

# LEMUR FOOD PLANTS

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Research on lemur diets began with J.-J. Petter's landmark 1956–1957 survey of lemur ecology (J.-J. Petter 1962), and further information accumulated steadily over the subsequent decades. Of the nearly 110 lemur species currently recognized, 61 lemur species have been the subject of at least one dietary study that has provided information on the taxa and parts of plants exploited for food. Building on Birkinshaw and Colquhoun (2003), published in the precursor of this book, and updating it with recent lemur-ecology studies, K. J. E. Steffens (2020) assembled a database of food plants exploited by lemurs, aggregating published lists and updating the taxonomy of plants following the online Catalogue of the Plants of Madagascar (Madagascar Catalogue 2020), which is part of the plants database Tropicos. The current contribution builds on this with additional unpublished data sets, limiting our scope to plants, both native and introduced, rather than other types of food items lemurs consume (e.g., arthropods, eggs, soil, etc.).

The 61 lemur species were documented to exploit foods from species in 155 vascular plant families (including introduced) and from species in 147 of 239 native vascular plant families. Currently, five plant families are recognized as endemic to Madagascar—Asteraceae, Barbeuiaceae, Phytolaccaceae, Sarcocaulaceae, and Sphaerosepalaceae—and lemurs have been recorded exploiting all of these except for Barbeuiaceae. The families that are exploited by the greatest numbers of lemur species are Rubiaceae (exploited by 50 species), Fabaceae (45 species), Moraceae (43 species), Malvaceae (42 species), and Apocynaceae (39 species). These families, with the exception of Moraceae, contain several hundred species that grow in a wide array of different vegetation types (Schatz 2001). Moraceae is a small family, with 42 native Malagasy species currently recognized. Its widespread utilization can be accounted for by the huskless, small-seeded fruits of most of the constituent genera (which are thus accessible to a wide range of lemur species, as well as frugivorous birds and bats) and the asynchronous fruit maturation among individuals of *Ficus*, both between species and to a certain extent within the same species (thus providing a more or less continuous supply of fruits throughout the year, including periods when other fruits are rare, particularly the dry season; see Rasplus et al., pp. 617–34). It might be expected that lemurs would avoid exploiting families whose plants contain latex, glycosides, and alkaloids (Simmen et al. 1999), but this does not seem to be the case, and such families are well represented in lemur diets (e.g., Apocynaceae, Clusiaceae, Moraceae, Sapotaceae).

Given the mainly arboreal lifestyle of lemur species, most of the exploited plants are trees, shrubs, and lianas. Notable exceptions are seen in *Haplemur* species and *Prolemur simus*, which are recorded to exploit terrestrial herbs of the Poaceae and Cyperaceae families (Figure 14.24c; see Larridon et al., pp. 580–85), and *Lemur catta*, which exploits herbs in a diversity of families (see Sautther and Cuozzo, pp. 1952–56). Most lemurs exploit an array of food items (e.g., leaves, fruits, flowers), whereas relatively few lemur species

would be considered strictly frugivorous. It is suggested that protein is a limiting factor for primate species (Ganzhorn et al. 2017), ultimately affecting life-history traits, and may have potentially led to a paucity of strictly frugivorous lemurs (Donati et al. 2017).

In general, lemur species inhabit every major habitat type on Madagascar; yet, relatively few records exist of them in mangroves (Gardner 2016). Only a few observations have been made of lemurs exploiting species from the mangrove genera *Avicennia*, *Rhizophora*, or *Sonneratia*. This may be related to the unpalatability of mangrove plant species, as most are rich in tannin and polyphenolic content (Donati et al. 2019), but also to a lack of research owing to the difficulty in accessing this habitat type. Similarly, the overall rarity of ferns in lemur diets is probably explained by a combination of factors, including the terrestrial habitat of most fern species; their lack of flowers, fruits, and seeds; their cyanogenic components; and the low palatability of tannin-rich fern fronds (May 1978). The unusual exploitation of ferns by *Propithecus diadema* may reflect the high tolerance to tannins by this genus compared to other lemur species (Simmen et al. 1999).

Given the large number of studies and observations of lemur feeding ecology that have been published over the past couple decades, we present information on exploited food plant families by lemur species from each of the five extant families. For a more detailed review, consult the database in K. J. E. Steffens (2020). The tables presented here indicate the plant part(s) within a given botanical family exploited by different lemur species. Eight different food-type classes are recognized. Some of these classes include the more precise food types distinguished by some researchers: in particular, leaf tips, new leaves, and petioles are included here in the class **leaves**; piths, shoots, and stems in the class **piths**; saps and gums in the class **exudates**; flowers, flower buds, and petals in the class **inflorescences** (note: **nectar** is in its own specific class); unripe and ripe fruits in the class **fruits** (note: **seeds** are in their own specific class when they are uniquely the consumed item). This has been done to simplify the general overview presented here and because the more precise food-type classes are inconsistently applied among researchers.

## CHEIROGALEIDAE

The Cheirogaleidae family includes *Allocebus trichotis*, *Microcebus* species (see Kappeler et al., pp. 1927–32), *Cheirogaleus* species (see Blanco, pp. 1922–26), *Mirza* species (see Kappeler, pp. 1932–34), and *Phaner* species; feeding data are available for representatives of all five genera. There are currently 41 recognized species within Cheirogaleidae, and 18 of these have been recorded to exploit foods from 82 plant families (Table 14.11). *Cheirogaleus major* exploits foods from 49 plant families, while other species with high plant family diversity in their diets include *Microcebus griseorufus* (35 families), *C. thomasi* (34 families), *M. ganzhorni* (34 families), and *M. ravelobensis*



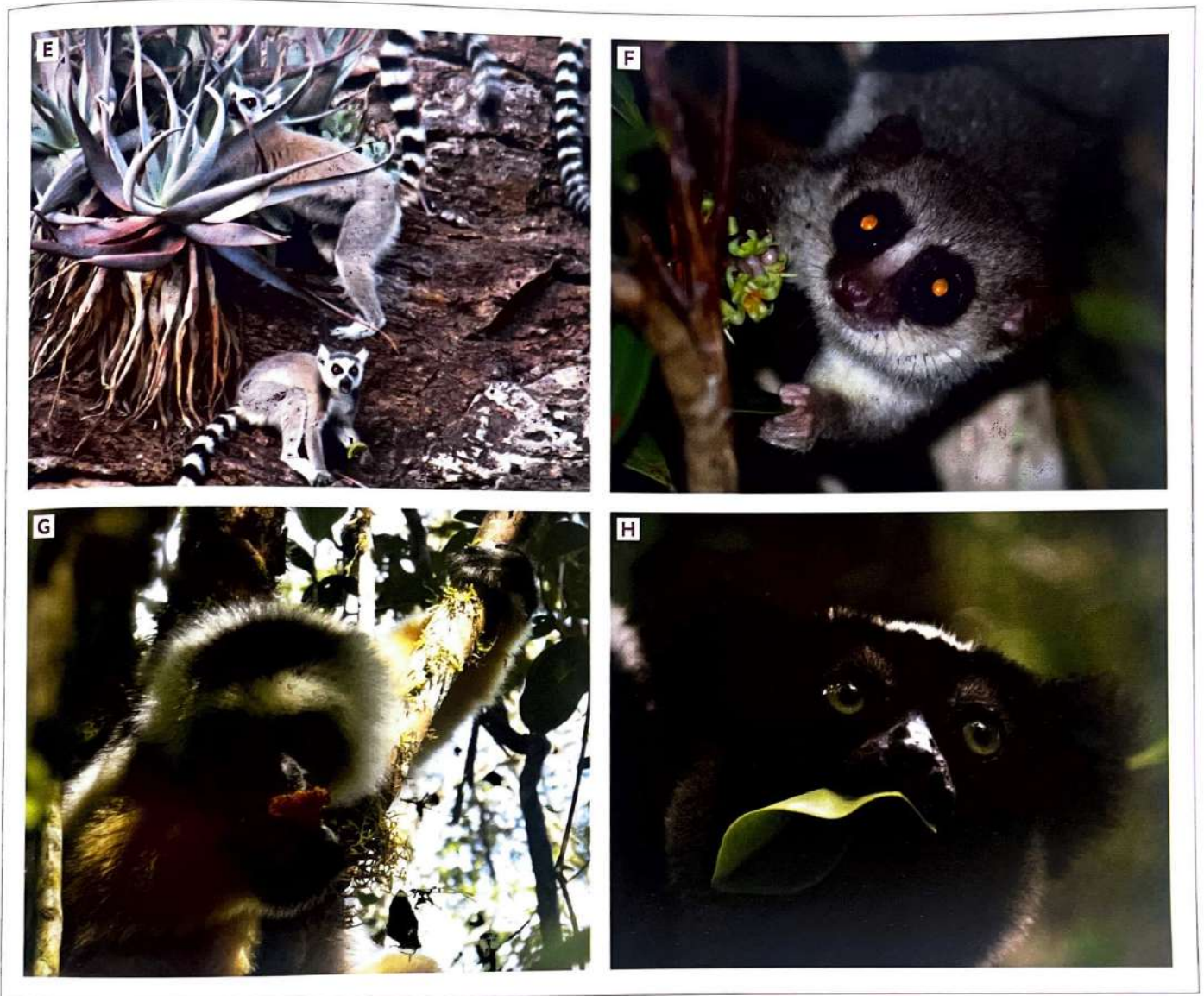
FIGURE 14.24 Lemurs and their food plants. A) *Eulemur fulvus* feeding on fruits of introduced *Solanum mauritianum* (Solanaceae) in Analamazaotra; B) *Lepilemur tymerlachsonorum* shortly after feeding on the flowers of *Ceiba pentandra* (Malvaceae), with the anterior portion of its body covered with the pollen, near Lokobe, Nosy Be; C) *Haplemur meridionalis* feeding on the pith/stem of *Cyperus* sp. (Cyperaceae) in Mandena; D) *Microcebus murinus* feeding on exudate of an unidentified tree species in Ankarafantsika; E) *Lemur catta* feeding on the leaves of *Aloe* sp. (Asphodelaceae) in Ifotaka; F) *Cheirogaleus thomasi* feeding on nectar from *Vaccinium emirnense* (Ericaceae) in Sainte Luce; G) *Propithecus diadema* feeding on the fruit of *Decarydendron* sp. (Monimiaceae) at Maromizaha; H) *Indri indri* feeding on the leaves of *Bakerella* sp. (Loranthaceae) in Mitsinjo Reserve, Andasibe. (PHOTOS A and C by T. M. Eppley; B by S. H. Roberts; D by E. Zimmermann; E by B. P. Semel; F by E. Račevska; G by M. Lutz; and H by M. A. Semel.)

(27 families). Though *C. major* is one of the most widespread species within this lemur family, the high diversity of families recorded in its diet seems to be more a result of the number of studies focused on it, and this is also likely the case with the range-restricted *M. ganzhorni*. Among the plant families most exploited by Cheirogaleidae species are Rubiaceae (exploited by 15 species), Combretaceae (11 species), and multiple plant families (native and introduced taxa) exploited by 10 lemur species each, including Anacardiaceae, Celastraceae, Fabaceae, and Malvaceae. For most of these, Cheirogaleidae species tend to focus on exploiting fruits, inflorescences, nectar (Figure 14.24f), and exudates (Figure 14.24d), with the highest diversity exploiting the

genera *Terminalia* (Combretaceae), *Canthium* (following Scharz 2001), *Gaertnera*, and *Hyperacanthus* (Rubiaceae).

## DAUBENTONIIDAE

The Daubentoniidae family includes only one extant species, *Daubentonia madagascariensis* (Aye-aye) (see Sterling et al., pp. 1975–78), which exploits foods from 13 different plant families (Table 14.12). Among the frequently exploited plant items are *Canarium* (Burseraceae) fruits and seeds, *Terminalia* (Combretaceae)

FIGURE 14.24 *continued*

seeds, and *Ravenala* (Strelitziaceae) nectar; it is well known that *D. madagascariensis* is insectivorous and thus focuses its diet on invertebrates; fruits, seeds, and nectar are largely supplemental (Sterling et al. 1994; Randimbiharinarina et al. 2018; Sefczek et al. 2020a).

## LEPILEMURIDAE

There are currently 26 recognized species within the family Lepilemuridae, all in the genus *Lepilemur* (see Radespiel et al., pp. 1935–40), but as most of these nocturnal lemur taxa are largely unstudied, feeding ecology data are available for only eight species. Despite the limited number of studies, *Lepilemur* species are known to exploit foods from 59 plant families (Table 14.13). Longer-term studies showed that seven different *Lepilemur* species each exploit between 16 and 22 families, with *L. mustelinus* exploiting the highest diversity, 22 families. Among the most frequently exploited plants, those of the Malvaceae (Figure 14.24b), including introduced species, are

utilized by eight *Lepilemur* species; the Fabaceae by seven *Lepilemur* species; Rubiaceae by six species; and Apocynaceae, Euphorbiaceae, Phyllanthaceae, and Sapindaceae by five species each. As folivores, Lepilemuridae species feed mostly on leaves, most frequently exploiting those of the genera *Albizia* (Fabaceae), *Canthium* (Rubiaceae), *Commiphora* (Burseraceae), *Diospyros* (Ebenaceae), *Grewia* (Malvaceae), *Strychnos* (Loganiaceae), and *Terminalia* (Combretaceae).

## LEMURIDAE

The family Lemuridae consists of 21 currently recognized species, and dietary data are available for all. Lemuridae species exploit food items from 136 plant families (Table 14.14). While some genera focus mostly on leaves and piths (*Hapalemur* spp., *Prolemur simus*; see Tan et al., pp. 1947–52 for general details on these genera), the genera *Eulemur* (see Johnson et al., pp. 1941–46) and *Varecia* (see Vasey et al., pp. 1957–63) tend to focus more heavily on ripe fruits

MAMMALS

TABLE 14.11. Plant parts consumed by different members of the Cheirogaleidae

PLANT FAMILIES EXPLOITED	CHEIROGALEIDAE SPECIES																	
	ALLOBEUS TRICHOTIS	CHEIROGALEUS CROSSLEYI	C. MAJOR	C. MEDIUS	C. THOMASI	MICROCEBUS BERTHAE	M. GANZHORNI	M. GRISEORUFUS	M. JOLLYAE	M. LEHILAHYSARA	M. MURINUS	M. MYOXINUS	M. RAVELOBENSIS	M. RUFUS	M. TANOSI	MIRZA COQUERELI	M. ZAZA	PHANER PALLESCENS
Acanthaceae	-	-	L	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Anacardiaceae	-	-	F	F	F	-	F	FL FX	-	-	E	-	FLE	-	F	-	-	E
Anacardiaceae (introduced)	-	F	F	-	-	-	-	-	-	-	-	-	I	-	-	-	-	-
Annonaceae	-	-	F	-	F	-	F	-	-	-	-	-	L	-	F	-	-	-
Aphloiaceae	-	-	FL	-	F	-	F	-	-	F	-	-	-	F	F	-	-	-
Apocynaceae	-	-	FL	F	F	-	F	FE	-	-	-	-	FLI	-	F	-	-	-
Aquifoliaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	F	-	-	-	-
Araliaceae	-	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Arecaceae	-	-	F	-	F	-	F	-	F	-	-	-	-	-	F	F	-	-
Asparagaceae	-	-	F	-	F	-	F	F	-	-	-	-	-	F	F	-	-	-
Asparagaceae (introduced)	-	-	-	-	I	-	-	N	-	-	-	-	-	-	F	-	-	-
Asteraceae	-	-	-	FI	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Asteropeiaceae	-	-	FI	-	FI	-	FI	-	-	-	-	-	-	-	-	-	-	-
Bignoniaceae	-	-	F	F	-	-	-	FEX	-	-	-	-	-	-	F	-	-	-
Boraginaceae	-	-	-	-	-	-	-	F	-	-	-	-	-	-	-	-	-	-
Burseraceae	-	-	-	-	-	-	-	FLE	-	-	E	-	E	-	-	-	-	-
Cactaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	E
Cactaceae (introduced)	-	-	-	-	-	-	-	E	-	-	-	-	-	F	-	-	-	-
Calophyllaceae	-	-	F	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Canellaceae	-	-	-	-	-	-	-	-	-	-	IE	-	L	-	-	-	-	-
Capparaceae	-	-	-	-	-	-	-	-	-	-	-	-	E	-	-	-	-	-
Celastraceae	-	-	FI	FI	FI	-	FI	FN	-	-	F	-	-	-	-	-	-	N
Chrysobalanaceae	-	-	-	-	-	-	-	E	-	-	FNE	-	E	-	F	-	-	I
Clusiaceae	-	-	L	-	-	-	-	-	-	-	-	-	L	-	-	-	-	-
Combretaceae	E	-	F	FI	F	-	F	FLIE	-	-	F	FE	-	-	-	-	-	-
Connaraceae	-	-	-	-	-	-	-	-	-	-	-	-	E	-	LIE	-	F	E
Convolvulaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	L	-	-	-	-
Cucurbitaceae	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-
Cunoniaceae	-	-	L	-	-	-	-	F	-	-	-	-	-	-	-	-	-	-
Cyperaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dichapetalaceae	-	-	-	-	-	-	-	-	I	-	-	-	-	-	-	-	-	-
Didiereaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	L	F	-	-	-
Dilleniaceae	-	-	F	-	F	-	F	-	X	-	-	-	-	-	-	-	-	-
Dioscoreaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ebenaceae	-	-	F	FX	-	-	-	-	-	-	F	-	-	-	-	-	-	-
								F					E					

PLANT FAMILIES EXPLOITED	CHEIROGALEIDAE SPECIES																	
	ALLOBEBUS TRICHOTIS	CHEIROGALEUS CROSSLEYI	C. MAJOR	C. MEDIUS	C. THOMASI	MICROCEBUS BERTHAE	M. GANZHORNI	M. GRISEORUFUS	M. JOLLYAE	M. LEHILAHTSARA	M. MURINUS	M. MYOXINUS	M. RAVELOBENSIS	M. RUFUS	M. TANOSI	MIRZA COQUEREJI	M. ZAZA	PHANER PALLESCENS
Ericaceae	-	-	F	-	FI	-	FI	-	-	-	-	-	-	-	F	-	-	-
Erythroxylaceae	-	-	F	F	F	-	F	-	-	-	E	-	-	-	-	-	-	-
Euphorbiaceae	-	-	FL	-	F	-	F	FL EX	-	-	E	-	-	-	-	-	-	-
Fabaceae	-	-	LIX	I	I	-	I	FLIN EX	-	-	FE	-	FE	-	-	N	-	E
Gentianaceae	-	-	F	-	-	-	-	-	-	-	-	-	F	F	-	-	-	-
Hernandiaceae	-	-	-	-	-	-	-	FLE	-	-	-	-	-	-	-	-	-	-
Hypericaceae	-	-	F	-	F	-	F	-	-	FI	-	-	-	F	F	-	-	-
Lamiaceae	-	-	F	F	F	-	F	FE	-	-	N	-	-	-	-	-	-	-
Lauraceae	-	-	FI	-	F	-	F	-	-	-	-	-	-	F	-	-	-	-
Loganiaceae	-	-	-	FS	-	F	-	FE	-	-	F	-	FL	-	-	-	-	-
Loranthaceae	-	-	FI	-	FI	-	FI	F	-	-	-	-	-	F	F	-	-	-
Lythraceae	-	-	-	F	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Malpighiaceae	-	-	-	-	-	-	-	F	-	-	-	-	-	-	-	-	-	-
Malvaceae	-	-	F	FIE	F	F	-	FLI EX	-	-	F	-	E	-	-	E	-	INE
Malvaceae (introduced)	-	-	-	-	-	-	-	-	-	-	N	-	-	-	-	-	-	-
Melastomataceae	-	-	-	-	-	-	F	-	-	F	-	-	-	F	-	-	-	-
Melastomataceae (introduced)	-	-	-	-	-	-	-	-	F	F	-	-	-	-	-	-	-	-
Meliaceae	-	-	F	-	F	-	F	FE	-	-	E	-	LE	-	-	-	-	E
Meliaceae (introduced)	-	-	-	-	-	-	-	E	-	-	-	-	-	-	-	-	-	-
Menispermaceae	-	-	F	-	F	-	F	-	-	-	-	-	-	F	-	-	-	-
Metteniusaceae	-	-	F	-	F	-	-	-	-	-	-	-	-	-	F	-	-	-
Monimiaceae	-	-	F	-	-	-	-	-	-	-	-	-	-	F	F	-	-	-
Moraceae	-	-	FL	-	F	-	F	-	F	-	E	-	LIE	F	F	-	-	-
Myrtaceae	-	-	FL	-	F	-	F	-	-	-	-	-	L	-	F	-	-	-
Myrtaceae (introduced)	-	-	FI	-	FI	-	FI	-	-	F	-	-	-	F	-	-	-	-
Ochnaceae	-	-	F	F	F	-	F	-	-	-	-	-	-	-	-	-	-	-
Oleaceae	-	-	-	-	-	-	-	FEX	-	-	-	-	F	-	-	-	-	-
Oleaceae	-	-	F	I	F	-	F	-	-	-	FE	-	FLE	-	F	-	-	-
Orchidaceae	-	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Passifloraceae	-	-	-	-	-	-	-	F	-	-	-	-	F	-	-	-	-	-
Phyllanthaceae	-	-	FL	F	F	-	FL	FLIE	-	-	FE	-	-	-	F	-	-	-
Physenaceae	-	-	-	-	-	-	-	FE	-	-	-	-	-	-	-	-	-	-
Poaceae (introduced)	-	-	L	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Primulaceae	-	-	FL	-	F	-	F	-	-	F	-	-	-	F	-	-	-	-
Putranjivaceae	-	-	-	-	-	-	-	-	-	F	-	-	-	-	-	-	-	-

(continued overleaf)

TABLE 14.11. continued

## CHEIROGALEIDAE SPECIES

PLANT FAMILIES EXPLOITED	ALLOEBUS TRICHOTIS	CHEIROGALEUS CROSSLEYI	C. MAJOR	C. MEDIUS	C. THOMASI	MICROCEBUS BERTHAE	M. GANZHORNI	M. GRISEORUFUS	M. JOLLYAE	M. LEHILAHTSARA	M. MURINUS	M. MYOXINUS	M. RAVELOBENSIS	M. RUFUS	M. TANOSI	MIRZA COQUERELI	M. ZAZA	PHANER PALLESCENS
Rhamnaceae	-	-	-	F	-	-	F	F	-	-	-	F	-	-	-	-	-	F
Rhizophoraceae	-	-	-	-	-	-	-	-	-	-	-	-	E	-	-	-	-	-
Rosaceae	-	-	L	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rosaceae (introduced)	-	-	L	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rubiaceae	-	I	FLI	FX	F	F	FI	FE	F	FI	FINE	-	FLIE	F	F	-	F	E
Rubiaceae (introduced)	-	-	F	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rutaceae	-	-	F	-	F	-	F	LEX	-	-	E	-	LE	-	F	-	-	E
Salicaceae	-	-	FL	-	F	-	F	-	-	-	E	-	FE	-	F	-	-	-
Salvadoraceae	-	-	-	-	-	-	-	FL EX	-	-	-	-	-	-	-	-	-	-
Santalaceae	-	-	-	-	-	-	-	F	-	-	-	-	-	F	-	-	-	-
Sapindaceae	-	-	F	F	F	-	F	-	-	-	F	-	L	-	F	-	-	-
Sapotaceae	-	-	F	-	-	-	-	F	-	-	-	-	-	-	-	-	-	-
Sarcocaulaceae	-	-	FI	-	FI	-	FI	-	-	-	-	-	-	-	-	-	-	-
Smilacaceae	-	-	F	-	F	-	F	-	-	-	-	-	-	-	F	-	-	-
Sphaerosepalaceae	-	-	-	-	-	-	-	FE	-	-	E	-	E	-	-	-	-	-
Stilbaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Strelitziaceae	-	I	N	-	-	-	-	-	-	-	-	-	-	F	-	-	-	-
Talinaceae	-	-	-	-	-	-	-	FX	-	-	-	-	-	-	-	-	N	-
Verbenaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Verbenaceae (introduced)	-	-	FI	-	-	-	-	-	-	-	I	-	-	-	-	-	-	-
Violaceae	-	-	-	F	-	-	-	-	-	F	-	-	-	-	-	-	-	-
Vitaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
References	3	13	6, 13, 14, 22, 23, 28, 35, 47	2, 8, 11, 12, 15, 20, 40	6, 23, 38	9	23, 25, 26	5, 17, 18, 32-34, 43	31	13, 14, 36	9, 16, 18, 20, 21, 24, 26, 29, 30, 37, 41, 43-45	10	19, 29, 30, 37, 45, 46	1, 31	6	20, 27	4, 39	2, 7, 9, 18, 40, 42, 43

Notes: Plants introduced to Madagascar are noted. Key to plant parts exploited: B, bark; E, exudates; F, fruits; I, inflorescences; L, leaves; N, nectar; P, piths and/or stems; S, seeds; X, no data available on which plant part was exploited.

Key to references: 1. Atsali (1999a); 2. Baum (1995); 3. Biebow (2009); 4. Birkinshaw and Colquhoun (1998); 5. Bohr et al. (2011); 6. Bollen et al. (2004a); 7. Charles-Dominique and Petter (1980); 8. D. J. Curtis and Zaramody (1998); 9. Dammhahn and Kappeler (2008a); 10. Dammhahn et al. (2009); 11. Fietz and Ganzhorn (1999); 12. Fietz et al. (2003); 13. Ganzhorn (1987); 14. Ganzhorn (1988); 15. Ganzhorn and Kappeler (1996); 16. Génin (2003); 17. Génin and Rambeloarivony (2018); 18. Génin et al. (2010); 19. Hagenah (2001); 20. Hladik et al. (1980); 21. Joly-Radko and Zimmermann (2010); 22. Kress et al. (1994); 23. Lahann (2007b); 24. Lutermann (2001); 25. R. D. Martin (1972a); 26. R. D. Martin (1973); 27. Pagès (1980); 28. J.-J. Petter et al. (1977); 29. Radespiel et al. (2006); 30. M. Rahelinirina (2002); 31. Ramananjato et al. (2020); 32. Randrianarimalalaso (2008); 33. Rasoazanabary (2011); 34. Rasoazanabary and Godfrey (2016); 35. Ratsirarson and Ranaivosy (2002); 36. O. H. Razafindratsima (unpublished data); 37. Reimann (2002); 38. S. H. Roberts (unpublished data); 39. Rode-Margono et al. (2016); 40. Scharfe and Schlund (1996); 41. Schmelting (2000); 42. Schülke (2003); 43. A. C. Smith (2010); 44. Sussman (1978); 45. Thorén et al. (2011); 46. Weidt (2001); 47. P. C. Wright and Martin (1995).

TABLE 14.12. Plant parts consumed by *Daubentonia madagascariensis* (Daubentoniidae)

PLANT FAMILIES EXPLOITED	PLANT PART
Anacardiaceae (introduced)	F
Arecaceae	F S
Arecaceae (introduced)	F
Burseraceae	F S B
Combretaceae	S
Euphorbiaceae	I
Fabaceae	F I B
Moraceae	X
Moraceae (introduced)	F S
Musaceae (introduced)	F N
Pandanaceae	X
Passifloraceae (introduced)	F
Poaceae (introduced)	L
Sapindaceae (introduced)	F
Strelitziaceae	N
References	1–15

Notes: Plants introduced to Madagascar are noted. Key to plant parts exploited: B, bark; E, exudates; F, fruits; I, inflorescences; L, leaves; N, nectar; P, piths and/or stems; S, seeds; X, no data available on which plant part was exploited.

Key to references: 1. Ancrenaz et al. (1994); 2. Andriamasimanana (1994); 3. Gardner (2009); 4. Goodman et al. (1996c); 5. Iwano (1991); 6. Iwano and Iwakawa (1988); 7. Lhota et al. (2008); 8. J.-J. Petter et al. (1977); 9. Pollock et al. (1985); 10. Randimbiharirina et al. (2018); 11. Sefczek et al. (2017); 12. Sefczek et al. (2020a); 13. Sterling (1994a); 14. Sterling and McCreless (2006); 15. Sterling et al. (1994).

and seeds. Though considered frugivores, both genera have been observed to rely on leaves and flowers during resource-limited seasons (Martinez and Razafindratsima 2014; Sato et al. 2016). *Lemur* is perhaps the most flexible of the lemurid genera, known to exploit a variety of food items (e.g., fruits, leaves, flowers, etc.) throughout its broad geographic distribution. In fact, *L. catta* (Figure 14.24e) exploits the highest diversity (94 families) of any lemur species, but it is important to note that this is also the most intensively studied species. Among the other species displaying a large food plant diversity are *V. variegata* (72 plant families), *E. rufifrons* (64 families), *E. coronatus* (63 families), and *E. collaris* (60 families). The plant families most frequently exploited by Lemuridae species are Moraceae (20 species), Rubiaceae (18 species), and—with 16 species each—Apocynaceae, Arecaceae, Fabaceae, and Malvaceae. Examples of frequently exploited genera include, for fruits, *Canarium* (Burseraceae), *Canthium* (Rubiaceae), and *Cryptocarya* (Lauraceae); and for fruits and leaves, *Diospyros* (Ebenaceae), *Erythroxylum*

(Erythroxylaceae), *Eugenia*, *Syzygium* (Myrtaceae), *Ficus* (Moraceae), and *Grewia* (Malvaceae).

Among the more unusual foods of lemurid species are aquatic plants; the stems of *Nymphaea lotus* (Nymphaeaceae) and the introduced and invasive *Eichhornia crassipes* (Pontederiaceae) are consumed by *H. alaotrensis* (Mutschler 1999). Presumably other lemurs rarely, if ever, exploit such aquatic plants, as normally they occupy habitats in which such plants are inaccessible to them. Furthermore, a number of Lemuridae species have been observed consuming fungi, but relatively few studies identify the fungi to finer taxonomic levels. For example, fungi of the families Auriculariaceae (two species) and Polyporaceae (unidentified genera) are regularly consumed by *H. aureus*, *H. griseus*, *H. meridionalis*, and *P. simus* (C. L. Tan 1999; Eppley et al. 2011, 2016a), while *V. variegata* frequently consumes Polyporaceae fungi at Manombo in the southeast (Ratsimbazafy et al. 2002).

## INDRIIDAE

The family Indriidae consists of 19 currently recognized species, and plant-food data are available for 13 of them, mostly concerning diurnal *Indri indri* (see Gamba et al., pp. 1967–71) and *Propithecus* species (see Lawler and Richard, pp. 1971–74), as the feeding ecology of species in the nocturnal genus *Avahi* (see Donati et al., pp. 1963) has been less explored. From these studies, 100 plant families have been recorded as food sources for Indriidae species (Table 14.15). *Propithecus verreauxi* exploits foods from 55 plant families, while other species with high plant family diversity in their diets include *P. tattersalli* (54 families), *P. diadema* (43 families; Figure 14.24g), *A. meridionalis* (38 families), and *P. candidus* (35 families). *Indri indri* exploits foods, mostly young leaves and some fruits, from 33 plant families. Among the plant families exploited by most Indriidae species are Anacardiaceae, Moraceae, and Sapotaceae (all exploited by 12 species); and Apocynaceae, Fabaceae, and Rubiaceae (11 species each). Indriidae species include both fruits and leaves in their diet (Figures 14.24g and h, respectively), frequently exploiting genera such as *Ocotea* (Lauraceae), *Oncostemum* (Primulaceae), *Protorhus* (now considered best placed in the genus *Abrahamia*; Anacardiaceae), *Symphonia* (Clusiaceae), *Syzygium* (Myrtaceae), and *Diospyros* (Ebenaceae). In areas where both *I. indri* and *Propithecus diadema* are sympatric, they exhibit little dietary overlap, with the former consuming mostly young leaves, and the latter consuming fruits, seeds, and flowers. The most unusual plants consumed within Indriidae are the fungus-like terrestrial inflorescences of the root parasites *Cytinus* (Cytinaceae) and *Langsdorffia* and *Ditepalanthus* (Balanophoraceae), all without chlorophyll, which have been reported to be exploited by *P. candidus* and *P. diadema*.

## INTRODUCED PLANTS

Plant species from at least 114 botanical families have been introduced to Madagascar via human migration, trade, and agricultural experimentation, though a large number of introduced tree species belong to only a small group of botanical families—for example, Myrtaceae, Fabaceae, Pinaceae, and Meliaceae (Kull et al. 2012).

TABLE 14.13. Plant parts consumed by different members of the Lepilemuridae

PLANT FAMILIES EXPLOITED	LEPILEMURIDAE SPECIES							
	LEPILEMUR EDWARDSI	L. FLEURETAE	L. MUSTELINUS	L. PETTERI	L. RUFICAUDATUS	L. SAHAMALAZENSIS	L. SEPTENTRIONALIS	L. TYMERLACHSONORUM
Anacardiaceae	X	L	-	-	-	L	-	-
Anacardiaceae (introduced)	-	-	-	-	-	L	LI	-
Annonaceae	X	-	L	-	-	-	L	-
Aphloiaceae	-	-	L	-	-	-	-	-
Apocynaceae	L	L	-	LX	-	L	L	-
Araliaceae	-	-	L	-	-	-	-	-
Asteraceae	-	-	-	-	-	L	-	-
Bignoniaceae	X	-	-	X	FLI	-	-	-
Burseraceae	-	-	-	LX	-	-	-	-
Buxaceae	-	-	-	-	F	-	-	-
Capparaceae	-	-	L	LX	-	-	-	-
Cardiopteridaceae	-	-	L	-	-	-	-	-
Celastraceae	L	-	-	X	FL	-	L	-
Chrysobalanaceae	-	-	-	-	-	L	-	-
Clusiaceae	X	L	L	-	-	L	-	-
Combretaceae	-	L	-	-	FSL	L	-	-
Connaraceae	-	L	-	-	-	-	L	-
Convolvulaceae	-	LI	-	LX	-	-	-	-
Cucurbitaceae	-	-	-	FLX	-	-	-	-
Cyperaceae	X	-	-	-	-	-	-	-
Dichapetalaceae	-	-	L	-	-	-	-	-
Didiereaceae	-	-	-	LIX	-	-	-	-
Dilleniaceae	-	F	-	-	-	-	-	-
Ebenaceae	X	-	-	-	FL	L	-	-
Erythroxylaceae	L	-	L	-	-	L	-	-
Euphorbiaceae	-	-	L	L	L	L	LI	-
Fabaceae	LX	LI	L	LIX	FLIB	L	FL	-
Fabaceae (introduced)	-	-	-	-	-	-	FL	-
Hernandiaceae	-	-	-	X	-	-	FL	-
Hypericaceae	-	-	F	-	-	-	-	-
Lamiaceae	LX	-	-	X	-	L	-	-
Lauraceae	-	-	L	-	-	-	-	-
Lecythidaceae	-	-	L	-	-	-	-	-
Loganiaceae	X	-	-	-	L	-	-	-
					FL	L	L	-



## LEPILEMURIDAE SPECIES

PLANT FAMILIES EXPLOITED	LEPILEMUR EDWARDSI	L. FLEURETAE	L. MUSTELINUS	L. PETTERI	L. RUFICAUDATUS	L. SAHAMALAZENSIS	L. SEPTENTRIONALIS	L. TYMERLACHSONORUM
Malvaceae	LX	L	F	LX	FLIX	L	FL	-
Malvaceae (introduced)	-	-	-	-	-	-	-	I
Melastomataceae	-	-	L	-	-	-	-	-
Menispermaceae	-	-	-	X	-	L	-	-
Moraceae	-	-	-	-	-	FL	FL	-
Moringaceae (introduced)	-	-	-	-	-	-	L	-
Myristicaceae	-	L	-	-	-	-	-	-
Myrtaceae	-	F	FL	-	-	-	L	-
Ochnaceae	L	-	-	-	-	-	-	-
Olacaceae	-	-	-	X	-	L	L	-
Oleaceae	LX	-	-	-	L	-	-	-
Phyllanthaceae	-	L	L	X	FL	L	-	-
Poaceae (introduced)	-	-	-	-	-	L	-	-
Polygalaceae	-	-	-	X	-	-	-	-
Primulaceae	-	-	L	-	-	-	-	-
Putranjivaceae	LX	-	-	-	-	-	-	-
Rhamnaceae	-	-	-	-	F	-	L	-
Rhizophoraceae	-	-	-	-	-	L	-	-
Rubiaceae	LX	FL	FL	LX	FLI	-	L	-
Rutaceae	X	-	-	-	L	-	-	-
Salicaceae	-	L	-	-	-	-	-	-
Salvadoraceae	-	-	-	L	-	-	-	-
Sapindaceae	L	-	L	-	L	L	L	-
Sapotaceae	-	L	-	-	-	-	-	-
Sarcocaulaceae	-	-	F	-	-	-	L	-
Scrophulariaceae	-	L	-	X	-	-	-	-
Sphaerosepalaceae	-	-	-	-	-	-	L	-
Violaceae	X	-	L	-	-	-	-	-
References	6, 7, 15, 19	2	6, 13, 14	3, 5, 10, 12	1, 5, 8, 9, 11, 17	18	4	16

Notes: Plants introduced to Madagascar are noted. Key to plant parts exploited: B, bark; E, exudates; F, fruits; I, inflorescences; L, leaves; N, nectar; P, piths and/or stems; S, seeds; X, no data available on which plant part was exploited.

Key to references: 1. Baum (1996); 2. Campera (2018); 3. Charles-Dominique and Hladik (1971); 4. Dinsmore et al. (2016); 5. Dröschler and Kappeler (2014a); 6. Ganzhorn (1988); 7. Ganzhorn (1993); 8. Ganzhorn (2002); 9. Ganzhorn and Kappeler (1996); 10. Hladik and Charles-Dominique (1974); 11. Hladik et al. (1980); 12. Nash (1998); 13. Ratsirason and Ranaivosasy (2002); 14. O. H. Razafindratsima (unpublished data); 15. Razanahoera (1988); 16. S. H. Roberts (unpublished data); 17. Scharfe and Schlund (1996); 18. Seiler (2012); 19. Thalmann (2001).

TABLE 14.14. Plant parts consumed by different members of the Lemuridae

PLANT FAMILIES EXPLOITED	LEMURIDAE SPECIES																						
	EULEMUR ALBIFRONS	E. CINEREICEPS	E. COLLARIS	E. CORONATUS	E. FLAVIFRONS	E. FULVUS	E. MACACO	E. MONGOZ	E. RUBRIVENTER	E. RUFIFRONS	E. RUFUS	E. SANFORDI	HAPALEMUR ALAOTRENSIS	H. AUREUS	H. GRISEUS	H. MERIDIONALIS	H. OCCIDENTALIS	LEMUR CATTA	PROLEMUR SIMUS	V. RUBRA	V. VARIEGATA EDITORUM	V. VARIEGATA SUBINCINCTA	V. VARIEGATA VARIEGATA
Acanthaceae	-	FL	-	FLI	-	L	FL	-	FLI	FLI	-	FL	-	F	FL	-	-	LX	-	-	F	S	-
Aizoaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	L	-	-	-	-	-
Amaranthaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	LX	-	-	-	-	-
Amaranthaceae (introduced)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	LIX	-	-	-	-	-
Anacardiaceae	F	FL	F	FSI	F	F	FLI	L	FX	F	-	-	-	-	-	-	-	FL IX	-	X	FLX	F	FLI
Anacardiaceae (introduced)	-	-	-	F	FL	-	FLI EB	F	-	-	-	F	-	-	-	-	-	FX	F	-	-	-	-
Anisophylleaceae	-	F	-	-	-	-	F	-	-	-	-	-	-	-	-	-	-	-	-	L	FL	-	F
Annonaceae	-	FL	FL	FLI	FL	FSL	FI	-	F	L	-	F	-	-	-	-	-	-	-	FL IX	FLX	F	FL
Annonaceae (introduced)	-	-	-	FI	-	-	FI	-	-	-	-	-	-	-	-	-	-	F	X	-	-	-	-
Aphloiaceae	-	-	-	LI	-	L	F	-	FL	FLI	-	FL	-	-	-	-	-	X	-	F	F	-	FL
Apiaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	L	-	L	-	-	-	-	-
Apocynaceae	FL	FL	I	FL	FL	FL	FL	FL	FLI NX	FL	-	F	-	-	FL	LP	-	FL IP BX	-	F	FX	F	F
Aquifoliaceae	-	-	-	-	-	L	-	-	FX	-	-	-	-	-	-	-	-	-	-	-	X	-	-
Araceae	L	-	FL	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Araceae (introduced)	-	-	-	-	-	-	L	-	-	-	-	-	-	-	-	-	LP	-	P	-	-	-	-
Araliaceae	-	F	F	FN	-	L	-	-	LI	-	-	F	-	-	-	-	-	-	-	-	-	-	-
Arecaceae	-	FI	F	F	F	F	FI	-	F	FL	-	F	-	F	F	FLP	-	FP X	FLI	F	FLI	-	F
Arecaceae (introduced)	-	-	-	-	-	-	F	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aristolochiaceae	-	-	-	-	-	-	-	-	-	F	-	-	-	-	-	-	-	-	-	-	-	-	-
Asclepiadaceae	-	-	L	-	-	-	-	-	-	-	-	-	-	-	-	-	-	LX	-	-	-	-	-
Asparagaceae	-	L	FI	FLI	FI	-	F	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Asparagaceae (introduced)	-	-	-	-	-	-	-	-	-	-	-	FI	-	-	-	F	-	-	-	FL	-	-	F
Asphodelaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	FL IX	-	-	-	-	-
Aspleniaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	LP	-	LIX	-	-	-	-	-
Asteraceae	-	FL	L	-	-	-	-	-	-	FLX	FL	-	-	-	-	-	-	-	-	-	L	-	-
Asteraceae (introduced)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	L	LP	-	FL IX	-	-	F	-	-
Asteropeiaceae	-	X	F	-	-	-	-	-	-	-	-	-	L	-	-	-	-	LX	-	-	-	-	-
Bignoniaceae	F	FI	F	-	-	-	F	-	-	FI	-	-	-	-	-	-	-	X	-	FL	-	-	-
Bignoniaceae (introduced)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	FL IX	-	F	-	-	-
Boraginaceae	-	-	-	F	-	-	FLI	FSL	-	FLI	-	-	-	-	-	-	-	I	-	-	-	-	-
Brassicaceae	-	-	F	-	-	-	-	-	-	-	-	-	-	-	-	-	-	FL IX	-	-	-	-	-
Bromeliaceae (introduced)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Burseraceae	F	-	F	F	FL	-	F	F	F	F	-	F	-	-	-	-	-	-	-	-	-	-	-

PLANT FAMILIES EXPLOITED	LEMURIDAE SPECIES																							
	EULEMUR ALBIFRONS	E. CINEREICEPS	E. COLLARIS	E. CORONATUS	E. FLAVIFRONS	E. FULVUS	E. MACACO	E. MONGOZ	E. RUBRIVENTER	E. RUFIFRONS	E. RUFUS	E. SANFORDI	HAPLEMUR ALAOTRENSIS	H. AUREUS	H. GRISEUS	H. MERIDIONALIS	H. OCCIDENTALIS	LEMUR CATTIA	PROLEMUR SIMUS	V. RUBRA	V. VARIEGATA EDITORUM	V. VARIEGATA SUBCINCTA	V. VARIEGATA VARIEGATA	
Burseraceae (introduced)	-	-	-	-	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Buxaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F	-	-	-	-	-
Cactaceae	-	-	-	-	-	-	-	-	F	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cactaceae (introduced)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	FLIX	-	-	-	-	-
Calophyllaceae	-	FL	F	-	-	F	FI	-	FLI	FI	-	-	-	-	-	-	-	-	-	-	FLX	FIX	-	F
Canellaceae	-	F	F	F	-	F	-	-	FL	F	-	F	-	-	-	-	-	-	-	-	-	F	-	-
Cannabaceae	-	-	-	FL	-	-	-	-	-	FLI	-	FLI	-	-	-	-	-	-	FLIX	-	-	F	-	-
Capparaceae	-	-	F	F	-	-	-	-	-	F	-	-	-	-	-	-	-	-	FLIX	-	-	-	-	-
Caricaceae (introduced)	-	-	-	-	-	-	FLI	-	-	-	-	-	-	-	-	-	-	F	F	-	-	-	-	-
Casuarinaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	L	-	-	-	-	-
Celastraceae	-	I	FLI	FLI	-	FL	FL	-	-	F	-	I	-	-	-	N	-	LIX	-	FL	F	-	-	-
Chrysobalanaceae	-	-	-	-	FI	-	FLI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	L	-	-
Clusiaceae	F	FLI	FLI	FN	FL	FL	F	-	FLI	FS	LI	FL	-	-	-	-	-	-	-	FL	IN	FLI	F	FLI
Colchicaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	LI	-	-	-	-	-
Combretaceae	F	FL	FI	F	FL	F	FL	FL	N	L	FL	IE	-	-	-	-	-	-	FLI	EX	FI	F	-	F
Commelinaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	LX	-	-	-	-	-
Connaraceae	FL	-	-	-	-	-	-	-	FL	F	-	-	-	-	-	-	-	-	-	-	-	L	-	-
Convolvulaceae	-	-	-	-	-	-	-	F	-	-	-	-	LP	-	-	-	-	-	FLI	NX	-	F	-	-
Crassulaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	LX	-	-	-	-	-
Cucurbitaceae	-	-	-	-	-	FSL	F	-	L	FL	-	-	-	-	-	-	-	-	FLX	-	F	-	F	-
Cucurbitaceae (introduced)	-	-	-	-	-	F	-	-	-	-	-	-	-	-	-	-	-	-	LX	-	-	-	-	-
Cunoniaceae	-	-	-	-	-	L	-	-	FIN	FLI	-	-	-	-	-	-	-	-	-	-	-	FIX	-	-
Cyperaceae	-	-	-	-	-	-	-	-	-	-	-	-	LIP	L	-	LIP	X	IP	L	-	F	-	-	-
Davalliaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	L	-	-	-
Dennstaedtiaceae	-	L	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dichapetalaceae	-	-	FL	F	-	FI	FL	-	FL	FL	-	F	-	-	-	-	-	-	L	-	F	F	-	F
Didiereaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	FLIX	-	-	-	-	-
Dilleniaceae	-	-	FLI	-	-	-	-	-	-	-	-	-	-	-	-	I	-	-	-	-	L	-	-	I
Dioscoreaceae	-	-	F	FS	-	-	-	-	-	-	-	-	-	-	-	-	-	-	LX	-	-	-	-	-
Ebenaceae	FL	FL	FI	FSI	FI	FL	FI	L	F	F	-	F	-	-	-	F	-	FX	-	FL	L	F	FL	
Elaeocarpaceae	-	-	F	-	-	-	-	-	FX	FL	IN	-	F	-	-	-	-	-	-	-	FLX	-	-	-
Ericaceae	-	-	F	-	-	-	-	-	IX	-	-	-	-	-	-	F	-	X	-	-	-	-	-	-
Erythroxylaceae	-	FLIX	F	FLIX	L	FL	-	-	LX	FL	-	FLI	-	F	-	F	-	F	-	IN	FL	-	FL	FL
Euphorbiaceae	-	FLI	FI	-	F	FL	FI	EB	N	F	FL	-	-	-	L	-	-	X	FLI	EX	FLI	N	FL	FL

(continued overleaf)

MAMMALS

TABLE 14.14. *continued*

PLANT FAMILIES EXPLOITED	LEMURIDAE SPECIES																							
	EULEMUR ALBIFRONS	E. CINEREICEPS	E. COLLARIS	E. CORONATUS	E. FLAVIFRONS	E. FULVUS	E. MACACO	E. MONGOZ	E. RUBRIVENTER	E. RUFIFRONS	E. RUFUS	E. SANFORDI	HAPLEMUR ALAOTRENSIS	H. AUREUS	H. GRISEUS	H. MERIDIONALIS	H. OCCIDENTALIS	LEMUR CATTIA	PROLEMUR SIMUS	V. RUBRA	V. VARIEGATA EDITORUM	V. VARIEGATA SUBCINCTA	V. VARIEGATA VARIEGATA	
Euphorbiaceae (introduced)	-	-	-	I	-	-	-	-	-	-	-	-	-	-	-	-	-	LI	-	-	-	-	-	-
Fabaceae	FLI	FLI	FLI	FSL IN	FLI	FLI	FSL IN	FS LI	FLI N	FLI NE BX	-	FI	-	-	FI	L	-	FS LIE BX	-	FLI N	FLI N	I	FL	
Fabaceae (introduced)	-	-	-	FI	-	I	FLI	I	-	LIE	-	-	-	-	-	-	-	FS LIX	X	-	F	-	-	-
Flacourtiaceae	-	-	FE	-	-	-	-	-	-	-	-	-	-	-	-	F	-	F	-	-	-	F	-	
Flagellariaceae	-	-	-	-	-	-	-	FLI	-	-	-	-	-	-	-	L	-	-	-	-	-	-	-	
Gentianaceae	-	F	F	-	-	-	-	-	FLX	F	-	-	-	-	-	-	-	-	-	F	I	-	F	
Hernandiaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	FL IX	-	-	-	-	-	
Hypericaceae	-	F	-	FI	FLI	-	FI	-	F	F	-	FL	-	-	-	-	-	X	-	-	FX	-	-	
Icacinaeae	F	F	F	-	-	-	F	-	L	-	-	-	-	-	-	-	-	X	-	-	-	-	-	
Lamiaceae	-	F	F	L	-	F	FI	-	X	FL	-	X	-	-	-	FI	-	FL IX	-	-	FL	-	-	
Lauraceae	FL	FL	FL	FL	F	FSL	FI	-	FL IX	FLI	-	F	-	-	L	-	-	X	-	FL IN	FLX	FL	FL	
Lauraceae (introduced)	-	-	-	F	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Liliaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	L	-	-	-	
Linaceae	-	F	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F	-	-	
Loganiaceae	FL	-	F	F	F	F	F	F	-	F	-	FI	-	-	-	-	-	FLX	-	FL	F	-	F	
Loranthaceae	-	L	FL	FS LI	-	-	F	-	FLI NX	FLI	-	FL	-	-	-	-	-	L	-	L	FLI	-	-	
Lygodiaceae	-	-	-	-	-	-	L	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Lythraceae	-	-	-	FI	-	-	L	-	-	FL	-	-	-	-	-	-	-	FL	-	-	-	-	-	
Malpighiaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	L	-	-	X	-	-	
Malvaceae	F	FLI	-	F	F	FI	FL	FL	FLI NX	FLI	F	FI	-	F	F	-	-	FL IX	-	FLI NX	FL IX	FS	F	
Malvaceae (introduced)	-	-	-	-	-	-	FLI N	FN	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Melastomataceae	F	F	F	F	-	FL	F	-	F	FLI	-	-	-	F	F	F	-	F	-	IN	FL	F	F	
Melastomataceae (introduced)	-	F	F	-	-	F	-	-	-	-	-	-	-	-	F	-	FX	-	-	F	F	-	-	
Meliaceae	FL	F	F	FL IN	-	F	-	-	FX	LI	-	FLI	-	-	-	-	-	FL IX	-	FL	FLI	FLI	-	
Meliaceae (introduced)	-	-	-	-	-	-	-	-	-	F	-	-	-	-	-	-	-	FL IX	-	-	-	-	-	
Menispermaceae	-	F	F	F	F	F	F	-	F	-	-	-	-	-	-	-	-	FL IX	-	-	-	-	-	
Metteniusaceae	-	FL	F	-	-	-	-	-	F	-	-	-	-	-	-	-	-	LX	-	-	F	S	-	
Molluginaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	FL	-	-	F	-	-	
Monimiaceae	-	F	F	F	-	FL	F	-	FL	FL	-	F	-	-	-	-	-	L	-	-	-	-	-	
Moraceae	F	F	FLI	FLX	FLI	FSL	FL	FS LI	FLX	FLI	FL	FLI	-	F	FL	F	FX	FLX	FX	FLI	FL X	F	FL	
Moraceae (introduced)	-	-	-	F	-	-	FLI	-	-	-	-	-	-	-	-	-	-	FLX	FX	FLI	FL X	F	FL	
Musaceae (introduced)	-	-	-	-	-	-	FI	-	-	-	-	-	-	-	-	-	-	X	-	FX	-	-	-	

PLANT FAMILIES EXPLOITED	LEMURIDAE SPECIES																						
	EULEMUR ALBIFRONS	E. CINEREICEPS	E. COLLARIS	E. CORONATUS	E. FLAVIFRONS	E. FULVUS	E. MACACO	E. MONGOZ	E. RUBRIVENTER	E. RUFIFRONS	E. RUFUS	E. SANFORDI	HAPLEMUR ALAOTRENSIS	H. AUREUS	H. GRISEUS	H. MERIDIONALIS	H. OCCIDENTALIS	LEMUR CATTIA	PROLEMUR SIMUS	V. RUBRA	V. VARIEGATA EDITORUM	V. VARIEGATA SUBCINCTA	V. VARIEGATA VARIEGATA
Myricaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-
Myristicaceae	F	-	F	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	FL	-	-	L
Myrtaceae	F	FL	FI	F	-	FL	F	-	FL IX	FL	-	F	-	-	-	F	-	FIX	-	FL IX	FL IX	FL	FL
Myrtaceae (introduced)	-	F	F	F	-	I	FI	-	FI	F	-	-	-	F	F	N	-	FIX	-	-	-	-	-
Nyctaginaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	LIX	-	-	-	-	-
Nyctaginaceae (introduced)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	LIX	-	-	-	-	-
Nymphaeaceae	-	-	-	-	-	-	-	-	-	-	-	-	LP	-	-	-	-	-	-	-	-	-	-
Ochnaceae	-	-	F	-	-	L	-	-	F	FL	-	-	-	-	-	-	-	-	-	L	-	-	-
Oleaceae	-	-	-	F	FL	F	-	-	-	-	-	-	-	-	-	-	-	FX	-	-	-	-	-
Oleaceae	F	FLI	FL	FL	-	FL	F	-	FX	FL	-	FLI	-	-	-	FLP	-	FLX	-	F	F	-	F
Opiliaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	LX	-	-	-	-	-
Orchidaceae	-	-	-	I	-	L	-	-	X	-	-	I	-	FLI	FLI	I	-	LI	-	LX	-	-	-
Pandanaceae	F	FLI	FL IP	F	-	-	FL	-	FI	F	-	-	-	-	-	FLP	-	P	-	F	F	-	-
Papaveraceae (introduced)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	LIX	-	-	-	-	-
Passifloraceae	-	-	-	FL	-	F	-	F	-	F	-	-	-	-	-	-	-	L	-	-	-	-	-
Phyllanthaceae	-	FL	F	FI	I	FL	F	F	FX	F	-	FL	-	-	-	FL	-	FL IX	-	FL	FL	F	F
Physenaceae	-	-	-	F	-	-	-	-	-	-	-	F	-	-	-	-	-	FLX	-	-	-	-	-
Pinaceae (introduced)	-	-	-	L	-	LI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Piperaceae	-	-	-	FLI	-	-	-	-	-	-	-	LI	-	-	-	-	-	-	-	-	-	-	-
Piperaceae (introduced)	-	-	-	-	-	-	F	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pittosporaceae	-	-	-	F	-	-	-	-	F	FL	-	F	-	-	-	-	-	-	-	-	X	-	-
Poaceae	-	L	-	LI	-	FI	-	-	L	-	-	FI	LP	LP	LIP	LP	LPX	LIX	LIP	-	-	-	-
Poaceae (introduced)	-	-	-	-	-	-	L	-	-	-	-	-	-	-	FLI	L	X	LI	FLX	-	-	-	-
Podocarpaceae	-	-	-	-	-	F	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F
Polygonaceae	-	-	-	-	-	-	-	-	-	-	-	-	L	-	-	-	-	L	-	-	-	-	-
Pontederiaceae (introduced)	-	-	-	-	-	-	-	-	-	-	-	-	IP	-	-	-	-	-	-	-	-	-	-
Primulaceae	-	FLI	F	FL	-	FS LI	F	-	FL IX	FL	-	FLI	-	L	F	F	-	FX	-	-	FLX	F	F
Proteaceae	-	-	-	-	-	-	-	-	FL IX	-	-	-	-	-	-	-	-	-	-	-	FLX	-	-
Putranjivaceae	-	-	F	FLI	-	-	-	-	-	-	-	FLI	-	-	-	-	-	-	-	F	-	-	-
Rhamnaceae	-	-	-	FL	-	F	-	FL NB	F	F	F	I	-	-	-	-	-	FL IX	-	FL	-	-	-
Rhizophoraceae	-	-	-	FL	F	L	F	-	-	-	-	F	-	-	-	-	-	-	X	-	-	-	-
Rosaceae (introduced)	-	-	-	F	-	-	-	-	-	-	-	FL	-	-	-	-	-	-	-	X	-	-	-
Rubiaceae	FLI	FLI	FLI	F	F	FSL	F	FSL	FL IX	FL IX	-	FI	-	F	F	F	-	FL IX	-	FLI NX	FLX	FI	FI
Rubiaceae (introduced)	-	-	-	F	-	-	F	-	-	-	-	L	-	-	-	-	-	-	X	FL	F	-	F

(continued overleaf)

TABLE 14.14. *continued*

PLANT FAMILIES EXPLOITED	LEMURIDAE SPECIES																							
	EULEMUR ALBIFRONS	E. CINEREICEPS	E. COLLARIS	E. CORONATUS	E. FLAVIFRONS	E. FULVUS	E. MACACO	E. MONGOZ	E. RUBRIVENTER	E. RUFIFRONS	E. RUFUS	E. SANFORDI	HAPALEMUR ALAOTRENSIS	H. AUREUS	H. GRISEUS	H. MERIDIONALIS	H. OCCIDENTALIS	LEMUR CAITA	PROLEMUR SIMIUS	V. RUBRA	V. VARIEGATA EDITORUM	V. VARIEGATA SUBCINCTA	V. VARIEGATA VARIEGATA	
Rutaceae	-	L	F	FLI	-	L	-	-	F	FLI	-	FI	-	F	-	F	-	FLIX	-	-	FL	-	F	
Rutaceae (introduced)	-	-	-	FI	-	-	FLI	-	F	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Salicaceae	-	FLX	FI	FI	F	FL	F	-	F	FL	-	FLI	-	-	F	-	-	FLX	-	FL	F	-	F	
Salvadoraceae	-	-	-	FL	-	-	-	-	-	FL	-	-	-	-	-	-	-	FLIBX	-	-	-	-	-	
Santalaceae	-	-	-	-	-	-	-	-	F	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Sapindaceae	-	FL	F	FSLIX	FLI	FLI	-	FSLX	FSI	-	FL	-	-	-	-	F	-	FLX	-	FLI	FLX	-	FL	
Sapindaceae (introduced)	-	-	-	-	-	F	-	S	-	-	-	-	-	-	-	-	X	-	X	-	L	-	-	
Sapotaceae	FL	FL	FI	FSI	-	F	FL	-	FL	F	-	FLI	-	-	-	-	-	-	-	FLX	FLINX	FSN	FL	
Sarcolaenaceae	-	F	FI	-	-	L	F	-	-	F	-	-	-	-	-	FN	-	FI	-	-	FN	-	FS	
Scrophulariaceae	-	-	-	-	-	F	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	
Smilacaceae	L	F	FL	FL	-	-	FL	-	FLX	FL	-	FL	-	L	FL	LP	-	P	-	-	-	-	-	
Solanaceae (introduced)	-	F	-	FI	-	-	-	-	-	-	-	F	-	-	-	-	-	FIX	-	-	-	-	F	
Sphaerosepalaceae	F	L	F	S	-	F	-	-	-	L	-	-	-	-	-	-	-	X	-	F	F	-	F	
Stemonuraceae	-	-	-	FLI	-	-	-	-	-	-	-	FLI	-	-	-	-	-	-	-	-	-	-	-	
Stilbaceae	-	F	-	-	-	-	-	-	F	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Strelitziaceae	FN	IN	I	-	-	-	FIN	-	-	L	-	-	-	-	-	-	IN	-	I	LIX	FLINX	FIN	FN	IN
Taccaceae	-	-	FP	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Talinaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Thelypteridaceae	-	-	-	-	-	-	-	-	-	-	-	-	L	-	-	-	-	FLX	-	-	-	-	-	
Toricelliaceae	-	-	-	-	-	-	-	-	F	F	-	-	-	-	-	-	-	-	-	-	-	-	-	
Urticaceae	-	-	-	-	-	-	-	L	L	F	-	-	-	-	-	-	-	-	-	-	-	-	-	
Urticaceae (introduced)	-	F	-	-	-	-	-	-	-	-	-	-	-	L	L	-	-	L	-	-	-	-	-	
Velloziaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	F	-	
Verbenaceae	-	-	FI	F	-	-	-	-	-	-	-	-	-	-	-	-	-	I	-	-	-	-	-	
Verbenaceae (introduced)	-	F	-	FLI	-	-	-	-	-	-	-	FI	-	-	-	-	-	L	-	-	-	-	-	
Violaceae	-	-	-	F	-	-	LI	FI	-	F	-	-	-	-	-	-	-	F	-	-	F	-	-	
Vitaceae	-	-	-	FSLI	-	-	F	FLN	F	FL	-	F	-	-	-	-	-	FLIX	-	-	-	-	-	
Ximeniaceae	-	-	-	-	-	F	-	-	-	-	-	-	-	L	-	-	-	FLX	-	-	F	F	-	
Zingiberaceae	F	F	-	-	-	-	F	-	-	-	-	-	-	-	-	-	-	FS	-	-	-	-	-	
Zygophyllaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	LX	-	-	-	

PLANT FAMILIES EXPLOITED	LEMURIDAE SPECIES																						
	<i>EULEMUR ALBIFRONS</i>	<i>E. CINEREICEPS</i>	<i>E. COLLARIS</i>	<i>E. CORONATUS</i>	<i>E. FLAVIFRONS</i>	<i>E. FULVUS</i>	<i>E. MACACO</i>	<i>E. MONGOZ</i>	<i>E. RUBRIVENTER</i>	<i>E. RUFIFRONS</i>	<i>E. RUFUS</i>	<i>E. SANFORDI</i>	<i>HAPALEMUR ALAOTRENSIS</i>	<i>H. AUREUS</i>	<i>H. GRISEUS</i>	<i>H. MERIDIONALIS</i>	<i>H. OCCIDENTALIS</i>	<i>LEMUR CAYTA</i>	<i>PROLEMUR SIMUS</i>	<i>V. RUBRA</i>	<i>V. VARIEGATA EDITORUM</i>	<i>V. VARIEGATA SUBCINCTA</i>	<i>V. VARIEGATA VARIEGATA</i>
References	31, 47, 62, 71, 98, 128-130	3, 59, 88	11, 14, 28, 29, 38, 112	15, 41, 46, 47, 66, 97, 120, 133	131	42-44, 50, 95, 103-106, 111, 127	1, 8-10, 17, 18, 83, 84, 116, 117	5, 20, 123	22, 24, 30, 51, 75-79, 81, 87, 100, 101, 113, 126, 135	24, 25, 27, 40, 45, 51, 59, 77-79, 81, 89, 100, 109, 114, 119, 121, 122, 135	21	16, 41, 66, 133	74, 84	39, 49, 69, 124, 139	39, 44, 49, 56, 57, 80, 84, 95, 124, 134, 139	33-38	67, 82	13, 19, 32, 36, 47, 48, 52-55, 60, 61, 63-65, 70, 75, 85, 86, 91, 92, 94, 107, 108, 113, 114, 115, 118, 122, 135-138, 140	2, 26, 39, 49, 69, 90, 96, 124, 125, 139	68, 71, 98, 99, 102, 128-130	6, 7, 23, 24, 40, 51, 58, 73, 93, 100, 101, 132	72	4, 12, 110

Notes: Plants introduced to Madagascar are noted. Key to plant parts exploited: B, bark; E, exudates; F, fruits; I, inflorescences; L, leaves; N, nectar; P, piths and/or stems; S, seeds; X, no data available on which plant part was exploited.

Key to references: 1. J. R. Andrews and Birkinshaw (1998); 2. Andriaholinirina et al. (2003); 3. Andriamaharoa et al. (2010); 4. Andrianarisata (1994); 5. Andriatsarafa (1988); 6. Balko (1998); 7. Beeby and Baden (2021); 8. Birkinshaw (1999); 9. Birkinshaw (2001); 10. Birkinshaw and Colquhoun (1998); 11. Bollen et al. (2004a); 12. Britt (2000); 13. Budnitz and Dainis (1975); 14. Campera (2012); 15. K. S. Chen et al. (2015); 16. K. S. Chen et al. (2016); 17. Colquhoun et al. (2009); 18. Colquhoun (2005); 19. Crawford et al. (2015); 20. D. I. Curtis (1997); 21. D. J. Curtis and Zaramody (1998); 22. Dague and Petter (1988); 23. Day et al. (2009); 24. Dew and Wright (1998); 25. de Winter et al. (2013); 26. Dolch et al. (2008); 27. Donati et al. (1999); 28. Donati et al. (2007b); 29. Donati et al. (2011); 30. DuBour (2018); 31. Duckworth et al. (1995); 32. Ellwanger and Gould (2011); 33. Eppley et al. (2011); 34. Eppley (2015); 35. Eppley et al. (2015a); 36. Eppley et al. (2015b); 37. Eppley et al. (2016a); 38. Eppley et al. (2017a); 39. Eppley et al. (2017b); 40. Erhart et al. (2018); 41. Freed (1996); 42. Ganzhorn (1985); 43. Ganzhorn (1987); 44. Ganzhorn (1988); 45. Ganzhorn and Kappeler (1996); 46. Gardner (2009); 47. Gardner (2016); 48. Gemmill and Gould (2008); 49. Glander et al. (1989); 50. Goodman et al. (1996c); 51. Goodman et al. (1997c); 52. L. Gould and Gabriel (2014); 53. L. Gould et al. (2009); 54. L. Gould et al. (2011); 55. L. Gould et al. (2015); 56. Grassi (2002); 57. Grassi (2006); 58. Holmes et al. (2016); 59. Johnson (2002); 60. Jolly (1966); 61. Kelley (2011); 62. Kress et al. (1994); 63. LaFleur (2012); 64. LaFleur and Gould (2009); 65. LaFleur and Sauther (2015); 66. Marrocoli et al. (2013); 67. Martinez (2008); 68. Martinez and Razafindratsima (2014); 69. Meier and Rumpler (1987); 70. Mertl-Millhollen et al. (2003); 71. Mogilevsky (2020); 72. Morland (1991a); 73. Moses and Semple (2011); 74. Mutschler (1999); 75. O'Mara (2012); 76. Overdorff (1988); 77. Overdorff (1992); 78. Overdorff (1993); 79. Overdorff and Strait (1998); 80. Overdorff et al. (1997); 81. Overdorff et al. (2002); 82. Patel et al. (2014); 83. J.-J. Petter (1962); 84. J.-J. Petter et al. (1977); 85. Pinkus et al. (2006); 86. S. V. Rakotoarisoa (1999); 87. Rakotonirina et al. (2010); 88. Ralainasolo et al. (2008); 89. Ralisoamalala (1996); 90. Randriahaingo et al. (2014); 91. Rasamimanana (1999); 92. Rasamimanana and Rafidinarivo (1993); 93. Ratsimbazafy et al. (2002); 94. Ratsirarson (1987); 95. Ratsirarson and Ranaivonasy (2002); 96. Ravaloharimanitra et al. (2011); 97. Ravelomalala (2015); 98. Razafindratsima (2009); 99. Razafindratsima and Razafimahatratra (2010); 100. Razafindratsima et al. (2014); 101. O. H. Razafindratsima (unpublished data); 102. Rigamonti (1993); 103. Sato (2012); 104. Sato (2013a); 105. Sato (2013b); 106. Sato et al. (2014); 107. Sauther (1992); 108. Sauther and Cuozzo (2009); 109. Scharfe and Schlund (1996); 110. Schmidt et al. (2010); 111. Semel (2015); 112. Serra (2011); 113. Simmen et al. (1999); 114. Simmen et al. (2003); 115. Simmen et al. (2006); 116. Simmen et al. (2007); 117. Snow (2011); 118. Soma (2006); 119. Spehn and Ganzhorn (2000); 120. K. J. E. Steffens (unpublished data); 121. Sussman (1975); 122. Sussman (1977a); 123. Sussman and Tattersall (1976); 124. C. L. Tan (1999); 125. C. L. Tan (2006); 126. Tecot (2008); 127. Valenta (2014); 128. (1997a); 129. Vasey (2000a); 130. Vasey et al. (2018); 131. Volampeno (2009); 132. F. J. White et al. (1995); 133. J. M. Wilson et al. (1989); 134. P. C. Wright (1986); 135. Yamashita (1996); 136. Yamashita (2002); 137. Yamashita (2003); 138. Yamashita (2008); 139. Yamashita et al. (2009); 140. Yamashita et al. (2015).

MAMMALS

TABLE 14.15. Plant parts consumed by different members of the Indriidae

PLANT FAMILIES EXPLOITED	INDRIIDAE SPECIES													
	AVAHI LANIGER	A. MERIDIONALIS	A. OCCIDENTALIS	A. PEYRIERASI	INDRI INDRI	PROPTHECUS CANDIDUS	P. COQUERELI	P. CORONATUS	P. DIADEMA	P. EDWARDSI	P. PERRIERI	P. TATTERSALLI	P. VERREAUXI	
Acanthaceae	FL	-	-	-	L	-	-	-	L	L	-	-	L	
Amaranthaceae (introduced)	-	-	-	-	-	-	-	-	-	-	-	-	L	
Anacardiaceae	-	X	LX	L	L	FLI	FLIX	LI	FSLI	FSL	L	FSLIX	FLIBX	
Anacardiaceae (introduced)	-	-	-	-	-	-	FLB	-	-	-	I	FSLIX	-	
Anisophylleaceae	-	L	-	-	FL	-	-	-	-	-	-	-	-	
Annonaceae	L	L	X	-	FLI	LI	X	-	L	S	-	X	X	
Annonaceae (introduced)	-	-	-	-	-	-	-	-	-	-	-	FSX	-	
Aphloiaceae	-	L	-	-	-	L	-	-	L	L	-	-	-	
Apocynaceae	-	L	X	L	L	FLI	-	L	FLI	FL	SL	FSLX	FLIX	
Apocynaceae (introduced)	-	-	-	-	-	-	-	-	-	-	-	-	L	
Araceae	-	-	-	-	-	-	-	-	-	-	-	X	-	
Araliaceae	-	-	-	-	L	FLI	-	-	FLI	FSL	-	X	-	
Arecaceae	-	-	-	-	-	-	-	-	-	-	-	F	-	
Aristolochiaceae	-	-	-	-	-	-	-	-	-	-	-	-	L	
Asclepiadaceae	-	-	-	-	-	-	-	-	-	-	-	-	FLP	
Asparagaceae	-	X	-	-	-	-	-	-	-	-	-	X	L	
Asteraceae	-	-	-	-	-	-	-	-	-	-	-	X	L	
Asteropeiaceae	-	X	-	-	-	-	-	-	-	-	-	X	L	
Balanophoraceae	-	-	-	-	-	I	-	-	I	-	-	-	-	
Balsaminaceae	-	-	-	-	-	-	-	-	L	-	-	-	-	
Bignoniaceae	-	-	-	-	-	-	LI	-	-	-	-	-	-	
Blechnaceae	-	-	-	-	-	L	-	-	-	-	-	-	X	
Boraginaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	
Burseraceae	-	X	X	-	L	FL	B	FL	-	-	-	F	L	
Buxaceae	-	-	-	-	-	-	-	-	-	-	-	FX	FSLIBX	
Calophyllaceae	-	-	-	-	SLI	FLI	X	-	-	-	-	-	F	
Canellaceae	-	X	-	-	-	-	-	-	FLI	FS	-	LX	-	



PLANT FAMILIES EXPLOITED	INDRIIDAE SPECIES												
	AVAH I LANIGER	A. MERIDIONALIS	A. OCCIDENTALIS	A. PEYRIERASI	INDRI INDRI	PROPTHECUS CANDIDUS	P. COQUERELEI	P. CORONATUS	P. DIADEMA	P. EDWARDSI	P. PERRIERI	P. TATTERSALLI	P. VERRAUXI
Cannabaceae	-	-	-	-	-	-	-	-	-	-	-	-	FL
Capparaceae	-	-	-	-	-	-	X	-	-	-	-	X	L
Celastraceae	-	LX	L	-	-	-	-	-	FS	-	-	X	FSL
Clusiaceae	FL	LX	X	-	FSL IB	FLI	X	-	FSLI	FSLI	-	SLI	-
Combretaceae	-	-	-	-	L	-	-	L	-	-	-	FS LX	FLIX
Connaraceae	-	-	-	-	-	-	-	-	L	-	-	X	-
Convolvulaceae	-	-	-	-	-	-	-	-	-	-	-	X	L
Cucurbitaceae	-	-	-	-	-	FLI	-	-	L	-	-	X	LI
Cunoniaceae	-	L	-	-	-	FLI	-	-	-	-	-	-	-
Cyatheaceae	-	-	-	-	-	-	-	-	L	-	-	-	-
Cytinaceae	-	-	-	-	-	I	-	-	LI	-	-	-	-
Dennstaedtiaceae	-	-	-	-	-	-	-	-	L	-	-	-	-
Dichapetalaceae	L	-	-	-	-	FLI	-	-	-	FS	-	-	-
Didiereaceae	-	-	-	-	-	-	-	-	-	-	-	-	I
Dilleniaceae	-	F	-	-	L	-	-	-	-	-	-	-	-
Dioscoreaceae	-	-	X	-	-	-	-	-	-	-	-	-	L
Dryopteridaceae	-	-	-	-	-	L	-	-	-	-	-	-	-
Ebenaceae	-	X	X	-	L	FL	-	L	-	-	L	IX	FS LX
Erythroxylaceae	LI	X	L	L	L	FLI	X	-	FSLI	FS LX	-	FIX	-
Euphorbiaceae	-	L	-	-	L	FLI	-	-	FSL IX	SL	-	X	FLI PX
Euphorbiaceae (introduced)	-	-	-	-	-	-	I	-	-	-	-	-	-
Fabaceae	-	LX	X	-	LI	FLI	FLX	LI	SL	FSL IX	FLI	FSL IX	FSLI PBX
Fabaceae (introduced)	-	-	-	-	-	-	-	-	-	-	-	X	FLIX
Flacourtiaceae	-	-	-	-	-	-	-	-	-	-	-	-	L
Gentianaceae	-	-	-	-	L	-	-	-	L	-	-	-	-
Hamamelidaceae	-	X	-	-	-	-	-	-	-	-	-	-	L
Hernandiaceae	-	-	-	-	-	-	-	-	-	-	-	-	-

(continued overleaf)

MAMMALS

TABLE 14.15. *continued*

PLANT FAMILIES EXPLOITED	INDRIIDAE SPECIES												
	A. VAHI LANIGER	A. MERIDIONALIS	A. OCCIDENTALIS	A. PEYRIERASI	INDRI INDRI	PROPHITHECUS CANDIDUS	P. COQUERELEI	P. CORONATUS	P. DIADEMA	P. EDWARDSI	P. PERRIERI	P. TATTERSALLI	P. VERREAUXI
Hypericaceae	L	L	X	L	-	-	-	-	-	F	-	-	-
Icacinaceae	-	-	-	-	-	L	-	-	-	-	-	-	L
Lamiaceae	-	-	X	-	-	-	X	L	-	F	-	F	FL
Lamiaceae (introduced)	-	-	-	-	-	-	-	-	-	-	-	X	-
Lauraceae	L	X	-	L	FSL IB	FLI	-	-	FSL	FSL	-	X	-
Lecythidaceae	-	-	-	-	-	-	-	-	-	-	-	X	LX
Loganiaceae	-	-	-	-	-	-	FI	-	-	-	-	-	FLX
Loranthaceae	-	-	-	-	L	FLI	-	-	FSLI	FL	-	X	-
Lygodiaceae	-	-	-	-	-	-	-	-	L	-	-	-	-
Lythraceae	-	-	-	-	-	-	-	-	-	-	-	-	FL
Malvaceae	L	L	LX	L	FLB	FLI	FLX	-	-	-	-	FSIX	FLIX
Malvaceae (introduced)	-	-	-	-	-	-	L	-	-	-	-	-	-
Melastomataceae	L	-	-	-	LB	FLI	-	L	F	F	-	FX	-
Meliaceae	-	L	L	-	-	-	X	-	FSL	S	-	IX	LI
Meliaceae (introduced)	-	-	-	-	-	-	-	-	-	-	-	-	FLIX
Metteniusaceae	-	X	-	-	-	-	-	-	-	-	-	-	-
Monimiaceae	-	LX	-	-	FI	FL	-	-	-	-	-	-	L
Montiniaceae	-	-	-	-	-	-	-	-	FL	F	-	-	-
Moraceae	L	LX	X	-	FL	FLI	F	FL	FSL	FSX	F	LX	FL
Musaceae (introduced)	-	-	-	-	-	-	-	-	-	-	-	X	-
Myristicaceae	-	LX	-	-	FSL IB	-	-	-	-	F	-	-	-
Myrtaceae	L	LX	-	L	FLI	FLI	-	-	FSL	FSL	-	X	-
Myrtaceae (introduced)	-	-	-	-	-	-	-	-	F	-	-	-	L
Nyctaginaceae (introduced)	-	-	-	-	-	-	-	-	-	-	-	-	-
Ochnaceae	L	LX	-	-	-	-	-	-	-	-	-	-	L
Olacaceae	-	-	L	-	-	-	-	-	FL	-	-	-	-
Oleaceae	-	X	X	-	L	-	-	L	L	-	L	LIX	FLI
								L	-	F	-	X	FX

PLANT FAMILIES EXPLOITED	INDRIIDAE SPECIES												
	AYAHI LANIGER	A. MERIDIONALIS	A. OCCIDENTALIS	A. PEYRIERASI	INDRI INDRI	PROPTHECUS CANDIDUS	P. COQUERELEI	P. CORONATUS	P. DIADEMA	P. EDWARDSI	P. PERRIERI	P. TATTERSALLI	P. VERREAUXI
Opiliaceae	-	-	-	-	-	-	-	-	-	-	-	-	L
Pedaliaceae	-	-	-	-	-	-	-	-	-	-	-	X	-
Phyllanthaceae	L	LX	X	-	FLIB	-	-	-	FL	F	-	X	FLIX
Physenaceae	-	-	-	-	-	-	-	-	-	-	-	LX	L
Pittosporaceae	L	-	-	-	-	FLI	-	-	FSL	FL	L	X	-
Plantaginaceae	-	-	-	-	-	-	-	-	-	-	-	X	-
Poaceae (introduced)	-	-	-	-	-	-	-	-	-	-	-	X	-
Primulaceae	L	-	-	L	L	FLI	-	-	FSL	FLX	-	X	-
Proteaceae	-	L	-	-	-	-	-	-	-	-	-	-	-
Putranjivaceae	-	-	-	-	-	-	X	-	FLI	-	-	FX	-
Rhamnaceae	-	-	-	-	-	LI	X	FL	-	-	-	FX	FSL IX
Rhamnaceae (introduced)	-	-	-	-	-	-	-	-	-	-	-	-	L
Rhizophoraceae	L	-	-	-	L	-	-	-	-	-	-	-	-
Rubiaceae	L	LX	LX	L	FL	FL	I	-	L	F	-	FSX	FLIX
Rubiaceae (introduced)	-	X	-	-	-	-	-	-	-	-	-	X	-
Rutaceae	L	-	LX	-	-	-	X	-	LI	FL	-	X	FLIX
Salicaceae	-	LX	-	-	L	FLI	-	-	L	-	-	X	FLX
Salvadoraceae	-	-	-	-	-	-	-	-	-	-	-	-	FL
Sapindaceae	L	LX	-	L	FL	FLI	X	LI	FSLI	FSL	-	SLX	FSL BX
Sapindaceae (introduced)	-	-	X	-	-	-	-	-	-	-	-	X	-
Sapotaceae	FL	L	L	L	-	FLI	LX	FL	SL	FS	LI	LX	FX
Sarcolaenaceae	-	X	-	-	L	FLI	-	-	I	-	-	FSI	FX
Scrophulariaceae	-	L	-	-	-	-	-	-	-	-	-	-	-
Simaroubaceae	-	L	-	-	-	-	-	-	-	-	-	-	I
Smilacaceae	-	-	-	-	-	-	-	-	L	FL	-	-	-
Solanaceae (introduced)	-	-	-	-	-	-	-	-	F	FL	-	X	FLI
Sphaerosepalaceae	-	-	X	-	-	-	X	FL	-	-	-	FX	FL

(continued overleaf)

TABLE 14.15. *continued*

PLANT FAMILIES EXPLOITED	INDRIIDAE SPECIES												
	AVAHILANIGER	A. MERIDIONALIS	A. OCCIDENTALIS	A. PEYRIERASI	INDRI INDRI	PROPTHECUS CANDIDUS	P. COQUERELI	P. CORONATUS	P. DIADEMA	P. EDWARDSI	P. PERRIERI	P. TATTERSALLI	P. VERREAUXI
Strelitziaceae	-	-	-	-	L	-	-	-	-	-	-	-	-
Talinaceae	-	-	-	-	-	-	-	-	-	-	-	F	LI
Theaceae	-	-	-	-	-	-	-	-	F	-	-	-	-
Violaceae	-	-	X	-	-	-	-	-	-	-	-	-	FLIX
Vitaceae	-	-	-	-	-	-	-	-	-	F	-	-	L
References	15, 19, 51	2, 38	15, 16, 53, 61	13, 22	6, 15, 43, 44, 46-48, 52, 62	20, 41, 56	14, 17, 43, 54	36, 45	9, 27, 29, 28, 30, 47, 48, 52	1, 10, 12, 21, 23-26, 39, 40, 64	32	35, 49, 58, 60	3-5, 7, 8, 11, 18, 31, 33, 34, 37, 42, 50, 55, 57, 59, 63-67

Notes: Plants introduced to Madagascar are noted. Key to plant parts exploited: B, bark; E, exudates; F, fruits; I, inflorescences; L, leaves; N, nectar; P, piths and/or stems; S, seeds; X, no data available on which plant part was exploited.

Key to references: 1. Arrigo-Nelson (2006); 2. Balestri (2018); 3. Baum (1995); 4. Baum (1996); 5. Böhning-Gaese et al. (1995); 6. Britt et al. (2002); 7. Carrai et al. (2003); 8. Charrier et al. (2007); 9. Day et al. (2009); 10. Dew and Wright (1998); 11. de Winter et al. (2013); 12. Erhart et al. (2018); 13. Faulkner and Lehman (2006); 14. Ganzhorn (1987); 15. Ganzhorn (1988); 16. Ganzhorn (1993); 17. Ganzhorn and Abraham (1991); 18. Ganzhorn and Kappeler (1996); 19. Ganzhorn et al. (1985); 20. Ganzhorn et al. (2017); 21. Goodman et al. (1997c); 22. C. Harcourt (1991); 23. Hemingway (1995); 24. Hemingway (1996); 25. Hemingway (1998); 26. Hemingway (1999); 27. Irwin (2008); 28. Irwin and Ravelomanantsoa (2004); 29. Irwin et al. (2007); 30. Irwin et al. (2014); 31. Jolly (1966); 32. Lehman and Mayor (2004); 33. Markham (2014); 34. Markham and Gould (2018); 35. Meyers (1993); 36. P. Müller (1997); 37. Norscia et al. (2006); 38. Norscia et al. (2012); 39. Overdorff and Strait (1998); 40. Overdorff et al. (2002); 41. Patel (2012); 42. Perofsky et al. (2017); 43. J.-J. Petter (1962); 44. J.-J. Petter et al. (1977); 45. Pichon et al. (2010); 46. Pollock (1977); 47. Powzyk (1997) (in Irwin 2006); 48. Powzyk and Mowry (2003); 49. Quéméré et al. (2013); 50. Ralisoamalala (1996); 51. Ratsirarson and Ranaivosasy (2002); 52. O. H. Razafindratsima (unpublished data); 53. Razanahoera (1988); 54. Richard (1974); 55. Richard (1977); 56. Sato et al. (2016); 57. Scharfe and Schlund (1996); 58. B. P. Semel and M. A. Semel (unpublished data); 59. Simmen et al. (2003); 60. E. L. Simons (1988); 61. Thalmann (2001); 62. Thalmann et al. (1993); 63. Veilleux et al. (2016); 64. Yamashita (1996); 65. Yamashita (2002); 66. Yamashita (2003); 67. Yamashita (2008).

Plant species from 42 of these introduced plant families have been identified as being exploited for food by lemurs. The highest diversity of introduced food plants is exploited by Lemuridae (35 plant families), followed by Indriidae (17 families), Cheirogaleidae (11 families), Daubentoniidae (seven families), and Lepilemuridae (five families). The plant families with introduced species exploited by the highest number of different lemur species include, in decreasing order, Myrtaceae, Anacardiaceae, Fabaceae, Rubiaceae, and Poaceae. Introduced plants exploited by the largest diversity of lemur species include, for their fruits, *Mangifera indica* (Anacardiaceae), *Psidium* spp. (Myrtaceae), *Miconia crenata* (previously known as *Clidemia hirta*; Melastomataceae), and *Solanum*

*mauritianum* (Solanaceae; Figure 14.24a). While these fruits typically constitute only small proportions of lemur diets, *Daubentonia madagascariensis* exhibits a relatively high diversity of introduced species in its diet, including fruits from *Cocos* sp. (Arecaceae), *Artocarpus* sp. (Moraceae), and *Litchi* sp. (Sapindaceae). However, this is more likely a reflection of the nature of vegetation at the study sites (i.e., to a greater or lesser extent anthropogenic) than the predilection of the species.

In areas of Madagascar where agricultural areas are intermixed with forested zones, different crop plants are incorporated in the diets of various lemur species. Further, invasive plant species, those exhibiting varying abilities to colonize and thrive in

disturbed habitats (Kull et al. 2012), are also consumed by several lemur species. Food items of the latter type include the fruits of *Psidium cattleianum* and *P. guajava* (Myrtaceae), *Lantana camara* (Verbenaceae), and *Miconia crenata*; and fruits, leaves, and flowers of *Pithecellobium dulce* (Fabaceae). As humans impact natural habitats, introduced plant species become increasingly abundant (Kull et al. 2013), and so the high diversity of non-native food plants utilized by lemur species might be best explained by the conversion of Madagascar's forests into more anthropogenic vegetation types within the last century (Vieilledent et al. 2018). Additionally, it could be due to the tendency of researchers to select more accessible field sites within close proximity to the forest edge ecotones. The data presented here appear to support the general idea that at some sites introduced plants can be an important component of lemur diets (Gérard et al. 2015).

## CONCLUSION

It is clear that lemurs exploit a significant proportion (>62%) of the island's woody flora (both native and introduced). Nevertheless, some taxa are clearly more important than others in terms of the number of different lemur species that exploit them, the number of different plant parts exploited, and their abundance in species' diets. With the exclusion of the family Poaceae (see Vorontsova et al., pp. 585–98), nonwoody taxa, especially aquatic plants, are

found rarely in lemur diets, with the notable exception being the flexible diet of *Lemur catta*. Still, the large number of plant taxa and plant parts exploited by all the lemur species whose feeding ecologies have thus far been studied reflects the remarkable plasticity in their dietary regimes.

Yet, despite the increase in lemur dietary studies since c. 2000, approximately 50 lemur species have never been the focus of feeding-ecology research, and among some species whose feeding ecology has been studied, this research was conducted in largely anthropogenic vegetation with abundant introduced flora, and complementary research is required in more natural habitats. Given that an understanding of species ecology is vital to creating effective conservation programs, dietary studies of these species should be considered high priority. Beyond general feeding-ecology descriptions, future directions should look to expand our understanding of 1) daily or seasonal macronutrient and micronutrient balancing (e.g., Irwin et al. 2014); 2) potential pharmacopeia use (e.g., Huffman 2003); and 3) the role of food traits such as visual and olfactory cues and specifically how lemurs may help shape these (e.g., Valenta and Nevo 2020). In summary, advances in lemur dietary research will ultimately help to reshape our understanding of the role of these animals within this unique island ecosystem, as well as inform the design of effective and urgently required initiatives to restore lemur habitat to Madagascar's sadly degraded landscapes.

Subject editors: Jörg U. Ganzhorn and Steven M. Goodman

## FOSSIL AND SUBFOSSIL BATS

K. E. Samonds, S. M. Goodman, J. L. Alumbaugh, and N. B. Simmons

Madagascar's living bats, totaling 46 species, show a high level of endemism and possess considerable ecological and morphological diversity (see Goodman et al., pp. 1894–911). While species endemism in Malagasy bats is lower than that of most other groups of terrestrial vertebrates, endemism is considerably higher than on other similar-size landmasses, and 80% of Malagasy bat species are known from nowhere else in the world. One of the nine chiropteran families that inhabit Madagascar is endemic to the island, Myzopodidae (see Ralisata et al., pp. 1917–22).

Madagascar was isolated by about 90 million years ago (Mya) (Storey et al. 1995), before the origin and evolution of modern bats (Teeling et al. 2005), and most groups are thought to have colonized the island by flying ~400 km across the Mozambique Channel from Africa, the closest available source (Goodman 2011; Rakotoarivelo et al. 2015; Foley et al. 2017). One notable exception is *Pteropus* (Pteropodidae), a taxon not known from continental Africa, whose ancestor likely came from Asia (Almeida et al. 2014). Some bat lineages have molecular divergence times within the Paleogene (Teeling et al. 2005), but most are thought to have

colonized the island more recently, many probably during the past 5 million years (Goodman 2011; Rakotoarivelo et al. 2015; Foley et al. 2017). Most extant Malagasy bat species have been the subject of molecular phylogenetic studies, and it seems likely on the basis of biogeography and divergence patterns that the modern bat fauna of the island represents 28 or 29 different colonization events by different bat lineages (see Goodman et al., pp. 1894–911).

*Triaenops/Paratriaenops* (Rhinonycteridae) may have had either two separate dispersal events to the island or a dispersal event from Madagascar to Africa (A. L. Russell et al. 2007), and *Scotophilus* (Vespertilionidae) may have had at least two separate dispersal events to Madagascar (Trujillo 2005).

The fossil record of the Cenozoic, a critical interval for interpreting the origin and evolution of most of the island's fauna, including bats, is unfortunately poorly represented in Malagasy formations (see Samonds et al., pp. 1859–62). The Madagascar fossil record is richest in two time periods: 1) Middle–Late Triassic to Late Cretaceous (Krause et al. 1997), which is too old to provide relevant context for distinctly more modern groups such as extant bats; and