

= 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 $2 \cdot 1 \cdot 32 \cdot 1 \cdot 3 \times 2 =$

24 . The permanent teeth erupt 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 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 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 size 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 km² (0 @-@ 39 sq mi) in dry forests to 250 ? 600 individuals per km² 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 = =

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 , 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 .

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 .

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 on average every 3 @. @ 5 years , although young males may transfer approximately 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 .

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 = = = =

Olfactory communication is critically important for strepsirrhines 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 .

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 (listen) , which expresses contentment . A complex call is the sequence of clicks , close @-@ mouth click series (CMCS) , open @-@ mouth click series (OMCS) and yaps (listen) 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 (listen) .

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

== Breeding and reproduction ==

The ring-tailed lemur is polygynandrous, 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 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.

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 used 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 use 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 endangered in 2014 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 .

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 mortality 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 .

= = Cultural references = =

The ring @-@ tailed lemur is known locally in Malagasy as maky (pronounced [?mak?i ?] , and spelled maki in French) or hira (pronounced [?hir?] or colloquially [?ir]) . Being the most widely recognized endemic primate on the island , it has been selected as the symbol for Madagascar National Parks (formerly known as ANGAP) . The Maki brand , which started by selling T @-@ shirts in Madagascar and now sells clothing across the Indian Ocean islands , is named after this lemur due to its popularity , despite the fact that the company 's logo portrays the face of a sifaka and its name uses the French spelling .

The first mention of the ring @-@ tailed lemur in Western literature came in 1625 when English traveler and writer Samuel Purchas described them as being comparable in size to a monkey and having a fox @-@ like long tail with black and white rings .

It has been popularized in Western culture by the Animal Planet television series Lemur Street , as well as by the character King Julien in the animated Madagascar film and TV franchise . The ring @-@ tailed lemur was also the focus of the 1996 Nature documentary A Lemur 's Tale , which was filmed at the Berenty Reserve and followed a troop of lemurs . The troop included a special infant named Sapphire , who was nearly albino , with white fur , bright blue eyes , and the characteristic ringed tail .

This species also played a role in the 1997 comedy film Fierce Creatures , starring John Cleese , who has a passion for lemurs . Cleese later hosted the 1998 BBC documentary In the Wild : Operation Lemur with John Cleese , which tracked the progress of a reintroduction of black @-@ and @-@ white ruffed lemurs back into the Betampona Reserve in Madagascar . The project had been partly funded by Cleese 's donation of the proceeds from the London premier of Fierce Creatures .