Plant Species Fed on by Wild Ring-Tailed Lemurs (*Lemur catta*) at Nine Sites

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Abstract

A key aspect of a primate’s ecology is its food source, the very nature of which is spatially and seasonally dependent and may be affected by anthropic pressures. One of the most endangered, yet best-studied, strepsirrhine primates is the ring-tailed lemur (*Lemur catta*), a species that has experienced significant human-induced habitat loss over many decades. To help understand feeding variability across time and space, I present a literature review of plant species (and parts) fed on by ring-tailed lemurs at nine sites in Madagascar: Ambatotsirongorongo, Andringitra Massif, Anja Reserve, Antserananomby, Berenty Reserve, Beza Mahafaly Special Reserve, Cap Sainte-Marie, Tsaranoro Valley Forest, and Tsimanampetsotsa National Park. I gathered literature using keyword searches on Google Scholar ([https://scholar.google.com/](https://scholar.google.com/)) and verified scientific names using the “Catalogue of the Plants of Madagascar” ([http://legacy.tropicos.org/Project/Madagascar](http://legacy.tropicos.org/Project/Madagascar)). From 24 studies, I identify 221 genera and 241 species of consumed plants, with 92 genera and 70 species consumed at two or more sites. Based on the available distribution data, 63% of species are endemic and 22% native. Sixty-seven plants are known only by Malagasy common names and excluded from analyses. When authors identify the plant tissue consumed, 52% of species in the diet are represented by a single tissue type, typically leaves (mature and immature) or fruit (ripe or unripe). This review highlights the importance of studying multiple populations when creating dietary summaries of species and should prove valuable to those exploring ecological trends and habitat use by ring-tailed lemurs.

Keywords Diet · Foraging · Frugivore–folivore · *Lemur catta* · Ring-tailed lemur

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Background and Summary

The ring-tailed lemur (Lemur catta) is one of the best-studied species of strepsirrhine primate, exploiting many different kinds of foods (Chandrashekar et al. 2020) and occupying diverse habitats, including rocky outcrop forests, gallery forests, deciduous forests, and spiny and xerophytic forests (Cameron and Gould 2013; LaFleur and Sauther 2015). It is endemic to Madagascar, an island recognized as a “Biodiversity Hotspot” (Kremen et al. 2008).

The most recent Red List assessment for ring-tailed lemurs (IUCN 2020) suggests a very small wild population, with only eight known sites with more than 100 individuals: Amoron’i Onilahy, Andringitra National Park, Anja Community Reserve, Berenty Private Reserve, Bezà Mahafaly Special Reserve, Isalo National Park, Ihorombe Region in Ihosy District, and Tsimanampesotse National Park. A further 73 lemurs were recorded in 53 ha at Tsaranoro in 2013, 50 lemurs were recorded in 30 ha in Ambatotsirongorongo in 2010, and it is unknown if a population still exists at Cap Sainte-Marie (LaFleur and Gould 2020). At their current rate of decline, ring-tailed lemur populations will not persist long-term, suggesting that introduction of captive animals may be the only hope for the survival of ring-tailed lemurs in the wild (Britt et al. 1998, 2004; LaFleur et al. 2016).

Rising anthropic pressures in Madagascar (Schwitzer et al. 2014) have created an “evolutionary disequilibrium” for its lemur populations as species began to explore recently available diurnal spaces, largely free of newly extinct large-bodied competitors (e.g., subfossil lemurs) and diurnal raptors (van Schaik and Kappeler 1996). Extreme reductions in habitat size and losses of continuous forests have restricted many populations of ring-tailed lemurs to fragmented and isolated forests (Gould and Sauther 2016), with low potential for male dispersal (Gould and Cowen 2020). The unintentioned introduction of red-fronted brown (Eulemur rufus) and collared lemurs (E. collaris) to Berenty in 1975–1983 (Pinkus et al. 2006) brought into question the long-term sustainability of resource partitioning between the native groups of ring-tailed lemurs, Verreaux’s sifaka (Propithecus verreauxi), and these newly introduced primates. Population growth suggests that they can coexist (Simmen et al. 2003), but ring-tailed lemurs and red-fronted brown lemurs compete directly for valuable and limited resources during the birth season (Pinkus et al. 2006).

The consumption of many human-introduced species of plants (e.g., Melia azedarach) is an important shift in the dietary repertoires of ring-tailed lemurs (Gould and Cowen 2020). The introduced tamarind tree (Tamarindus indica), which provides a reliable food source during the dry season when many endemic plants are scarce, is a keystone species for ring-tailed lemurs in the gallery forests of Berenty and Bezà (Soma 2006). While tamarind fruit is a valuable fallback food at Bezà, it can cause severe dental pathology (Sauther and Cuozzo 2009). The incompatibility between thin enamel and the consumption of hard and mechanically challenging fruit, likely reflects how new tamarind is to the lemurs’ diet, with morphology not having caught up with behavior (Cuozzo and Sauther 2006). This hypothesis of an evolutionary disequilibrium in the tamarind-dominated gallery forests of Bezà is further supported by the lack of similar patterns of tooth loss and wear in a sample of subfossil ring-tailed lemurs (ca. 500 to ca. 600 years BP) from Ankilitelo Cave (Cuozzo and Sauther 2015). Additionally, isotopic analyses from extant and subfossil ring-tailed
lemurs (pre- and post-900 BP, respectively) suggest an ecological retreat from predominately dry forests and spiny scrub-living populations in the past to more riparian habitats today (Crowley et al. 2012).

To help understand feeding variability across time and space, I present a literature review of plant species consumed by ring-tailed lemurs from nine study sites in Madagascar. Although other reviews exist (e.g., Goodman et al. 2006; Gould and Gabriel 2015; LaFleur and Sauther 2015; Simmen et al. 2006), this is the most extensive and comprehensive to date with regard to the number of sites examined. The data are from 1974–2016, with the earliest publication (Sussman 1974) including fieldwork from 1969. Study sites (Fig. 1; Table I) are Ambatotsirongorongo (25°4.703′ S, 46°47.246′E; Razafindramanana 2011), Andringitra Massif (22°11.52′S, 46°54.27′E and 22°10.89′S, 46°53.60′E; Goodman and Langrand 1996), Anja Reserve (21°51′S, 46°50′E; Gabriel 2013), Antserananombia (21.7°S, 44.1°E; Kelley et al. 2007), Berenty Reserve (25°0.5′S, 46°18.5′E; Gould et al. 2011), Bezà Mahafaly Special Reserve (23°30′S, 44′E; Gemmil and Gould 2008), Cap Sainte-Marie (25°33.390′S, 45°3.277′E; Kelley 2011), Tsaranoro Valley Forest (22°05′S, 46°46′E; Gabriel 2013), and Tsimanampetsotsa National Park (24°03′S, 43°46′E; LaFleur 2012).

The data comprise 221 plant genera and 241 species consumed by ring-tailed lemurs (Table I; Data Citation 1). Of species for which distribution data are available (N = 209), 131 (63%) are endemic, 45 (22%) native, and 26 (12%) naturalized. Seven species (3%) are not specifically placed within a single category. Ninety-two genera and 70 species of plants are consumed at two or more sites (Table II), with *Ficus*

![Fig. 1](https://example.com/fig1.png)  
**Fig. 1** Sites used in this study (downloaded from Google Earth (n.d.) version 9.3.115.1).
(Moraceae) consumed at all sites. Of species consumed at two or more sites with
distribution data \((N = 62)\), 26 (42%) are endemic, 22 (35%) native, and 11 (18%)
naturalized (three lacked definitive classifications). The greatest overlap in species
consumed is between Bezà and Berenty \((N = 33)\). While this high overlap may be a
result of the greater number of studies conducted at these sites (i.e., their plants are
better sampled than at other sites), it may also indicate ecological similarities, as both
contain riverine gallery forests (Yamashita et al. 2016).

Table I  Numbers of plants eaten by ring-tailed lemurs at nine sites, based on a literature search

| Site                          | Families\(^a\) | Genera\(^a\) | Species\(^a, b\) | Studies included |
|-------------------------------|----------------|--------------|------------------|-----------------|
| Ambatotsirongorongo           | 24             | 33           | 23               | 1               |
| Andringitra Massif            | 16             | 19           | 16               | 2               |
| Anja Reserve                  | 17             | 22           | 20               | 2               |
| Antserananomby                | 14             | 17           | 12               | 2               |
| Berenty Reserve               | 55             | 102          | 95               | 8               |
| Bezà Mahafaly Special Reserve | 48             | 96           | 83               | 12              |
| Cap Sainte-Marie              | 33             | 49           | 43               | 2               |
| Tsaranoro Valley Forest       | 19             | 25           | 19               | 2               |
| Tsimanampetsotsa National Park| 21             | 24           | 26               | 3               |
| Total                         | 91             | 221          | 241              | 24              |

\(^a\) Excludes doubtful taxonomic status according to http://legacy.tropicos.org/Project/Madagascar.
\(^b\) Identified species (excluding sp. or spp.) using http://legacy.tropicos.org/Project/Madagascar.

Table II  Number of genera and species consumed by ring-tailed lemurs at different sites, based on a literature search

| Site (number of overlapping genera; number of overlapping species)\(^b\) |
|-----------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|
| Ambatot                     | Andring                    | Anja                        | Antseran                    | Berenty                     | Bezà                        | Cap St                      | Tsaranoro                   | Tsiman                      |
| 2; 0                        | 6; 2                        | 2; 1                        | 6; 2                        | 7; 1                        | 3; 2                        | 5; 2                        | 1; 1                        |                             |
| Andring                     | 2; 1                        | 3; 0                        | 5; 1                        | 6; 1                        | 3; 0                        | 4; 3                        | 2; 0                        |                             |
| Anja                        | 6; 2                        | 3; 1                        | 7; 2                        | 8; 2                        | 4; 0                        | 9; 7                        | 2; 0                        |                             |
| Antseran                    | 2; 1                        | 3; 0                        | 3; 1                        | 13; 9                       | 12; 8                       | 6; 2                        | 2; 0                        | 4; 1                        |
| Berenty                     | 6; 2                        | 5; 1                        | 7; 2                        | 13; 9                       | 49; 33                      | 26; 14                      | 7; 2                        | 12; 4                       |
| Bezà                        | 7; 1                        | 6; 1                        | 8; 2                        | 12; 8                       | 49; 33                      | 22; 11                      | 6; 0                        | 13; 7                       |
| Cap St                      | 3; 2                        | 3; 0                        | 4; 0                        | 6; 2                        | 26; 14                      | 22; 11                      | 7; 0                        | 12; 5                       |
| Tsaranoro                   | 5; 2                        | 4; 3                        | 9; 7                        | 2; 0                        | 7; 2                        | 6; 0                        | 7; 0                        | 4; 1                        |
| Tsiman                      | 1; 1                        | 2; 0                        | 2; 0                        | 4; 1                        | 12; 4                       | 13; 7                       | 12; 5                       | 4; 1                        |

\(^a\) Localities: Ambatot = Ambatotsirongorongo; Andring = Andringitra Massif; Anja = Anja Reserve; Antseran = Antserananomby; Berenty = Berenty Reserve; Bezà = Bezà Mahafaly Special Reserve; Cap St = Cap Sainte-Marie; Tsaran = Tsaranoro Valley Forest; Tsiman = Tsimanampetsotsa National Park.

\(^b\) Overlap between genera and identified species.
To demonstrate how ring-tailed lemurs use these plants in their diets, I identified plant parts consumed across all nine sites. Plant parts are identified as “fruit” (ripe and unripe), “leaf” (mature and immature), “flower” (mature and bud), and “other” (wood, exudate, stem, new growth). Of the 225 identified species with data on plant part consumed, one part species are 52% (N = 116) of this sample, two part are 29% (N = 66), three part are 16% (N = 35), and four part are 4% (N = 8; Fig. 2; Electronic Supplementary Material [ESM] Appendix S1). The most frequently consumed parts for each of these categories are leaves (48% of one-part species); fruit and leaves (52% of two-part species); and fruit, leaves, and flowers which make up 69% of three-part species.

Differences between populations in plant species and parts may be related to 1) seasonality and the month(s) data were collected, 2) the geographic distribution of the plant species in question (i.e., availability), or 3) group and/or population-level preferences. The diversity of plant species (and plant parts) consumed may protect lemurs against changes in availability, particularly seasonal changes (Hemingway and Bynum 2005). This diversification strategy is also apparent through ring-tailed lemur feeding and foraging behaviors on cultivated and non-native plants in areas where anthropic pressures continue to increase (Sauther and Cuozzo 2009).

**Future Directions**

Sixty-seven plants are reported by Malagasy common names (Table III), with only one consumed at two sites (“Hidy” at Anja Reserve and Tsaranoro Valley Forest). I exclude these plants from the analyses but include them in site summaries (Data Citation 1).

![Fig. 2](image-url) Plant parts consumed from all identified plant species for which part data are available (N = 225; ESM Appendix S1). Data labels provide N species (% species) contribution within each category.
Of plant parts identified in Table III, leaves are reported for 38 Malagasy names, fruit reported for 22 names, and flowers for 11 names. Future efforts in defining ring-tailed lemur dietary repertoires should identify the scientific names of these plants to provide a more complete picture of overall plant part feeding. As ring-tailed lemurs near extinction in the wild, it is critical that we identify and preserve their most valued food sources—especially the many endemic plant species they fed on—and protect the lands that sustain them.

**Methods**

To determine plant species (and plant parts, when information was available) fed on by wild ring-tailed lemurs, I searched Google Scholar (https://scholar.google.com/) using multiple relevant keyword searches, including “Lemur catta diet” (this was not a systematic review). I culled the output from these searches for papers that included tables and descriptions of specific plants consumed by ring-tailed lemurs and examined

### Table III

| Site (N plants) | Plant (plant part) |
|----------------|--------------------|
| Ambalotisorongorongo (13) | Eimahavano (mature leaf); Foto (ripe fruit); Holatra (mature leaf); Nonoka (mature leaf, ripe fruit); Sipotiky (mature leaf); Trakavola (new and mature leaf); Tsimahavanono (mature leaf); Tsipotika (ripe fruit); Tsiriky (mature leaf, flower); Tsivonjavonja (mature leaf); Vahimbisika (mature leaf); Voatavo (new and mature leaf); Volombato (mature leaf) |
| Andringitra Massif (0) | * |
| Anja Reserve (7) | Hidy (buds, fruit, leaves); Kasoa Mena (fruit); Komoay (?); Mamatsikariva (fruit); Ombianty (leaves); Tsara (leaves); Vahatonara (?) |
| Antserananomby (0) | * |
| Berenty Reserve (0) | * |
| Beza Mahafaly (22) | Amбириндола (leaves); Amelo (leaves); Angaranfke (leaves); Atapiso (leaves); Atratra (flower); Daliste (leaves); Fale (fruit); Fatikakoho (mature leaves); Fitarsaoampona (leaves); Kidresy (mature leaves); Kijeradolo (leaves); Kongo (leaves); Lavaenafe (leaves); Lobankanjirike (leaves, flower); Mamayho (flower bud, flower, ?); Sakarvironala/Sakaviron’ala/Sakavironala (mature leaves); Saritabuara/Sarytabuara (young and mature leaves); Taboarandolo (leaves, stem, ?); Tarasoampona (leaves, buds); Tsyvoanisoa (?) Vanadioa (leaves); Vihipinde (leaves) |
| Cap Sainte-Marie (4) | Fatikekolahy (leaves); Kolovy (other); Miatika (fruit and seeds); Rothmannia (fruit and seeds) |
| Tsaranoro Valley Forest (7) | Anakatsimba (fruit); Fandafika (fruit); Fanera (flower, fruit); Fopoho (fruit); Hazodrea (fruit); Hidy (flower, fruit, leaves); Mena Tendo (fruit) |
| Tsimanampetsotsa National Park (15) | Anango (flower); Fatra (fruit); Hazontan-dahy (young and mature leaves, stem); Kisenindolo (fruit); Lampana (young leaves); Manolosasavy (fruit); Matitihena (flower); Rantsandiak[a] (fruit, flower); Rodrotse (flower); Somangiligahy (fruit); Talilahi (fruit); Tsikova (young leaves); Vahe (Voamena; fruit and seeds); Vaheantenenteo (leaves); Vahanose (leaves) |

Sources can be found in Data Citation 1.
pertinent publications and their references exhaustively. I identified 24 studies that presented such data. For each study, I recorded the following data, when available: family, genus, and species name; plant part consumed (including ripeness or maturity); and common name (Malagasy or English). I recorded the plant names exactly as reported in the source, including misspellings. When available, I also recorded miscellaneous feeding behaviors (e.g., licking items), common names for unidentified plants (e.g., liana) or animals (e.g., insect), and Malagasy names for which a scientific name was not available.

I verified all scientific names using the “Catalogue of the Plants of Madagascar” (Tropicos; http://legacy.tropicos.org/Project/Madagascar), the most complete and current online database of the flora of Madagascar, curated by the Missouri Botanical Gardens. I recorded names (including family, genus, and species) as they appear on Tropicos in a column next to the names reported by the author(s). Where I could not find species names on Tropicos (including a review of synonymies that have been used, as well as species for which similarities in spelling may have caused confusion), I recorded the entry as Genus sp. I also recorded the distribution and lifeform/habit, for each species, when this was available in Tropicos.

**Ethical Note**

No animals were used nor licenses necessary for this literature review. I declare no conflict of interest.

**Data Availability** All of the data in this study are freely available in the Dryad Digital Repository (Data Citation 1) as an Excel file (XLSX) and a CSV file.

**Data Records**

The data are available in the Dryad Digital Repository (Data Citation 1) as an Excel file (XLSX) and a CSV file. The primary data sheet includes site, coordinates (degrees, minutes, seconds), decimal degrees coordinates (converted using http://rcn.montana.edu/Resources/Converter.aspx), family, genus, species, and subspecies names (according to Tropicos), the name of the plant as described in the source, the plant’s distribution and lifeform/habit (Tropicos), the part of the plant consumed (as described by the author), a breakdown of the plant parts consumed (leaf, fruit, seed, flower, other, and unknown), and the common name for the plant. When applicable, I also include nonplant foods (e.g., insects). References are available in the References sheet in the Excel file and also as an attached word document. Data notes are available in the Excel file and also as an attached PDF document.

**Technical Validation**

The data set includes species names as originally given by the author(s), as well as the current standing of the name. I replicate the source’s spelling of the name and description of
plant part consumed. I aimed to include as many sources for each site as possible. However, some sites (e.g., Bezà and Berenty) are better represented in the literature than others (e.g., Ambatotsiriongorongo). Additionally, because field research was not conducted every month at each site, some plant species and parts that are consumed seasonally may not be included. Finally, many plant species included in the data set are known only by their Malagasy names and therefore are excluded from analyses of plant species presence, overlap, and plant part consumed.

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s10764-020-00184-1.

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**Data Citations**
1. Canington, Stephanie. (2020). Plant species fed on by wild ring-tailed lemurs (Lemur catta) at nine sites., v12, Dryad, Dataset, https://doi.org/10.5061/dryad.1vhmgqqs

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