additionally, Molecular data suggests a deep genetic divergence and sister group

relationship between the true lemurs (*Eulemur*) the remaining three genera: *Lemur*, *Hapalemur*, and *Prolemur*.

The Ring-tailed Lemur is thought to share closer affinities to the bamboo lemurs of the genera *Hapalemur* and *Prolemur* than to the other two genera in its family. This has been supported by comparisons in communication, chromosomes, genetics, and several morphological traits, such as scent gland similarities. However, other data concerning immunology and other morphological traits fail to support this close relationship. For example, *Hapalemur* and *Prolemur* have short snouts, while the Ring-tailed Lemur and the rest of Lemuridae have long snouts. (However, differences in the relationship between the orbit (eye socket) and the muzzle suggest that the Ring-tailed Lemur and the true lemurs evolved their elongated faces independently.)

The relationship between the Ring-tailed Lemur and bamboo lemurs (both *Hapalemur* and *Prolemur*) is the least understood. Molecular analysis suggests that either the bamboo lemurs diverged from the Ring-tailed Lemur, making the group monophyletic and supporting the current 3-genera taxonomy, or that the Ring-tailed Lemur is nested in with the bamboo lemurs.

The karyotype of the Ring-tailed Lemur has 56 chromosomes, of which four are metacentric (arms of nearly equal length), four are submetacentric (arms of unequal length), and 46 are acrocentric (the short arm is hardly observable). The X chromosome is metacentric and the Y chromosome is acrocentric.

Taxonomic classification

Linnaeus first used the genus name *Lemur* to describe "*Lemur tardigradus*" (the Red Slender Loris, now known as *Loris tardigradus*) in his 1754 catalog of the Museum of King Adolf Frederick. In 1758, his 10th edition of *Systema Naturae* listed the genus *Lemur* with three included species, only one of which is still considered to be a lemur while another is no longer considered to be a primate. These species include: *Lemur tardigradus*, *Lemur catta* (the Ring-tailed Lemur), and *Lemur volans* (the Philippine Colugo, now known as *Cynocephalus volans*). In 1911, Oldfield Thomas made *Lemur catta* the type species for the genus, despite the term initially being used to describe lorises. On January 10, 1929, the International Commission on Zoological Nomenclature (ICZN) formalized this decision in its publication of Opinion 122.

The Ring-tailed Lemur shares many similarities with ruffed lemurs (genus *Varecia*) and true lemurs (genus *Eulemur*), and its skeleton is nearly indistinguishable from that of the true lemurs. Consequently, the three genera were once grouped together in the genus *Lemur* and more recently are sometimes referred to as subfamily Lemurinae (within family Lemuridae). However, ruffed lemurs were reassigned to the genus *Varecia* in 1962, and due to similarities between the Ring-tailed Lemur and the bamboo lemurs, particularly in regards to molecular evidence and scent glands similarities, the true lemurs were moved to the genus *Eulemur* by Yves Rumpler and Elwyn Simons (1988) as well as Colin Groves and Robert H. Eaglen (1988). In 1991, Ian Tattersall and Jeffrey H.

Schwartz reviewed the evidence and came to a different conclusion, instead favoring to return the members of *Eulemur* and *Varecia* to the genus *Lemur*. However, this view was not widely accepted and the genus *Lemur* remained monotypic, containing only the Ring-tailed Lemur. Because the differences in molecular data are so minute between the Ring-tailed Lemur and both genera of bamboo lemurs, it has been suggested that all three genera be merged.

Anatomy and physiology

The Ring-tailed lemur is a relatively large lemur. Its average weight is 2.2 kilograms (4.9 lb). Its head–body length ranges between 39 and 46 cm (15 and 18 in), its tail length is 56 and 63 cm (22 and 25 in), and its total length is 95 and 110 cm (37 and 43 in). Other measurements include a hind foot length of 102 and 113 mm (4.0 and 4.4 in), ear length of 40 and 48 mm (1.6 and 1.9 in), and cranium length of 78 and 88 mm (3.1 and 3.5 in).

The Ring-tailed Lemur's tail is longer than its body

The species has a slender frame and narrow face, fox-like muzzle. The Ring-tailed Lemur's trademark—a long, bushy tail—is ringed in alternating black and white transverse stripes, numbering 12 or 13 white rings and and 13 or 14 black rings, and always ending in a black tip. The total number of rings nearly matches the approximate number of caudal vertebrae (~25). Its tail is longer than its body and is not prehensile. Instead, it is only used for balance, communication, and group cohesion.

The pelage (fur) is so dense that it can clog electric clippers. The ventral (chest) coat and throat are white or cream. The dorsal (back) coat varies from gray to rosy-brown, sometimes with a brown pygal patch around the tail region, where the fur grades to pale gray or grayish brown. The dorsal coloration is slightly darker around the neck and crown. The hair on the throat, cheeks, and ears is white or off-white and also less dense, allowing the dark skin underneath to show through. The muzzle is dark grayish and the nose is black, and the eyes are encompassed by black triangular patches. Facial vibrissae (whiskers) are developed and found above the lips (mystacal), on the cheeks (genal), and on the eyebrow (superciliary). Vibrissae are also found slightly above the wrist on the underside of the forearm. The ears are relatively large compared to other lemurs and are covered in hair, which has only small tufts if any. Although slight pattern variations in the facial region may be seen between individuals, there are no obvious differences between the sexes.

Unlike most diurnal primates, but like all strepsirhine primates, the Ring-tailed Lemur has a tapetum lucidum, or reflective layer behind the retina of the eye, that enhances night vision. The tapetum is highly visible in this species because the pigmentation of the ocular fundus (back surface of the eye), which is present in—but varies between—all lemurs, is very spotty. The Ring-tailed Lemur also has a rudimentary foveal depression on the retina. Another shared characteristic with the other strepsirrhine primates is the rhinarium), a moist, naked, glandular nose supported by the upper jaw and protruding beyond the chin. The rhinarium continues down where it divides the upper lip. The upper lip is attached to the premaxilla, preventing the lip from protruding and thus requiring the lemur to lap water rather than using suction.

Scent glands on a male: the brachial glands on the upper chest (top), and antebrachial gland and spur on the forearm (bottom)

The skin of the Ring-tailed Lemur is dark gray or black in color, even in places where the fur is white. It is exposed on the nose, palms, soles, eyelids, lips, and genitalia. The skin is smooth, but the leathery texture of the hands and feet facilitate terrestrial movement. The anus, located at the joint of the tail, is covered covered when the tail is lowered. The area around the anus (circumanal area) and the perineum are covered in fur. In males, the scrotum lacks fur, is covered in small, horny spines, and the two sacs of the scrotum are divided. The penis is nearly cylindrical in shape is covered in small spines, as well as two pairs of larger spines on both sides. Males have a relatively small baculum (penis bone) compared to their size. The scrotum, penis, and prepuce are usually coated with a foul-smelling secretion. Females have a thick, elongated clitoris that protrudes from the labia of the vulva. The opening of the urethra is closer to the clitoris than the vagina, forming a "drip tip."

Females have two pairs of mammary glands (four nipples), but only one pair is functional. The pair anterior pair (closest to the head) are very close to the axillae (armpit). Furless scent glands are present on both males and females. Both genders have small, dark antebrachial (forearm) glands measuring 1 cm long and located on the inner surface of the forearm nearly 25 cm (9.8 in) above the wrist joint. (This trait is shared between both the *Lemur* and *Hapalemur* genera.) The gland is soft and compressible, bears fine dermal ridges (like fingerprints), and is connected to the palm by a fine, 2 mm–high, hairless strip. However, only the male has a horny spur that overlays this scent gland. The spur develops with age through the accumulation of secretions from an underlying gland that may connect through the skin through as many as a thousand minuscule ducts. The males also have brachial (arm) glands on the axillary surface of their shoulders (near the armpit). The brachial gland is larger than the antebrachial gland, covered in short hair around the periphery, and has a naked crescent-shaped orifice near the center. The gland secretes a foul-smelling, brown, sticky substance. The brachial gland is barely developed if present at all in females. Both genders also have apocrine and sebaceous glands in their genital or perianal regions, which care covered in fur.

Its fingers are slender, padded, mostly lacking webbing, and semi-dexterous with flat, human-like nails. The thumb is both short and widely separated from the other fingers. Despite being set at a right angle to the palm, the thumb is not opposable since the ball of the joint is fixed in place. As with all strepsirrhines, the hand is ectaxonic (the axis passes through the fourth digit) rather than mesaxonic (the axis passing through the third digit) as seen in monkeys and apes. The fourth digit is the longest, and only slightly longer than the second digit. Likewise, the fifth digit is only slightly longer than the second. The palms are long and leathery, and like other primates, they have dermal ridges to improve grip. The feet are semi-digitigrade and more specialized than the hands. The big toe is opposable and is smaller than the big toe of other lemurs, which are more arboreal. The second toe is toe is short, has a small terminal pad, and has a toilet-claw (sometimes referred to as a *grooming claw*) specialized for personal grooming, specifically to rake through fur that is unreachable by the mouth. The toilet-claw is a trait shared among nearly all prosimian primates. Unlike other lemurs, the Ring-tailed Lemur's heel is not covered by fur.

Like other lemurs, the Ring-tailed lemur has a claw-like nail (toilet-claw) on their second toe (above) and dermal ridges on its hands to improve its grip (center). Unlike other lemurs, it lacks fur on its heel (below).

Dentition

The front, lower dentition includes a toothcomb (4 incisors and 2 canine teeth), while the first premolars resemble canines.

The Ring-tailed Lemur has a dentition of $\frac{2.1.3.3}{2.1.3.3} \times 2 = 36$, meaning that on each side of the jaw it has two incisors, one canine tooth, three premolars, and three molar teeth. Its deciduous dentition is $\frac{2.1.3}{2.1.3} \times 2 = 24$. The permanent teeth erupts in the following order: m 1/1 (first molars), i 2/2 (first incisors), i 3/3 (second incisors), C1 (upper canines), m 2/2 (second molars), c1 (lower canines), m 3/3 (third molars), p 4/4 (third premolars), p 3/3 (second premolars), p 2/2 (first premolars).

Its lower incisors (i1 and i2) are long, narrow, and finely spaced while pointing almost straight forward in the mouth (procumbent). Together with the incisor-shaped (incisiform) lower canines (c1), which are slightly larger and also procumbent, form a structure called a toothcomb, a trait unique to nearly all strepsirrhine primates. The toothcomb is used during oral grooming, which involves licking and tooth-scraping. It may also be used for grasping small fruits, removing leaves from the stem when eating,

and possibly scraping sap and gum from tree bark. The toothcomb is kept clean using a sublingual organ—a thin, flat, fibrous plate that covers a large part of the base of the tongue. The first lower premolar (p2) following the toothcomb is shaped like a canine (caniniform) and occludes the upper canine, essentially filling the role of the incisiform lower canine. There is also a diastema (gap) between the second and third premolars (p2 and p3).

The upper incisors are small, with the first incisors (I1) space widely from each other, yet closely to the second incisors (I2). Both are compressed between buccolingually (between the cheek and the tongue). The upper canines (C1) are long, have a broad base, and curve down and back (recurved). The upper canines exhibit slight sexual dimorphism, with males exhibiting slightly larger canines than females. Both sexes use them in combat by slashing with them. There is a small diastema between the upper canine and the first premolar (P2), which is smaller and more caniniform than the other premolars. Unlike other lemurs, the first two upper molars (M1 and M2) have prominent lingual cingulae, yet do not have a protostyle.

Ecology

The Ring-tailed Lemur can leap from tree to tree

The Ring-tailed Lemur is diurnal and semi-terrestrial. It is the most terrestrial of lemur species, spending as much as 33% of its time on the ground. However it is still considerably arboreal, spending 23% of its time in the mid-level canopy, 25% in the upper-level canopy, 6% in the emergent layer and 13% in small bushes. Troop travel is 70% terrestrial.

Troop size, home range, and population density vary by region and food availability. Troops typically range in size from 6 to 25, although troops with over 30 individuals have been recorded. The average troop contains 13 to 15 individuals. Home range sizes varies between 6 and 35 hectares (15 and 86 acres). Troops of the Ring-tailed Lemur will maintain a territory, but overlap is often high. When encounters occur, they are agonistic, or hostile in nature. A troop will usually occupy the same part of its range for three or four days before moving. When it does move, the average traveling distance is 1 km (0.62 mi). Population density ranges from 100 individuals per 1 km^2 (0.39 sq mi) in dry forests to 250–600 individuals per km^2 in gallery and secondary forests.

The Ring-tailed Lemur has both native and introduced predators. Native predators include the Fossa (*Cryptoprocta ferox*), the Madagascar Harrier-hawk (*Polyboroides radiatus*), the Madagascar Buzzard (*Buteo brachypterus*) and the Madagascar Ground Boa (*Boa madagascariensis*). Introduced predators include the Small Indian Civet (*Viverricula indica*), the Domestic Cat and the Domestic Dog.

Geographic range and habitat

The Ring-tailed Lemur can be found in several protected areas, including Isalo National Park in Madagascar.

Endemic to southern and southwestern Madagascar, the Ring-tailed Lemur ranges further into highland areas than other lemurs. It inhabits deciduous forests, dry scrub, montane humid forests, and gallery forests (forests along riverbanks). It strongly favors gallery forests, but such forests have now been cleared from much of Madagascar in order to create pasture for livestock. Depending on location, temperatures within its geographic range can vary from −12 °C (10 °F) at Andringitra Massif to 48 °C (118 °F) in the spiny forests of Beza Mahafaly Special Reserve.

This species is found as far east as Tôlanaro, inland towards the mountains of Andringitra on the southeastern plateau, among the spiny forests of the southern part of the island, and north along the west coast to the town of Belo sur Mer. Historically, the northern limits of its range in the west extended to the Morondava River near Morondava. It can still be found in Kirindy Mitea National Park, just south of Morondava, though at very low densities. It does not occur in Kirindy Forest Reserve, north of Morondava. Its distribution throughout the rest of its range is very spotty, with population densities varying widely.

The Ring-tailed Lemur can be easily seen in five national parks in Madagascar: Andohahela National Park, Andringitra National Park, Isalo National Park, Tsimanampetsotse National Park, and Zombitse-Vohibasia National Park. It can also be found in Beza-Mahafaly Special Reserve, Kalambatritra Special Reserve, Pic d'Ivohibe Special Reserve, Amboasary Sud, Berenty Private Reserve, Anja Community Reserve, and marginally at Kirindy Mitea National Park. Unprotected forests that the species has been reported in include Ankoba, Ankodida, Anjatsikolo, Anbatotsilongolongo, Bereny, Mahazoarivo, Masiabiby, and Mikea.

Within the protected regions it is known to inhabit, the Ring-tailed Lemur is sympatric (shares its range) with as many as 24 species of lemur, covering every living genus except *Allocebus*, *Indri*, and *Varecia*. Historically, the species used to be sympatric with the critically endangered Southern Black-and-white Ruffed Lemur (*Varecia variegata editorum*), which was once found at Andringitra National Park; however, no sightings of the ruffed lemur have been reported in recent years.

List of species sympatric with the Ring-tailed Lemur

• Verreaux's Sifaka (*Propithecus verreauxi*) • Milne-Edwards' Sifaka (*Propithecus edwardsi*) • Peyrieras' Woolly Lemur (*Avahi peyrierasi*)	• Greater Dwarf Lemur (*Cheirogaleus major*) • White-footed Sportive Lemur (*Lepilemur leucopus*) • Small-toothed Sportive Lemur (*Lepilemur*	• Southern Lesser Bamboo Lemur (*Hapalemur meridionalis*) • Greater Bamboo Lemur (*Prolemur simus*) • Common Brown Lemur (*Eulemur fulvus*)

• Gray Mouse Lemur (*Microcebus murinus*) • Brown Mouse Lemur (*Microcebus rufus*) • Reddish-gray Mouse Lemur (*Microcebus griseorufus*) • Aye-aye (*Daubentonia madagascariensis*) • Fat-tailed Dwarf Lemur (*Cheirogaleus medius*)	*microdon*) • Petter's Sportive Lemur (*Lepilemur petteri*) • Red-tailed Sportive Lemur (*Lepilemur ruficaudatus*) • Wright's Sportive Lemur (*Lepilemur wrightae*) • Hubbard's Sportive Lemur (*Lepilemur hubbardorum*) • Golden Bamboo Lemur (*Hapalemur aureus*)	• Red-fronted Lemur (*Eulemur rufifrons*) • Red-bellied Lemur {*Eulemur rubriventer)* • Collared Brown Lemur (*Eulemur collaris*) • Coquerel's Giant Mouse Lemur (*Mirza coquereli*) • Pale Fork-marked Lemur (*Phaner pallescens*)

In western Madagascar, sympatric Ring-tailed Lemurs and Red-fronted Lemurs (*Eulemur rufifrons*) have been studied together. Little interaction takes place between the two species. While the diets of the two species overlap, they eat in different proportions since the Ring-tailed Lemur has a more varied diet and spends more time on the ground.

Behavior

Diet

The Ring-tailed Lemur is an opportunistic omnivore primarily eating fruits and leaves, particularly those of the tamarind tree (*Tamarindus indica*), known natively as *kily*. When available, tamarind makes up as much as 50% of the diet, especially during the dry, winter season. The Ring-tailed Lemur eats from as many as three dozen different plant species, and its diet includes flowers, herbs, bark and sap. It has been observed eating decayed wood, earth, spider webs, insect cocoons, arthropods (spiders, caterpillars, cicadas and grasshoppers) and small vertebrates (birds and chameleons). During the dry season it becomes increasingly opportunistic.

Social systems

Troops are classified as multi-male groups, with a matriline as the core group. As with most lemurs, females socially dominate males in all circumstances, including feeding priority. Dominance is enforced by lunging, chasing, cuffing, grabbing and biting. Young females do not always inherit their mother's rank and young males leave the troop between three and five years of age. Both sexes have separate dominance hierarchies;

females have a distinct hierarchy while male rank is correlated with age. Each troop has one to three central, high-ranking adult males who interact with females more than other group males and lead the troop procession with high-ranking females. Recently transferred males, old males or young adult males that have not yet left their natal group are often lower ranking. Staying at the periphery of the group they tend to be marginalized from group activity.

The Ring-tailed Lemur will sit facing the sun to warm itself in the mornings

For males, social structure changes can be seasonal. During the six month period between December and May a few males immigrate between groups. Established males transfer every 3.5 years, although young males may transfer every 1.4 years. Group fission occurs when groups get too large and resources become scarce.

In the mornings the Ring-tailed Lemur sunbathes to warm itself. It faces the sun sitting in what is frequently described as a "sun-worshipping" posture or Lotus position. However, it sits with its legs extended outward, not cross-legged, and will often support itself on nearby branches. Sunning is often a group activity, particularly during the cold mornings. At night, troops will split into sleeping parties huddling closely together to keep warm. A group of huddled Ring-tailed Lemurs is referred to as a *lemur ball*.

Despite being quadrupedal the Ring-tailed Lemur can rear up and balance on its hind legs, usually for aggressive displays. When threatened the Ring-tailed Lemur may jump in the air and strike out with its short nails and sharp upper canine teeth in a behaviour termed *jump fighting*. This is extremely rare outside of the breeding season when tensions

are high and competition for mates is intense. Other aggressive behaviours include a *threat-stare*, used to intimidate or start a fight, and a submissive gesture known as *pulled-back lips*.

Border disputes with rival troops occur occasionally and it is the dominant female's responsibility to defend the troop's home range. Agonistic encounters include staring, lunging approaches and occasional physical aggression, and conclude with troop members retreating toward the center of the home range.

Olfactory communication

Male Ring-tailed Lemurs will scent-mark saplings and branches by spur-marking

Olfactory communication is critically important for prosimians like the Ring-tailed Lemur. Males and females scent mark both vertical and horizontal surfaces at the overlaps in their home ranges using their anogenital scent glands. The Ring-tailed Lemur will perform a handstand to mark vertical surfaces, grasping the highest point with its feet while it applies its scent. Use of scent marking varies by age, sex and social status. Male lemurs use their antebrachial and brachial glands to demarcate territories and maintain intragroup dominance hierarchies. The thorny spur that overlays the antebrachial gland on each wrist is scraped against tree trunks to create grooves anointed with their scent. This is known as *spur-marking*.

In displays of aggression, males engage in a social display behaviour called *stink fighting*, which involves impregnating their tails with secretions from the antebrachial and brachial glands and waving the scented tail at male rivals. During the mating season, males wave their scented tails at females as a form of sexual overture; this usually results in the female cuffing or biting the male and elicits subordinate vocalizations from the would-be paramour.

Ring-tailed Lemurs have also been shown to mark using urine. Behaviorally, there is a difference between regular urination, where the tail is slightly raised and a stream of urine is produced, and the urine marking behavior, where the tail is held up in display and only a few drops of urine are used. The urine-marking behavior is typically used by females to mark territory, and has been observed primarily at the edges of the troop's territory and in areas where other troops may frequent. The urine marking behavior also is most frequent during the mating season, and may play a role in reproductive communication between groups.

Auditory communication

The Ring-tailed Lemur is one of the most vocal primates and has a complex array of distinct vocalizations used to maintain group cohesion during foraging and alert group members to the presence of a predator. Calls range from simple to complex. An example of a simple call is the purr, which expresses contentment. A complex call is the sequence of clicks, close-mouth click series (CMCS), open-mouth click series (OMCS) and yaps used during predator mobbing. Some calls have variants and undergo transitions between variants, such as an infant "whit" (distress call) transitioning from one variant to another.

The most commonly heard vocalizations are the moan (low-to-moderate arousal, group cohesion), early-high wail (moderate-to-high arousal, group cohesion), and clicks ("location marker" to draw attention).

Breeding and reproduction

In the wild, females typically give birth to a single offspring

The Ring-tailed Lemur is polygynous, although the dominant male in the troop typically breeds with more females than other males. Fighting is most common during the breeding season. A receptive female may initiate mating by presenting her backside, lifting her tail and looking at the desired male over her shoulder. Males may inspect the female's genitals to determine receptiveness. Females typically mate within their troop, but may seek outside males.

The breeding season runs from mid-April to mid-May. Estrus lasts 4 to 6 hours, and females mate with multiple males during this period. Within a troop, females stagger

their receptivity so that each female comes into season on a different day during the breeding season, reducing competition for male attention. Gestation lasts for about 135 days, and parturition occurs in September or occasionally October. In the wild one offspring is the norm, although twins may occur. Ring-tailed Lemur infants have a birth weight of 70 g (2.5 oz) and are carried ventrally (on the chest) for the first 1 to 2 weeks, then dorsally (on the back).

The young lemurs begin to eat solid food after two months and are fully weaned after five months. Sexual maturity is reached between 2.5 and 3 years. Male involvement in infant rearing is limited, although the entire troop, regardless of age or sex, can be seen caring for the young. Alloparenting between troop females has been reported. Kidnapping by females and infanticide by males also occur occasionally. Due to harsh environmental conditions, predation and accidents such as falls infant mortality can be as high as 50% within the first year and as few as 30% may reach adulthood. The longest-lived Ring-tailed Lemur in the wild was a female at the Berenty Reserve who lived for 20&nbps; years. In the wild, females rarely live past the age of 16, whereas the life expectancy of males is not known due to their social structure. The longest-lived male was reported to be 15 years old. The maximum lifespan reported in captivity was 27 years.

Cognitive abilities and tool use

Historically, the studies of learning and cognition in non-human primates have focused on simians (monkeys and apes), while strepsirrhine primates, such as the Ring-tailed Lemur and its allies, have been overlooked and popularly dismissed as unintelligent. A couple of factors stemming from early experiments have played a role in the development of this assumption. First, the experimental design of older tests may have favored the natural behavior and ecology of simians over that of strepsirrhines, making the experimental tasks inappropriate for lemurs. For example, simians are known for their manipulative play with non-food objects, whereas lemurs are only known to manipulate non-food objects in captivity. This behaviour is usually connected with food association. Also, lemurs are known to displace objects with their nose or mouth more so than with their hands. Therefore, an experiment requiring a lemur to manipulate an object without prior training would favor simians over strepsirrhines. Second, individual Ring-tailed Lemurs accustomed to living in a troop may not respond well to isolation for laboratory testing. Past studies have reported hysterical behaviour in such scenarios. As a result of these early studies lemurs were often omitted from further research.

The notion that lemurs are unintelligent has been perpetuated by the view that the neocortex ratio (as a measure of brain size) indicates intelligence. In fact, primatologist Alison Jolly noted early in her academic career that some lemur species, such as the Ring-tailed Lemur, have evolved a social complexity similar to that of cercopithecine monkeys, but not the corresponding intelligence. After years of observations of wild Ring-tailed Lemur populations at the Berenty Reserve in Madagascar and as well as baboons in Africa, she more recently concluded that this highly social lemur species does not demonstrate the equivalent social complexity of cercopithecine monkeys, despite general appearances.

Regardless, research has continued to illuminate the complexity of the lemur mind, with emphasis on the cognitive abilities of the Ring-tailed Lemur. As early as the mid-1970s, studies had demonstrated that they could be trained through operant conditioning using standard schedules of reinforcement. The species has been shown to be capable of learning pattern, brightness and object discrimination, skills common among vertebrates. The Ring-tailed Lemur has also been shown to learn a variety of complex tasks often equaling, if not exceeding, the performance of simians.

More recently, research at the Duke Lemur Center has shown that the Ring-tailed Lemur can organize sequences in memory and retrieve ordered sequences without language. The experimental design demonstrated that the lemurs were using internal representation of the sequence to guide their responses and not simply following a trained sequence, where one item in the sequence cues the selection of the next. But this is not the limit of the Ring-tailed Lemur's reasoning skills. Another study, performed at the Myakka City Lemur Reserve, suggests that this species along with several other closely related lemur species understand simple arithmetic operations.

Since tool use is considered to be a key feature of primate intelligence, the apparent lack of this behavior in wild lemurs, as well as the lack of non-food object play, has helped reinforce the perception that lemurs are less intelligent than their simian cousins. However, another study at the Myakka City Lemur Reserve examined the representation of tool functionality in both the Ring-tailed Lemur and the Common Brown Lemur and discovered that, like monkeys, they utilized tools with functional properties (e.g., tool orientation or ease of use) instead of tools with nonfunctional features (e.g., color or texture). Although the Ring-tailed Lemur may not use tools in the wild, it can not only be trained to use a tool, but will preferentially select tools based on their functional qualities. Therefore, the conceptual competence to utilize a tool may have been present in the common primate ancestor, even though the use of tools may not have appeared until much later.

Conservation status

In addition to being listed as *Near Threatened* in 2008 by the IUCN, the Ring-tailed Lemur has been listed since 1977 by CITES under Appendix I, which makes trade of wild-caught specimens illegal. Although there are more endangered species of lemur, the Ring-tailed Lemur is considered a flagship species due to its recognizability.

Ring-tailed lemurs are a common sight at Berenty Private Reserve in southern Madagascar

Three factors threaten Ring-tailed Lemurs. First and foremost is habitat destruction. Starting nearly 2,000 years ago with the introduction of humans to the island, forests have been cleared to produce pasture and agricultural land. Extraction of hardwoods for fuel and lumber, as well mining and overgrazing, have also taken their toll. Today, it is estimated that 90% of Madagascar's original forest cover has been lost. Rising populations have created even greater demand in the southwest portion of the island for fuel wood, charcoal, and lumber. Fires from the clearing of grasslands, as well as slash-and-burn agriculture destroy forests. Another threat to the species is harvesting either for food (bush meat) or pets. Finally, periodic drought common to southern Madagascar can impact populations already in decline. In 1991 and 1992, for example, a severe drought caused an abnormally high morality rate among infants and females at the Beza Mahafaly Special Reserve. Two years later, the population had declined by 31% and took nearly four years to start to recover.

The Ring-tailed Lemur resides in several protected areas within its range, each offering varying levels of protection. At the Beza Mahafaly Special Reserve, a holistic approach to in situ conservation has been taken. Not only does field research and resource management involve international students and local people (including school children), livestock management is used at the peripheral zones of the reserve and ecotourism benefits the local people.

Outside of its diminishing habitat and other threats, the Ring-tailed Lemur reproduces readily and has fared well in captivity. For this reason, along with its popularity, it has

become the most populous lemur in zoos worldwide, with more than 2500 in captivity as of 2009. It is also the most common of all captive primates. Ex situ facilities actively involved in the conservation of the Ring-tailed Lemur include the Duke Lemur Center in Durham, NC, the Lemur Conservation Foundation in Myakka City, FL and the Madagascar Fauna Group headquartered at the Saint Louis Zoo. Due to the high success of captive breeding, reintroduction is a possibility if wild populations were to crash. Although experimental releases have met success on St. Catherines Island in Georgia, demonstrating that captive lemurs can readily adapt to their environment and exhibit a full range of natural behaviors, captive release is not currently being considered.

Ring-tailed Lemur populations can also benefit from drought intervention, due to the availability of watering troughs and introduced fruit trees, as seen at the Berenty Private Reserve in southern Madagascar. However, these interventions are not always seen favorably, since natural population fluctuations are not permitted. The species is thought to have evolved its high fecundity due to its harsh environment; therefore, interfering with this natural cycle could significantly impact the gene pool.

Chapter- 8

Ruffed Lemur

Ruffed lemurs

Black-and-white Ruffed Lemur
(*Varecia variegata*)

Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Mammalia
Order:	Primates
Family:	Lemuridae
Genus:	***Varecia*** Gray, 1863

Type species
Lemur varius É. Geoffroy

(= *Lemur macaco variegatus* Kerr,

1792)

Species
Varecia variegata
Varecia rubra

Distribution of *Varecia spp.*
red = *V. rubra*; orange = *V. v. subcincta*;
green = *V. v. variegata*; blue = *V. v. editorum*

The **ruffed lemurs** of the genus ***Varecia*** are strepsirrhine primates and the largest extant lemurs within the family Lemuridae. Like all living lemurs, they are found only on the island of Madagascar. Formerly considered to be a monotypic genus, two species are now recognized: the Black-and-white Ruffed Lemur, with its three subspecies, and the Red Ruffed Lemur.

Ruffed lemurs are diurnal and arboreal quadrupeds, often observed leaping through the upper canopy of the seasonal tropical rainforests in eastern Madagascar. They are also the most frugivorous of the Malagasy lemurs, and they are very sensitive to habitat disturbance. Ruffed lemurs live in multi-male/multi-female groups and have a complex and flexible social structure, described as fission-fusion. They are highly vocal, and have loud, raucous calls.

Ruffed lemurs are seasonal breeders and highly unusual in their reproductive strategy. They are considered an "evolutionary enigma" in that they are the largest of the extant species in Lemuridae, yet exhibit reproductive traits more common in small, nocturnal lemurs, such as short gestation periods (~102 days) and relatively large average litter sizes (~2–3). Ruffed lemurs also build nests for their newborns (the only primates that do so), carry them by mouth, and exhibit an absentee parental system by stashing them while they forage. Infants are altricial, although they develop relatively quickly, traveling independently in the wild after 70 days and attaining full adult size by six months.

Threatened by habitat loss and hunting, ruffed lemurs are facing extinction in the wild. However, they reproduce readily in captivity, and have been gradually re-introduced into the wild since 1997. Organizations that are involved in ruffed lemur conservation include the Durrell Wildlife Conservation Trust, the Lemur Conservation Foundation (LCF), the Madagascar Fauna Group (MFG), Monkeyland Primate Sanctuary in South Africa, Wildlife Trust, and the Duke Lemur Center (DLC).

Evolutionary history

No mammalian fossil record exists for Madagascar until recent times. Consequently, little is known about the evolution of ruffed lemurs, let alone the entire order Lemuriformes, which comprises the endemic primate population of the island.

Although there is still much debate about the origins of lemurs on Madagascar, it is generally accepted that a single rafting event, similar to the one that brought New World monkeys to South America, occurred around 50–80 million years ago and allowed ancestral lemurs to cross the Mozambique Channel and colonize the island, which had already split from Africa (while it was joined to the Indian subcontinent), approximately 160 million years ago. The resulting founder effect and either non-existent or inferior competition resulted in speciation as the lemur ancestors radiated out to fill open or insufficiently guarded niches. Today, the endemic primate fauna of Madagascar contains over three-quarters of the extant species of the suborder Strepsirrhini, which had been abundant throughout Laurasia and Africa during the Eocene epoch.

Taxonomic classification

Color print of the two ruffed lemur species from Alfred Grandidier's *L'Histoire politique, physique et naturelle de Madagascar*. (1892)

The ruffed lemur genus, *Varecia*, is a member of the family Lemuridae. The extinct genus, *Pachylemur* most closely resembled the ruffed lemurs but died out after the arrival of humans. The genus *Varecia* contains two species, Red Ruffed Lemurs and Black-and-white Ruffed Lemurs, the latter having three subspecies.

- **Family Lemuridae**
  - Genus *Eulemur*: true lemurs
  - Genus *Hapalemur*: lesser bamboo lemurs

- Genus *Lemur*: the Ring-tailed Lemur
- Genus †*Pachylemur*
- Genus *Prolemur*: the Greater Bamboo Lemur
- **Genus *Varecia***: ruffed lemurs
  - Black-and-white Ruffed Lemur, *Varecia variegata*
    - Variegated Black-and-white Ruffed Lemur, *Varecia variegata variegata*
    - Southern Black-and-white Ruffed Lemur, *Varecia variegata editorum*
    - Northern Black-and-white Ruffed Lemur, *Varecia variegata subcincta*
  - Red Ruffed Lemur, *Varecia rubra*

Changes in taxonomy

Ruffed lemurs, along with several species of brown lemur were once included in the genus *Lemur*. In 1962, the ruffed lemurs were reassigned to the genus *Varecia*.

The Red Ruffed Lemur and the Black-and-white Ruffed Lemur were formerly recognized as subspecies, *Varecia variegata rubra* and *Varecia variegata variegata* respectively. In 2001 both were elevated to species status, a decision that was later supported by genetic research. Three subspecies of Black-and-white Ruffed Lemur, which had been published decades earlier, were also recognized as *variegata*, *editorum*, and *subcincta*, although studies have not been entirely conclusive.

Subfossil remains of two extinct lemur species were initially classified under the genus *Varecia*. Found at sites in central and southwestern Madagascar, *Varecia insignis* and *V. jullyi* were very similar to modern ruffed lemurs, but more robust and assumed to be more terrestrial, and thus more prone to predation by early human settlers. More recent studies have shown that these extinct species had a diet similar to that of modern ruffed lemurs, and that they were also arboreal in nature. Enough differences were demonstrated to merit a new genus, *Pachylemur*. These close relatives of ruffed lemurs are now named *Pachylemur insignis* and *P. jullyi*.

Anatomy and physiology

Profile of a typical ruffed lemur overbite

Ruffed lemurs are the largest extant members of the family Lemuridae, with an average head-body length between 43 to 57 cm (17 to 22 in) and a total length from 100 to 120 cm (39 to 47 in), while ranging in weight from 3.1 to 4.1 kg (6.8 to 9.0 lb). The thick, furry tail is longer than the body, averaging 60 and 65 cm (24 and 26 in) in length and is used primarily for balance while moving through the trees. Ruffed lemurs exhibit neither sexual dimorphism nor sexual dichromatism, and females have three pairs of mammary glands.

Foot of a ruffed lemur, showing the toilet-claw on the second toe

Ruffed lemurs are characterized by their long, canine-like muzzle, which includes a significant overbite. The face is mostly black, with furry "ruffs" running from the ears to the neck. Depending on the species, these ruffs are either white (*V. variegata*) or deep reddish (*V. rubra*). Likewise, the coloration of the fluffy fur also varies by species, while the coloration pattern varies by subspecies in the Black-and-white Ruffed Lemur. There are also intermediates in color variation between the two species.

As with all lemurs, the ruffed lemur has special adaptations for grooming, including a toilet-claw on its second toe, and a toothcomb.

Locomotion

Ruffed lemurs are considered arboreal quadrupeds, with the most common type of movement being above-branch quadrupedalism. While in the canopy leaping, vertical clinging, and suspensory behavior, are also common, while bridging, bimanual movement, and bipedalism are infrequently seen. When moving from tree to tree, ruffed lemurs will look over the shoulder while clinging, launch themselves into the air, and twist mid-air so that their ventral surface lands on the new tree or limb. Suspensory behavior is more common in ruffed lemurs than in other lemur species. When ruffed

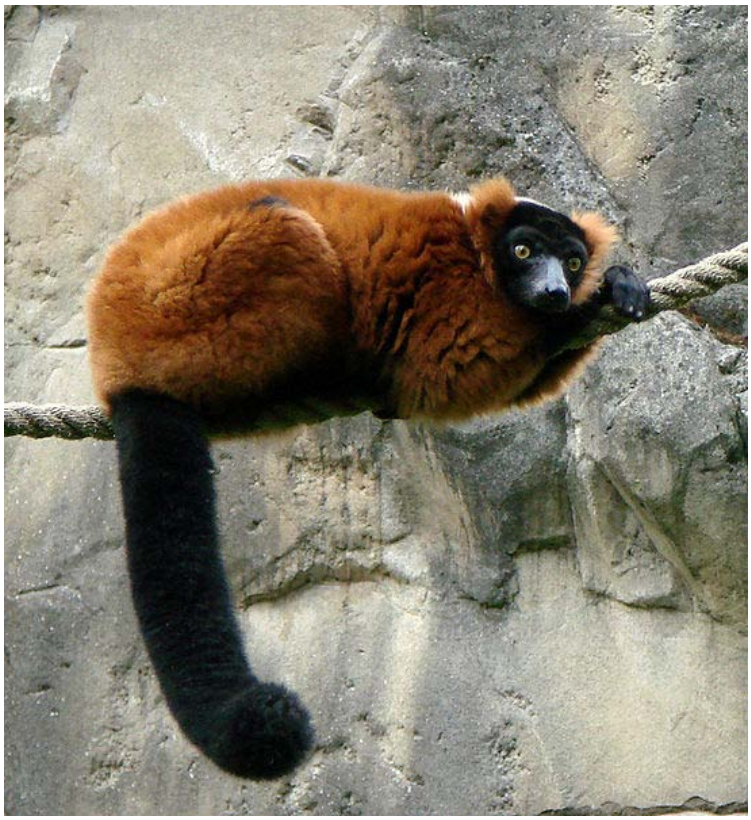
lemurs come down to the ground, they continue to move quadrupedally, running with bounding hops and the tail held high.

Ecology

Being highly arboreal and the most frugivorous of the lemurs, they thrive only in primary forest with large fruiting trees, where they spend most of their time in the upper canopy. By spending the majority of their time in the crown of tall forest trees, they are relatively safe from predators such as the Fossa.

Ruffed lemurs are active primarily during the day (diurnal), during which time they feed primarily on fruits and nectar, often utilizing suspensory postures while feeding. The seeds of the fruit they eat pass through their digestive tract and are propagated throughout the rainforests in their feces, helping to ensure new plant growth and a healthy forest ecosystem. These lemurs are also significant pollinators of the Traveller's Tree (*Ravenala madagascariensis*). Without destroying the inflorescence, they lick the nectar from deep inside the flower using their long muzzles and tongues, collecting and transferring pollen on their snouts and fur from plant to plant. This relationship is thought to be a result of co-evolution.

Geographic range and habitat



Red Ruffed Lemur (*V. rubra*)

Like all lemurs, this genus is found only on the island of Madagascar off the southeastern coast of Africa. Confined to the island's seasonal eastern tropical rainforests, it is uncommon to rare throughout its range, which historically ran from the Masoala Peninsula in the northeast to the Mananara River in the south. Today, the Black-and-white Ruffed Lemur has a much larger range than the Red Ruffed Lemur, although it is very patchy, extending from slightly northwest of Maroantsetra, on Antongil Bay, in the north down the coast to the Mananara River near Vangaindrano in the south. Additionally, a concentrated population of Black-and-white Ruffed Lemurs, of the subspecies *Varecia variegata subcincta*, can also be found on the island reserve of Nosy Mangabe in Antongil Bay. It is suspected that this population was introduced to the island in the 1930s. The Red Ruffed Lemur, on the other hand, has a very restricted range on the Masoala Peninsula.

Historically, the confluence of the Vohimara and Antainambalana Rivers may have been a zone of hybridization between these two species, although no conclusive results have indicated current interbreeding. In general, the Antainambalana River appears to isolate the Red Ruffed Lemurs from the neighboring subspecies of Black-and-white Ruffed Lemur, *V. v. subcincta*. The subspecies *V. v. variegata* can be found further south, and *V. v. editorum* is the southernmost subspecies. The ranges of these two southern subspecies overlap and intermediate forms are reported to exist, although this has not been confirmed.

The rainforests in which these animals live are seasonal, with two primary seasons: the hot, wet season (November through April), and the cool, dry season (May through October). The primary habitat for both species, at any season, is in the crowns of trees, where they spend the majority of their time 15 and 25 m (49 and 82 ft) above ground. With the seasonal availability of resources being similar regardless of location, there is little to no difference in tree usage between species. From September through April, more fruit is available, so females prefer the lianas in the crowns of trees. Both sexes utilize the lower, major branches during the hot, rainy season. The tree crowns are predominantly used from May through August, when young leaves and flowers are in abundance.

Sympatric relations

The following lemur species can be found within the same geographic range as ruffed lemurs:

- Greater Dwarf Lemur (*Cheirogaleus major*)
- Eastern Lesser Bamboo Lemur (*Hapalemur griseus griseus*)
- Weasel Sportive Lemur (*Lepilemur mustelinus*)
- Diademed Sifaka (*Propithecus diadema*)
- Common Brown Lemur (*Eulemur fulvus*)
- Red-bellied Lemur (*Eulemur rubriventer*)
- Eastern Woolly Lemur (*Avahi laniger*)
- Indri (*Indri indri*)
- Brown Mouse Lemur (*Microcebus rufus*)

- Aye-aye (*Daubentonia madagascariensis*)
- White-headed Lemur (*Eulemur albifrons*)

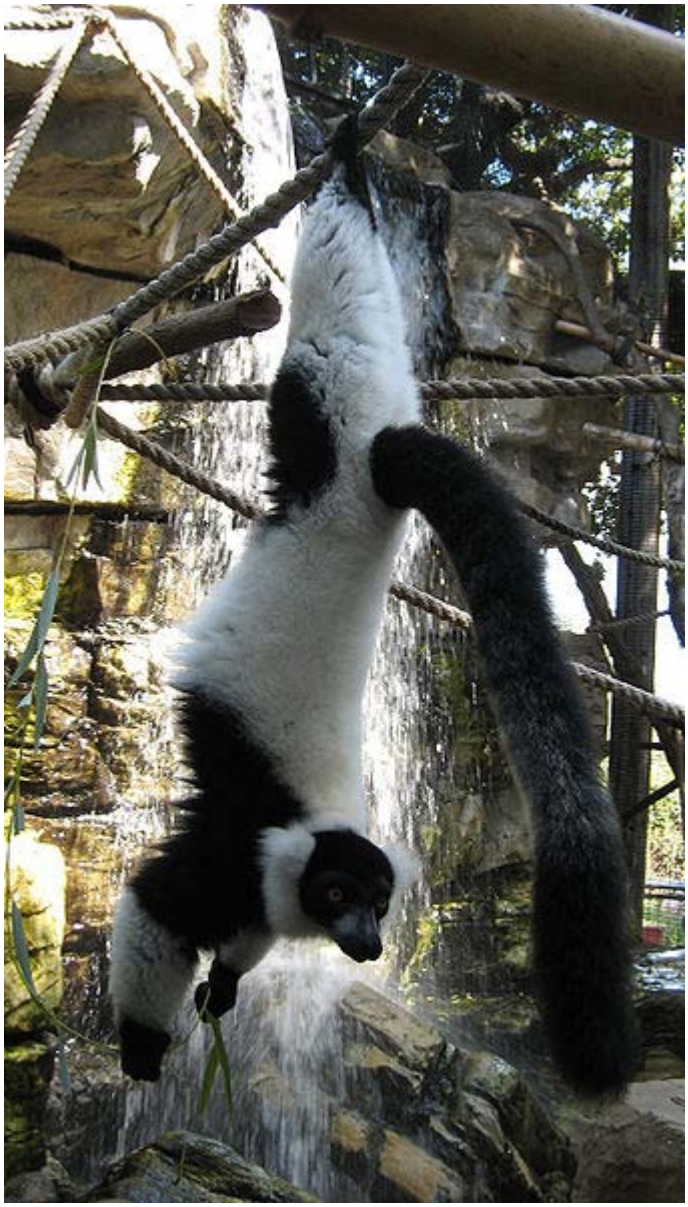
Ruffed lemurs either demonstrate feeding dominance or divide resources by using different forest strata. They are dominant over Red-bellied Lemurs, while Eastern Lesser Bamboo Lemurs avoid encountering them all together. White-headed Lemurs, on the other hand, utilize the understory and lower canopy, below 15 m (49 ft), while the ruffed lemurs utilize the upper canopy, above 15 m (49 ft). Play has even been observed between infant ruffed lemurs and White-headed Lemurs.

Behavior

Ruffed lemurs, on average, spend 28% of the day feeding, 53% resting, and 19% traveling, although differences in resting and feeding durations have been observed between males and females, with females resting less and feeding more. They are diurnal; although peak activity occurs during the early morning and late afternoon or evening, resting usually occurs around midday. When resting, ruffed lemurs often sit hunched or upright. They are also frequently seen lying prone over a branch or sunbathing in a supine position with the limbs outstretched. When feeding, they will often hang upside-down by their hind feet, a type of suspensory behavior, which allows them to reach fruits and flowers.

Being highly arboreal, they spend the majority of their time in the high canopy throughout the day. Ruffed lemurs spend the majority of their time between 15 to 20 m (49 to 66 ft) above the forest floor, followed by 20 to 25 metres (66 to 82 ft) up, and are least frequently seen at 10 to 15 metres (33 to 49 ft). During the hot season, they will relocate to the lower canopy to help regulate their body temperature. In the cold season, ruffed lemurs are least active and may dedicate 2% of their resting time to sunbathing in order to warm up.

Long-term field research has shown that range size, group size, social systems, and territorial behavior vary widely, and may be greatly affected by food distribution and quality. It is generally agreed that the ruffed lemur social system is multi-male/multi-female with a fission-fusion society, although some populations of Black-and-white Ruffed Lemur have been reported as monogamous. This social flexibility is suspected to improve survivability despite an inflexible feeding ecology.



Suspensory feeding by a Black-and-white Ruffed Lemur

Diet

Being the most frugivorous members of the family Lemuridae, consuming an average of 74–90% fruit, ruffed lemurs also consume nectar (4–21%), and supplement the rest of their diet with young leaves (3–6%), mature leaves (1%), flowers (3–6%), and some seeds. Ruffed lemurs have also been reported to come to the ground to eat fungi and exhibit geophagy.

The majority of their diet is made up of relatively few common plant species, with a few species providing more than 50% of the diet. Fig species of the genus Ficus, for example, account for 78% of the fruit consumed by Red-ruffed Lemurs on the Masoala Peninsula.

Although plant species and diets vary by location, the most common food plants reported from the field include the following:

- Canarium
- Cryptocarya
- Ocotea
- Ravensara (Family Lauraceae)
- Ficus
- Eugenia/Syzygium
- Grewia

Fruit trees do not appear to be selected by species, but by availability and accessibility of edible fruit. And despite predominance of a few plant species in the ruffed lemur diet, the remainder of their diet consists of between 80 and 132 other species from 36 plant families.

The availability of food reflects the seasonal nature of the forests in which they live. During the hot season, fruit, flowers, and young leaves are more abundant, whereas the cold, wet season offers more young leaves and flowers. Despite this, the diet changes little between seasons, except that females will consume more high-protein, low-fiber items, such as young leaves and flowers, during pregnancy and lactation in order to offset the energy costs of reproduction. Nectar is only available sporadically, yet constitutes a major food source when the flowers bloom. The nectar of the Traveller's Palm (*Ravenala madagascariensis*) is a favorite among ruffed lemurs.

Social systems

The social organization of ruffed lemurs is widely variable in both group organization and group composition, although no notable difference can be seen between the two species. Ruffed lemurs are typically described as multi-male groups with a fission-fusion social structure, although this can vary by season and locality.

In a study done at Masoala Peninsula on Red ruffed lemurs three levels of organization were identified and defined: communities, core groups, and subgroups. Communities are individuals that affiliated regularly with each other, but rarely with conspecifics outside of the community. Although the entire multi-male/multi-female community lives within a discrete home range, all individuals are never seen in the same location at the same time. Instead, individuals form dispersed social networks, known as core groups, within the community. Core groups are individuals that shared the same core area within a community territory throughout the year. Core groups typically consist of two reproductive females, as well as reproductive males and subadults, ranging in size from two individuals to nine. Females within the groups are cooperative, but male encounters are often agonistic. Subgroups, on the other hand, vary daily in size, composition, and duration, and consist of associated individuals from either the same core group or different core groups, depending on the season. It is from the consistent, daily changes in these subgroups that occur throughout the year, as well as the seasonal formations of core

groups in core areas, that demonstrate the fission-fusion nature of ruffed lemur social structure.

Ruffed lemur sunning position

In another study done at Nosy Mangabe on Black-and-white Ruffed Lemurs a fourth level or organization was defined: affiliates. Affiliates were individuals with more persistent social bonds and more frequent interactions, usually within a core group, but sometimes also between core groups within a subgroup. Adult females typically had many affiliates, whereas adult males rarely interacted with conspecifics, living a more solitary existence.

Past studies have reported other social organizations in ruffed lemurs including monogamous pair bonding. This may have been due to the use of short-term, seasonal field studies instead of yearlong studies that take into consideration the effects that changing seasons have on ruffed lemur communities. For instance, during the cold, rainy season, which corresponds with the breeding season, interactions between core groups within a community are significantly reduced. During this time small subgroups form consisting of a mature female, a mature male, and sometimes offspring. This can be misinterpreted as monogamous pair bonding.

Ranging behavior can also exhibit seasonal variability. During the hot, wet season, females range widely, either alone or in groups of up to six individuals. In the cool, dry season, smaller core groups stabilize in order to occupy concentrated areas. Therefore, during seasons when fruit is abundant, subgroups are larger while scarcity is met with more solitary behavior. This suggests that although their feeding ecology is inflexible, being tied to widely distributed, patchy, and sometimes scarce fruit, ruffed lemurs instead adapt the social system in order to survive.

In terms of dominance, the ruffed lemur's social structure is not as clear-cut as other lemur societies where female dominance is the norm. Although it is historically reported that "males were subordinate to females," especially with captive and free-ranging ruffed lemur populations demonstrating this, wild populations cannot be definitively labeled as matriarchal due to inter-group variation.

There are also social differences between males and females. Females typically have many affiliates and bond strongly with other females both within and outside their core areas, but do not affiliate with individuals outside the community range, except during mating season. Males, on the other hand, are more solitary, interact with only a couple of conspecifics, have weak social bonds with other males, and rarely associate with others outside their core group. Furthermore, field studies suggest that only females play a role in communal home range defense. Males may scent-mark and remain relatively silent, but otherwise show little involvement during disputes.

Community range or territory size can vary widely, from 16 to 197 ha (0.16 to 2.0 km^2; 0.062 to 0.76 sq mi) while group size can range from a single pair to 31 individuals. Population density is also noticeably variable. These wide ranges can be attributed to differing levels of protection and degree of environmental degradation, with better protection and a less degraded environment resulting in higher population density and more moderately sized community ranges. (The duration and seasonality of the studies involved may also have contributed to low group size estimates and community ranges. A study at the Betampona Reserve, for instance, observed monogamous pairs with two to five infants maintaining ranges of 16 to 43 ha (0.16 to 0.43 km^2; 0.062 to 0.17 sq mi).) Core areas at Ambatonikonilahy constituted approximately 10% of the overall community range and showed a close relationship with the location of the largest fruiting trees.

The average daily traveling distance for ruffed lemurs varies between 436 to 2,250 metres (1,430 to 7,380 ft), averaging 1,129 metres (3,704 ft) per day. Activity patterns within the community range vary by gender and season. Males generally stay within a core area all year, whereas females only confine themselves to a core area during the cold wet season, then expand their range throughout the community range during the hot, rainy season. Females expand their traveling range slightly after giving birth, still staying within the core area, but gradually range further in December when they begin stashing their infants with other community members while they look for food. Females range the furthest later during the hot, rainy season. Both activity level and reproductive activity can be summarized in the following table.

Seasonal behavior

Season	Months	Stage	Reproductive cycle	Females activity	Male activity
hot, rainy season	November – April	early	Infant rearing	Expanding travel & infant stashing	Remains in core area
		late	Infant rearing	Expands travel throughout community range	Remains in core area
cool, dry season	May – October	early	Mating season	Remains in core area	Remains in core area
		late	Gestation and birth	Remains in core area & nest building	Remains in core area

Although males demonstrate little involvement in territorial disputes between neighboring communities, and ruffed lemur communities lack cohesiveness, females communally defend the community range against females of other communities. These disputes occur mostly during the hot, rainy season, when resources are more abundant and occur near the boundaries of community ranges. Spacing is maintained by scent marking and vocal communication. Ruffed lemurs are known for their loud, raucous calls that are answered by neighboring communities and subgroups within the same community.

During agonistic encounters between communities, chasing, scent-marking, calling, and occasional physical contact can be seen. Other social behaviors appear to vary between wild and captive ruffed lemurs, as illustrated by the following table.

Behavioral differences: captive vs. wild

	Wild behaviors	Captive behaviors
Aggressive/Agonistic behaviors	• attacks • cuffs • grapples • chases	• stare • charge • chase • lunge • cuff

		• feint-to-cuff • bipedal hop • pounce on • push down • bite
Submissive behaviors	• chatter vocalizations	• chatter vocalizations • displacement • head turning/eye aversion • cowering/flinching • grimacing • backing away • fleeing • jumping away
Affiliate/Affinitive behaviors	• female greeting behavior (intertwining and scent marking) • play • social grooming • squeal approach / anogenital inspections (males, mating season only)	• group movement • huddling together with bodily contact • greeting by sniffing • play (wrestling, grappling, chasing, fleeing and solitary play) • social grooming

Some affiliative behaviors are seasonal or gender-specific, such as the male squeal approach and anogenital inspections performed during the mating season. Another example is the female greeting behavior, where two females will use their anogenital scent glands to mark each other's backs, jump over one another, writhe together, and emit squealing vocalizations. This behavior is not seen during the end of the cool, dry season or around gestation. The frequency of other affiliative behaviors can be affected by age. All ruffed lemurs over five months of age allogroom, and, in captivity, subadults participate in play more frequently than adults.

Cognitive abilities

Historically, relatively few studies of learning and cognition have been performed on strepsirrhine primates, including ruffed lemurs. However, a study at the Myakka City Lemur Reserve demonstrated that ruffed lemurs, along with several other members of the family Lemuridae, could understand the outcome of simple arithmetic operations.

Communication

Olfactory communication

As with all prosimian primates, olfactory communication is used extensively by ruffed lemurs – scent marking in territorial defense and disputes, as well as female greeting displays. The scents communicate the sex, location, and identity of their owner.

Females predominantly scent mark with their anogenital scent glands, by squatting to rub their anogenital region along horizontal surfaces, such as tree limbs. Males, on the other hand, favor using the glands on their neck, muzzle, and chest, by embracing horizontal and vertical surfaces and rubbing themselves over them. Both sexes will occasionally scent mark in ways characteristic of the opposite sex.

In greeting displays, female ruffed lemurs will leap over one another, scent marking the other individual's back in the process.

Auditory communication

Ruffed lemurs are highly vocal, with an extensive vocal repertoire with calls being used in multiple contexts. Calls can also vary seasonally. During the hot, rainy season, the loud, raucous calls that are a hallmark of ruffed lemurs allow groups to remain in contact and maintain spacing. These loud calls can be heard up to 1 kilometre (0.6 mi) away.

Ruffed lemurs utilize alarm calls that differentiate between ground and aerial predators. For instance an *abrupt roar* or *huff* alerts the group to an avian predator, and a *pulsed squawk* or *growl-snort* communicates the existence of a mammalian ground predator. When sounding these calls, such as the pulsed squawk, adults direct them at the predator after moving to a safe position. Once the alarm call is sounded by one individual, the resulting chorus can even reach the furthest ranging community members.

In captivity, ruffed lemur vocalizations have been studied and divided into three general groups: high-, medium-, and low-amplitude calls.

High-amplitude calls

Call	Inferred Function
Roar/shriek chorus	• Intergroup communication and spacing • Intragroup communication (unspecified social functions)
Abrupt roar	• Signals disturbances • Promotes intergroup spacing • Avian predator alert
Pulsed squawk	• Mammalian predator alert • Indicates high arousal

	• Call group together
Wail (*V. variegata* only)	• Signals end of disturbance • Calls group together
Bray	• May serve a mating function (males only)
Quack	• May serve a mating function (males only)

The well-known *roar/shriek chorus* is spontaneous, occurring most often during period of high activity, as well as being contagious, involving communal participation including infants three to four months old. *Abrupt roars* are also more common during high activity and aside from alerting group members to the presence of an avian predator, they probably also help maintain contact with individuals outside of visual range or indicate an aggressive/defensive response to a disturbance. In the wild, both of these calls are emitted more during the hot, rainy season due to heighten activity. All high-amplitude calls are delivered with from a "taut" body posture.

Medium-amplitude calls

Call	Inferred Function
Growl	• Alerts group to low-level disturbance • Announces individual's approach
Growl-snort	• Alerts group to mammalian predator or other startling context
Chatter	• Signals submission • Signals subordinate status
Whine	• Behavioral frustration • Signals submission • Signals appeasement during mating season (males only)

Medium-amplitude calls operate over a shorter range or often involve moderately arousing situations, such as frustration or submission. Low-amplitude calls also generally operate over a short range, yet also cover a wider range of aggravation levels.

Whines are highly variable between individual ruffed lemurs. *Cough*, *grumble*, *squeak*, and *squeal* have only been observed and researched in the wild.

Low-amplitude calls

Call	Inferred Function
Grunt	• Indicates mild aggravation
Huff	• Indicates intense aggravation or high level arousal • Aggravation when avian predator is present
Mew	• Contact call between mother and infant • Occasionally used for coordination between individuals while traveling
Cough	• Aggression between a female and male during mating/birth seasons
Grumble	• Advertises the presence of a male to another
Squeak	• Infant distress signal
Squeal	• Female affiliation

The calls of ruffed lemurs vary only slightly between the two species. In fact, in captivity, it has been documented that Red Ruffed Lemurs understand and even join in the alarm calls of Black-and-white Ruffed Lemurs. One minor difference between the vocal repertoires of these two species is in the pulse rate and frequency of the *pulsed squawk*, which is much faster and higher in Red Ruffed Lemurs than in Black-and-White Ruffed Lemurs. The difference in this vocalization is only interspecific, showing no signs of significant sexual dimorphism within each species.

Red Ruffed Lemurs do not appear to produce a bona fide *wail* vocalization. In Black-and-white Ruffed Lemurs, *pulsed squawks* sometimes slow down as the group calms down, and integrate with the *wail*, creating *pulsed squawk-wail intermediates*. Red Ruffed Lemurs also produce *pulsed squawk-wail intermediate* sounds, but they do not exhibit long, drawn-out *wails* like the Black-and-white Ruffed Lemurs.

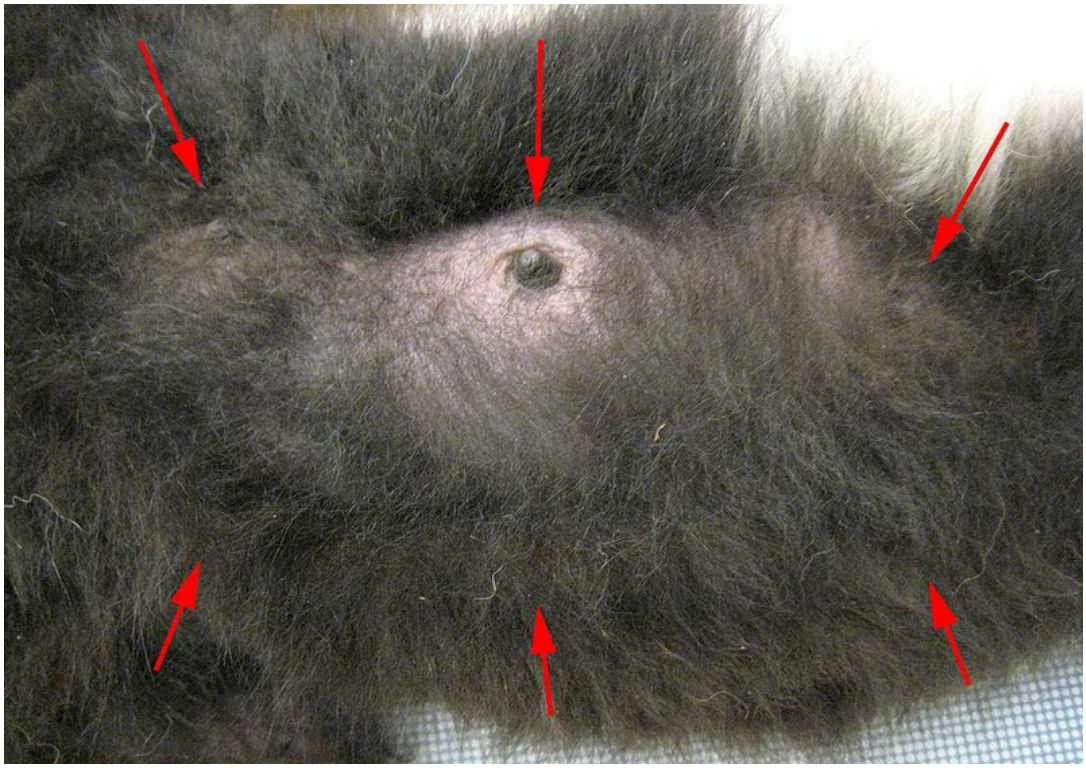
Breeding and reproduction

Contrary to initial reports of monogamy, ruffed lemurs in the wild exhibit seasonal polygamous breeding behavior, with both males and females mating with more than one partner within a single season. Mating is not restricted to just community members, but also involves members of neighboring communities. Females mate primarily with males with whom they had affiliative relations prior to mating season, although some matings occurred with roaming males from other communities.

Shortly before mating season begins, females exhibit swelling of the sex skin, which reaches its peak around the middle of their 14.8 day estrous cycle. Male sexual physiology also undergoes its own change, with testicular volume increasing during mating season, peaking around the time of breeding. Aggression also increases during the mating season, both between members of the same sex and by females towards the male attempting to mate with her. Females have been observed grappling, cuffing, and biting the male during copulation. Either sex may approach the other when the female is in estrus. Initially they may *roar-shriek* with each other. When a male approaches a female he often lowers his head and squeals, inspecting the female's genitalia by licking or sniffing, scent-marking, and offering a submissive chattering vocalization. When a female approaches a male, she may posture herself for mounting. Mating pairs often copulate many times during the course of a mating bout.

The mating season lasts from May through July, during the cold, rainy season, resulting in birth and peak lactation coinciding with the time that fruit is the most plentiful. The gestation period of ruffed lemurs is the shortest of the family Lemuridae, averaging 102 days (with a range of 90 to 106 days). Gestation in the wild last slightly longer than in captivity, averaging 106 days. Just like the mating season, parturition is also seasonal, synchronized to the end of the cold, dry season and the start of the productive hot, rainy season.

In addition to an abnormally short gestation period, ruffed lemurs share another feature with small, nocturnal lemurs by producing the largest litters of the family Lemuridae. Litters typically include two or three infants, although up to five have been reported. Birth weights in captivity average between 83 to 101.7 g (2.9 to 3.59 oz) and range from 70 to 140 grams (2.5 to 4.9 oz). Ruffed lemur infants are altricial, and are born with their eyes open and a full coat of fur.



Female ruffed lemurs have three pairs of mammary glands for feeding their large litters

Ruffed lemurs are the only known primates to build arboreal nests, used exclusively for birth and for the first week or two of life. Starting three weeks prior to birth, females begin constructing the nest from twigs, branches, leaves, and vines, locating it within her core area and 10 to 25 metres (33 to 82 ft) above ground. The nests have only one apparent entry point, and are shallow and dish-shaped. During the first couple of weeks, the mother is mostly solitary and does not travel far from the nest, spending as much as 70–90% of her time with the newborns (in captivity). In order to find food, she will leave the infants alone in the nest or, after the first couple of weeks, will carry them in her mouth and stash them in concealed locations in the canopy while she forages. Since this early developmental period corresponds with the end of the cold, dry season, which offers the least amount of fruit, energy is conserved for lactation while travel is limited. As the hot, rainy season begins, fruit availability rises, lactation demands rise as well, and females increase their travel distance in search of food.

Unlike other diurnal primates, which usually carry their infants with them, ruffed lemur mothers will stash their young by concealing them in the canopy foliage, leaving them to rest and sit quietly for several hours while she forages and performs other activities. Mothers continue to transport their offspring by mouth, moving them one at a time by grasping the infant's belly crosswise. This form of transport usually stops around 2.5 months of age when the infants become too heavy to carry.

Ruffed lemurs are cooperative breeders, with parental care being shared by all community members. For example, mothers will stash their offspring with other mothers

or leave them to be guarded by other community members, including non-breeding individuals of both genders. While the mother is away, community members will not only care for and guard them, but also sound alarm calls if danger is detected or if leaving the infant alone. They will also respond to alarm calls by others. These coordinated vigilance displays further involve communal transmission of the alarm call, with nearby community members repeating the alarm call, potentially summoning the mother back to her offspring. Infant transport by other members of the community has also been recorded. Females have been observed nursing infants of their close relatives, while close kin have adopted rejected infants, acting as foster parents.

Male care for infants has been documented in ruffed lemur societies. During early development, adult males may guard the nests of multiple core group females, as well as help care for the infants that were likely fathered by other males. During the season when females practice infant stashing, males effectively lighten the reproductive burden of up to several mothers by guarding, huddling, grooming, travelling, playing with and feeding the young.

Female ruffed lemurs produce relatively rich milk compared to other lemurs, and consequently, their young develop faster than those of other lemurs. Infants develop rapidly, attaining approximately 70–75% adult weight by the age of four months. They begin climbing and clinging at one month of age, advancing to the point of independently following their mother and group members through the canopy at heights of 50 to 100 metres (160 to 330 ft) by two to three months. Full adult mobility is attained at three to four months of age. Socially, they begin exchanging contact calls with their mother at three weeks, and select their mother as their play partner 75–80% of the time during the first three months. Participation in greeting displays and utilization of more extensive vocalizations commences around four months, while scent marking does not start until six months of age. Infants begin testing solid food starting around 40 days to two months with weaning occurring between four to six months in the wild, although some individuals have continued to nurse until seven to eight months.

Infant mortality is often high among ruffed lemurs, but can also be highly variable. In some seasons, as many as 65% are unable to reach three months of age, possibly due to falls and related injuries, although in some seasons infant mortality is as low as 0%. For those that do survive to adulthood, sexual maturity is attained at 18 to 20 months in females and 32 to 48 months in males. Sexual maturity may take longer to reach in the wild compared to captivity. For females, the inter-birth interval, or time between successive offspring, is typically one year, and in captivity, females can remain reproductively active until the age of 23. The life expectancy for both species of ruffed lemur is estimated at 36 years in captivity, although it is likely to be considerably less in the wild.

Conservation status

In a land where approximately 90% of the original island forest has been destroyed, ruffed lemurs cling to only a small fraction of their original range. Completely dependent

upon large fruiting trees, neither species appears to be flexible with its habitat choice, with selective logging resulting in significantly lower population densities. Although they can survive in very disturbed habitats with lower population densities, they are still especially vulnerable to habitat disturbance. Decreased genetic diversity, in tandem with hunting, natural disasters, predation, and disease, can easily wipe out small populations.

The Black-and-white Ruffed Lemur was elevated by the IUCN to Critically Endangered (A2cd) status from Endangered status in 2008. They cite that "the species is believed to have undergone a decline of 80% over a period of 27 years, due primarily to a decline in area and quality of habitat within the known range of the species and due to levels of exploitation." The total area of all known localities in which Black-and-white Ruffed Lemurs exist is estimated at less than 8,000 km^2 (3,100 sq mi), while the total wild population is estimated between 1,000 and 10,000.

The Red Ruffed Lemur was downgraded to Endangered status from Critically Endangered status by the IUCN in 2008. The justification given includes its limited range, its restriction to only the Masoala Peninsula, and its risk from ongoing habitat loss and hunting. This species occupies a range of no more than 4,000 km^2 (1,500 sq mi), while the total wild population is estimated between 29,000 and 52,000 individuals. Red Ruffed Lemurs are only protected within the boundaries of the Masoala National Park. Historically, this species has been considered more threatened due to its highly restricted range, compared to the widely distributed Black-and-white Ruffed Lemur. However, its protection within the island's largest national park has slightly improved its chances at survival.

There are several organizations involved in ruffed lemur conservation, including the Durrell Wildlife Conservation Trust, the Lemur Conservation Foundation (LCF), the Madagascar Fauna Group (MFG), Monkeyland Primate Sanctuary in South Africa, Wildlife Trust, and the Duke Lemur Center (DLC). To conservation organizations, the ruffed lemurs are considered indicator, umbrella, and flagship species.

Threats in the wild

As with other primates, one of the principal threats to both ruffed lemur species is habitat loss due to slash-and-burn agriculture, logging, and mining. Both species appear to be very sensitive to logging, and are thought to be the most vulnerable of rainforest lemurs. The hardwoods that are favored for construction materials and selectively logged are also preferred by ruffed lemurs for their fruits and potentially affect their travel routes through the canopy. Deforestation, on the other hand, is a result of the need to provide firewood and to support subsistence agriculture and cash crops. For Red Ruffed Lemurs, Slash-and-burn agriculture, known locally as *tavy*, is practiced seasonally on the Masoala peninsula between October and December, and its practice is expanding. Additionally, cattle are sometimes allowed to free-range over these former agricultural clearings, preventing forest re-growth.

Another principal threat to the survival of ruffed lemurs is hunting. Local human populations still hunt and trap ruffed lemurs with traditional weapons, using them as a source of subsistence. Studies from villages in the Makira Forest have revealed that ruffed lemur meat is not only a desired food, but is being hunted unsustainably. On the Masoala peninsula, the calls of Red Ruffed Lemurs help hunters locate them. On this peninsula, firearms are used in addition to traditional traps, known as *laly*, which involve a 5 metres (16 ft) strip of cleared forest with snares set on the few remaining branches that allow the lemurs to cross. Although hunting is illegal, the laws are generally not enforced and the local inhabitants show little concern about their hunting practices, which occur mostly from May to September. Hunting is the biggest concern in the Masoala peninsula because it is likely to continue, whereas logging and slash-and-burn agriculture could be curtailed. In other regions, hunters can scare away ruffed lemurs from their favorite food sources, even if they are hunting other prey. Lastly, these animals are taken from their natural habitats to display for tourists or are sold as exotic pets.

Frequent cyclones also pose a threat, particularly to concentrated or small populations. In late January 1997, cyclone Gretelle destroyed 80% of the Manombo forest canopy. With their habitat, including most of their food resources, effectively destroyed, the ruffed lemurs of the forest broadened their diet, remaining surprisingly frugivorous. Their body weights dropped and no births were reported for four years, but they managed to stave off starvation. This event demonstrated not only their flexibility in the face of natural disasters, which may highlight the evolutionary reasons behind their reproductive capacity and litter size, but also the threat faced by already stressed populations.

Predation in the wild appears to be very rare for ruffed lemurs, probably because living in the high canopy makes them challenging to catch. Evidence of predation by raptors, such as the Henst's Goshawk (*Accipiter henstii*) suggests it occurs at a low rate. The Fossa (*Cryptoprocta ferox*) could present a potential risk if it found an individual lower in the forest canopy, but no confirmation has been presented to indicate that they prey upon ruffed lemurs. Instead, only re-introduced, captive-bred ruffed lemurs have been killed by Fossa, likely due to their inexperience with predators. Nesting behavior poses the biggest risk of predation, making them susceptible to carnivorous mammals, such as the Ring-tailed Mongoose (*Galidia elegans*) and Brown-tailed Mongoose (*Salanoia concolor*).

Captive breeding and reintroductions

Captive populations of both ruffed lemur species exist in American and European zoos, representing a safeguard against extinction. In the United States, captive breeding is managed by the Species Survival Plan (SSP), a program developed by the Association of Zoos and Aquariums (AZA). Although the populations are very limited in their genetic diversity, these species thrive in captivity, making them an ideal candidate for reintroduction into protected habitat, if it is available. Although reintroduction is seen as a last resort among conservationists, a combination of in situ conservation efforts, such as legal protection, public education, the spread of sustainable livelihoods, and reforestation offer hope for ruffed lemurs. In the meantime, reintroductions offer conservation research

opportunities and allow the limited genetic diversity maintained by the SSP to improve the genetic diversity of dwindling Malagasy ruffed lemur populations.

A captive release first occurred in November 1997, when five Black-and-white Ruffed Lemurs (*Varecia variegata variegata*) born in the United States were returned to Madagascar for release in the Betampona Strict Nature Reserve in eastern Madagascar. Popularly known as the *Carolina Five*, these individuals had lived their entire lives in the Natural Habitat Enclosures at the Duke Lemur Center (DLC). Since then, two more groups totaling 13 captive-born ruffed lemurs have been reintroduced into the same reserve, once in November 1998 and again in January 2001. These latter two groups also received "boot camp training" in the DLC forested free-range enclosures prior to release. So far, the results have shown some success, with 10 surviving longer than one year, 3 individuals integrating into wild groups, and 4 offspring have been born to or sired by released lemurs, all of which were parent-raised. Saraph, a male released with the first group, was reported to be doing well seven years post-release, living in a social group with a wild female and their offspring. Research has been ongoing since the initial release, as illustrated in the 1998 BBC documentary *In the Wild: Operation Lemur with John Cleese*. The research has provided useful information about their adaptation to life in the wild.