

NON-NATIVE HABITAT USE BY ENDEMIC TERRESTRIAL MALAGASY MAMMALS

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It has been estimated that approximately 1200 introduced vascular plant species exist on Madagascar (Kull et al. 2012), compared to the conservative approximation of 11,220 native vascular plants (Callmander et al. 2011). Though 8.9% of these—slightly more than 100 species—are considered invasive (Kull et al. 2014), many introduced plants constitute elements of habitat and food resources for endemic animals, and in some cases the plants are used by local people; according to Gérard et al. (2015), 100 endemic vertebrate species on Madagascar have been identified as using introduced plant species.

Since 1953, approximately 44% of Madagascar's forest cover was lost, and 46% of remaining forest habitat is less than 100 m from a forest edge (Vieilledent et al. 2018). Further, numerous forest-dependent land vertebrates, including 95% of lemur species (C. Schwitzer et al. 2014), are threatened with extinction, and as their natural habitats disappear, degraded areas are often (at least initially) colonized by introduced plant species, some of them invasive (Kull et al. 2013). As such, it is important to understand the role of introduced plants and associated habitats, as well as agroecosystems, in lemur and other endemic mammal survival. The purpose of this contribution is to summarize what is known about endemic Malagasy nonvolant mammals, specifically lemurs, tenrecs, and nesomyine rodents, using non-native habitats, which includes what we consider anthropogenic grasslands and degraded formerly forested areas.

ORDER PRIMATES

Families Cheirogaleidae, Lepilemuridae, Lemuridae, Indriidae, and Daubentoniidae

There are an estimated 108 recognized lemur species, all endemic to Madagascar (see Goodman and Soarimalala, pp. 1737–69), many of which occupy and utilize a variety of different habitat types. Given the widespread diversity of both lemur and introduced plant species, we examine herein lemur use of these non-native habitats.

In terms of cash-crop plantations, it was recently confirmed that a number of lemur species utilize *Theobroma cacao* (Cacao) plantations, at least occasionally, near Ambanja (Webber et al. 2020). These plantations are grown under both native and introduced shade trees, which commonly include introduced *Albizia* species (silk trees), *Artocarpus heterophyllus* (Jackfruit), and *Cananga odorata* (Ylang-ylang). Among the lemur species recorded in these plantations are *Lepilemur dorsalis* (Gray's Sportive Lemur), *Mirza zaza* (Northern Giant Mouse Lemur), *Phaner parienti* (Sambirano Fork-marked Lemur), *Microcebus* species (mouse lemurs), and *Cheirogaleus* species (dwarf lemurs). There were also local reports mentioned in the Webber et al. (2020) study of *Eulemur macaco*

(Black Lemur) and *Haplemur* species (bamboo lemurs) moving through this non-native woody plant habitat, though the authors were unable to confirm this.

Cash-crop plantations are becoming more common throughout eastern Madagascar, where many lemur species have also been observed in plantations of *Vanilla planifolia* (Bourbon Vanilla), including *E. coronatus* (Crowned Lemur), *M. tavaratra* (Tavaratra Mouse Lemur), *C. shethi* (Ankarana Dwarf Lemur), *C. crossleyi* (Crossley's Dwarf Lemur), and *C. major* (Greater Dwarf Lemur) (Hending et al. 2018). These plantations are often within a few hundred meters of, or sometimes within, native forest fragments, thus possibly acting as corridors and forest habitat extensions. Similarly, shade-grown *Coffea* (coffee) plantations, which often mix native and introduced plant species, have been shown to provide habitat for *M. rufus* (Rufous Mouse Lemur; Deppe et al. 2007) and *Prolemur simus* (Greater Bamboo Lemur; P. C. Wright et al. 2008).

Other agricultural areas, especially those in close proximity to native forest, are well known to provide habitat to several lemur species. Degraded forests dominated by *Mangifera indica* (Mango) in different portions of the island are frequently inhabited by lemurs, including *Cheirogaleus major* (J.-J. Petter et al. 1977), *Mirza coquereli* (Coquerel's Giant Mouse Lemur; Kappeler 2003), *Lepilemur edwardsi* (Milne-Edwards' Sportive Lemur; Ganzhorn 1987), *Daubentonia madagascariensis* (Aye-aye; J.-J. Petter et al. 1977), *Propithecus coquereli* (Coquerel's Sifaka; Ganzhorn and Abraham 1991), and *P. edwardsi* (Milne-Edwards' Sifaka; Lehman and Mayor 2004). *Litchi chinensis* (Lychee) has been recorded as habitat for *Microcebus rufus* (Deppe et al. 2007), *C. major* (J.-J. Petter et al. 1977), and *D. madagascariensis* (J.-J. Petter et al. 1977), and noted as frequently visited by *Eulemur collaris* (Red-collared Brown Lemur) along the periphery of native forest (Eppley et al. 2017b). *Eulemur rubriventer* (Red-bellied Lemur) and *Haplemur griseus* (Gray Bamboo Lemur) have been observed utilizing habitat largely consisting of *Psidium cattleianum* (Strawberry Guava) in degraded forested areas of Ranomafana National Park (Overdorff 1988; Grassi 2006), while *E. collaris* often utilizes this introduced species in the southeast (Eppley et al. 2017b).

Among other recorded non-native habitat–lemur associations, unspecified citrus trees can provide habitat to *M. rufus* in the southeast near Ranomafana (Deppe et al. 2007), while the introduced *Syzygium aromaticum* (Clove) is used as a regular nesting site by *M. rufus* (J.-J. Petter et al. 1977). Heavily degraded forest dominated by *Anacardium occidentale* (Cashew) in the west is utilized regularly by *Mirza coquereli* (Kappeler 2003). Both *Cocos nucifera* (Coconut) and *Terminalia catappa* (Indian Almond) are occasionally used as nest-site habitat by *D. madagascariensis* (J.-J. Petter et al. 1977). In agricultural fields adjacent to Masoala National Park, both *Miconia crenata* (Soapbush, previously known as *Clidemia hirta*) and *Oryza sativa* (rice) are utilized by *H. occidentalis*

(Western Bamboo Lemur; Martinez 2008). In the southwest, cultivated crop habitat of *Ipomoea batatas* (Sweet Potato) is heavily relied upon by *Lemur catta* (Ring-tailed Lemur; LaFleur and Gould 2009). *Tamarindus indica* (Tamarind) has been recorded as a reputed habitat for *Propithecus verreauxi* (Verreaux's Sifaka; Yamashita 2002) and extensively recorded being used by populations of *L. catta* in the riparian forests of Bezà-Mahafaly (L. Gould et al. 2011) and Berenty (Mertl-Millhollen et al. 2011). *Tamarindus* does not have any invasive properties, and recent phylogeographic studies across its tropical range indicate that it is probably native to Madagascar (Diallo et al. 2007).

Timber plantations occur in different areas of the island and, despite being utilitarian, are well known to provide vertical structure, enabling many lemur species to travel arboreally more easily. Among the most widespread timber trees are species of *Eucalyptus* (Géard et al. 2015). In the dry west near Kirindy Forest CNFEREF (Centre National de Formation, d'Etudes et de Recherche en Environnement et Foresterie), *Eucalyptus* has been observed to provide habitat for *Microcebus murinus* (Gray Mouse Lemur), *Cheirogaleus major*, *Mirza coquereli*, and *Phaner pallescens* (Pale Fork-marked Lemur; Ganzhorn et al. 1999a; Ganzhorn 2003). In the north, *Eucalyptus* plantations have been inhabited by *Microcebus arnholdi* (Montagne d'Ambre Mouse Lemur), *C. andysabini* (Sabin's Dwarf Lemur), *P. electromontis* (Montagne d'Ambre Fork-marked Lemur), and *E. sanfordi* (Sanford's Brown Lemur) (Ganzhorn et al. 1997). In the central east, these introduced plantations were used by *Lepilemur mustelinus* (Weasel Sportive Lemur; Ganzhorn 1988), *Avahi laniger* (Eastern Woolly Lemur; Ganzhorn 1987), *E. rubriventer* (Overdorff 1988), and *Indri indri* (Indri; Ganzhorn 1987), while in the southeast they were used by *A. meridionalis* (Southern Woolly Lemur; Scobie et al. 2017). Old, sometimes abandoned *Eucalyptus* plantations often have an understory overgrown with other introduced plants, including *Miconia crenata* and *Lantana camara*, which are utilized by *M. lehilahytsara* (Goodman's Mouse Lemur), *Cheirogaleus major*, *E. fulvus* (Brown Lemur), and *H. griseus*. These plantations occasionally have an understory dominated by introduced *Bambusa* (bamboo) species, utilized by both *H. griseus* and *C. major* (Ganzhorn 1987).

Similar plantations consist of *Acacia* species and *Cassia siamea*, which are used by *M. murinus*, *M. rufus*, *Mirza coquereli*, and *P. pallescens* (Ganzhorn et al. 1999a; Ganzhorn 2003). Corridors of *A. mangium* are used by *Microcebus ganzhorni* (Ganzhorn's Mouse Lemur) to travel between littoral forest fragments in the southeast (Andriamandimbiarisoa et al. 2015). Plantations of *Araucaria araucana* (Monkey Puzzle Tree) provide habitat for *Cheirogaleus andysabini*, *P. electromontis*, *E. coronatus*, and *E. sanfordi* (Ganzhorn et al. 1997).

Additional introduced utilitarian trees that provide potential habitat for lemurs include *Aucoumea klaineana* (Okoumé), used by *Avahi laniger* near littoral forests in the central east (Ratsirarson and Ranaivonasy 2002); and *Ceiba pentandra* (Kapok), the flowers and fruits of which provide >80% of the diet of *E. mongoz* (Mongoose Lemur), as reported by J.-J. Petter et al. (1977). At Manombo, in the southeast, *Varecia variegata* (Black and White Ruffed Lemur) was recorded to heavily rely on two introduced and invasive plant species, *Cecropia peltata* (Trumpet Tree) and *Miconia crenata* (Ratsimbazafy et al. 2002).

In the southeast, *Melaleuca quinquenervia* (Broad-leaved Paperbark Tree) has invaded many wetland areas along the coast. Though invasive, this tree is harvested for timber by local people. The littoral forests within this region are highly fragmented, and *Melaleuca* provides both structural habitat, which certain lemurs use as corridors to travel between fragments, and occasional food, specifically the tree's fragrant flowers (Figure 14.18). Among the species that have been observed utilizing *M. quinquenervia* are *Microcebus ganzhorni*, *Cheirogaleus medius* (Fat-tailed Dwarf Lemur), *A. meridionalis*, *E. collaris*, and *Haplemur meridionalis* (Southern Bamboo Lemur) (Bollen 2003; Eppley et al. 2015a). Additionally, the introduced grass *Stenotaphrum dimidiatum* grows well in partially exposed areas within *Melaleuca* woodlands and forms a foraging habitat frequently used by *H. meridionalis* (Eppley et al. 2017b).

Another introduced plant, *Argemone mexicana* (Mexican Poppy), is heavily utilized by *Lemur catta* in and around Bezà-Mahafaly in the southwest and can constitute a large portion of this animal's annual diet, especially during drought (LaFleur and Gould 2009).

ORDER RODENTIA

Family Nesomyidae

A few species of rodents belonging to the endemic subfamily Nesomyinae, most of which are considered forest-dependent, have been documented in different types of introduced or non-natural

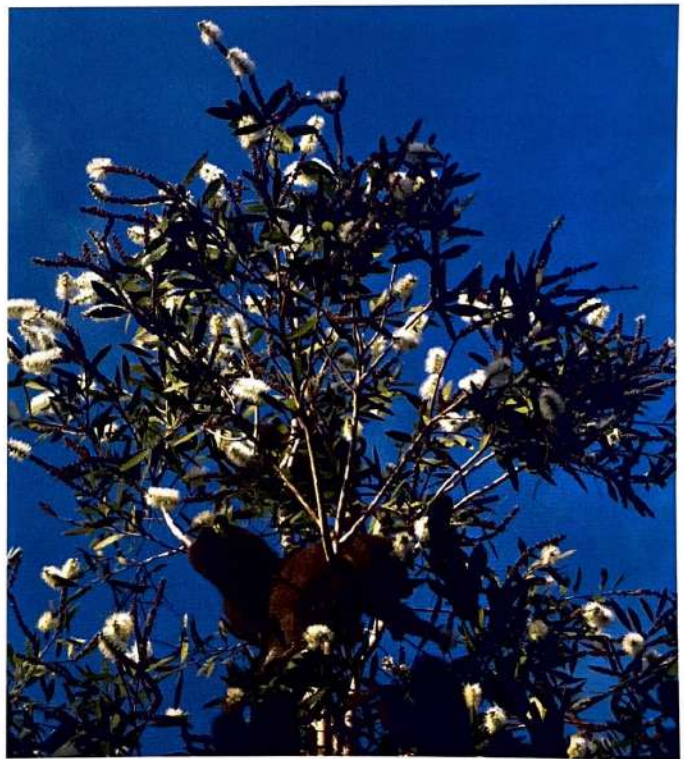


FIGURE 14.18 *Haplemur meridionalis* (Southern Bamboo Lemur) foraging on flowers of the introduced tree *Melaleuca quinquenervia* in the Mandena littoral forest, southeast Madagascar. (PHOTO by T. M. Eppley.)

plant habitats. Two different nesomyine species have been found in fallow rice fields in close proximity to relatively intact moist evergreen forest near Ranomafana National Park and the corridor linking this site to Andringitra National Park: *Nesomys rufus* (Eastern Red Forest Rat) and *Brachyuromys betsileoensis* (Lesser Short-tailed Rat; Jansa and Carleton 2003a; S. M. Goodman and V. Soarimalala, unpublished data). In the region of Moramanga, at a site about 12 km from the nearest natural moist evergreen forest block, Randriamoria et al. (2015) found *B. betsileoensis* in an area of grassland in close vicinity to a dispersed planting of *Pinus* and a recently harvested rice field. Among the nesomyine rodents, this species is exceptional in that it lives in non-native forest formations and has also been documented in marsh areas of the east and montane ericoid thicket.

In heavily degraded littoral forest of the lowlands of the central east, D. Rakotondravony et al. (1998a) found *Eliurus webbi* (Webb's Tufted-tail Rat) associated with a plantation of *Aucoumea klaineana* in close proximity to natural forest. In northern Madagascar, around the medium-altitude moist evergreen forest of Montagne d'Ambre, *E. minor* (Lesser Tufted-tail Rat) has been associated with *Eucalyptus* plantations (Goodman et al. 1997a). Highly degraded monocultures of *Ziziphus mauritiana* (Indian Jujube) bordering partially disturbed dry deciduous forest in the central west are used as habitat by tufted-tail rats (*Eliurus* sp.; Ganzhorn 2003). In an area of montane forest on the Ankaratra Massif that is reputed to be replanted with native *Weinmannia* trees and includes numerous introduced and invasive plant species dominated by *Pinus*, the nesomyine rodent *Monticolomys koopmani* (Koopman's Mountain-dwelling Mouse) was trapped in largely non-native woody vegetation (Goodman et al. 1996a).

ORDER AFROSORICIDA

Family Tenrecidae

Members of this family compose three different subfamilies: Oryzorictinae, which is largely forest-dependent, and Tenrecinae and Geogalinae, which occur in natural forest, degraded formations, and grassland habitats. In the case of the Tenrecinae, numerous documented cases record its members' occurrence outside natural forest formations (Deppe et al. 2007; Soarimalala and Goodman 2011), and this subfamily is not discussed here.

One rather exceptional oryzorictine is the aquatic *Microgale mergulus* (Web-footed Shrew Tenrec; formerly placed in the genus *Limnogale*), known to occur in streams and small rivers passing through areas outside natural moist evergreen forests, including *Pinus* plantations (Benstead and Olson 2003). *Oryzorictes hova* (Hova Mole Tenrec) is found in rice fields and open marshy habitats as well as natural forest formations, while *O. tetradactylus* (Four-toed Mole Tenrec) is found in native montane ericoid thicket above forest line (Goodman 2003a).

Over the past decades, much of the field research on Malagasy small mammals has focused on natural forest habitats and to a large extent has not provided insight into members of this family, particularly Oryzorictinae, occurring outside these formations. Recent work by Randriamoria et al. (2015), however, affords new insights

into species that are not necessarily forest-dependent. At different trapping localities in the Moramanga District, the authors found five species of shrew tenrecs of the genus *Microgale* occurring outside natural moist evergreen forest. An individual of *M. cowani* (Cowan's Shrew Tenrec) was found in an area dominated by sugarcane, bananas, and the introduced *Lantana camara*, and another individual in herbaceous vegetation in close proximity to a rice field; the maximum straight-line distance of these trapping localities to natural forest was less than 500 m. Two individuals of *M. majori* (Major's Long-tailed Shrew Tenrec) were trapped in *savoka* (regenerating humid forest habitat) dominated by Asteraceae (*Psiadia altissima* and *Helichrysum cirrhosum*) and other non-native vegetation, including *L. camara*. Other individuals of this species were trapped in plantations of introduced *Eucalyptus*. The direct distance between sites where these animals were trapped and native forest was 775 m to 3 km. Another species, *M. pusilla* (Least Shrew Tenrec), which was previously known to occur in marsh areas outside of natural forest (Soarimalala and Goodman 2011), was trapped in a variety of settings: near a rice field, in areas of *savoka* with *L. camara*, *Psidium cattleianum*, *Psiadia altissima*, and *H. cirrhosum*. The last shrew tenrec captured outside the forest by Randriamoria et al. (2015) was *M. thomasi* (Thomas's Shrew Tenrec), which was in *savoka* dominated by *Psidium cattleianum* and *L. camara*, and the site was about 100 m from natural forest.

In an area of medium-altitude moist evergreen forest on the Ankaratra Massif reputedly replanted with *Weinmannia* and numerous introduced plant species, some of them invasive, dominated by *Pinus*, the shrew tenrec *M. thomasi* was captured in largely non-native woody vegetation (Goodman et al. 1996a). At another site in the Central Highlands, in this case Ankazomivady, *M. cowani* was found in secondary grasslands about 100 m from a native medium-altitude moist evergreen forest fragment (S. M. Goodman and V. Soarimalala, unpublished data). This species, like some other members of this genus, is also known from natural montane ericoid thicket above forest line on different massifs, such as Marojejy and Andringitra, confirming that it is not strictly forest-dependent (Langrand and Goodman 1997; Goodman and Jenkins 2000).

Remarkably little is known about the natural history of the Geogalinae, specifically *Geogale aurita* (Large-eared Tenrec), which is reputed to show a marked preference for termites (Stephenson 2003). A survey near Ampoza of the organisms occurring in what is presumed to be secondary grasslands found *G. aurita* in areas of secondary grasslands and at the grasslands-dry spiny thicket ecotone (Tingle et al. 2003).

CONCLUSION

Though it is difficult to measure the contribution of introduced and invasive plant species to habitats used by Malagasy native nonvolant mammals, it would appear that in some cases, under specific conditions at certain sites, these plants play an important role (Gérard et al. 2015). Although the ultimate survival of all forest-dwelling mammal species, which has been extensively discussed in the literature for lemurs, should be considered precarious because of a multitude of anthropogenic and climatic pressures (C. Schwitzer et al. 2014), the observations that certain lemur and other small mammal

species are able to cope with some habitat degradation should be seen as positive. However, it is important to underline that in most cases, sites with non-native habitat where these mammal species have been found are in close proximity to native forest, which in virtually all cases serve as the critical corridor or buffer zone to allow the dispersal of certain mammal species into the non-native

formations. We suspect that if the native blocks are severely degraded or disappear, this system will break down, and for largely forest-dependent mammal species, the non-native plant areas will no longer serve as critical habitat for their continued existence.

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PHYLOGENETIC OVERVIEW OF THE LEMURIFORMES

A. D. Yoder

It is astonishing to reflect upon how much has changed in phylogenetic methods and theory since this contribution was written for the precursor of this book close to 20 years ago (A. D. Yoder 2003). Leading up to that time, the subject of lemuriform origins was considered controversial. The most essential aspect of this controversy was the question of whether or not lemurs constitute a clade. Early in the period of phylogenetic systematic investigation, a number of researchers focused on morphological characters of the basicranium, concluding that certain unusual aspects of the arterial and bony morphology shared by Malagasy dwarf lemurs (Cheirogaleidae) and Afro-Asian lorises indicate a cladistic relationship between the two that excludes other Malagasy lemurs (Szalay and Katz 1973; Cartmill 1975). Because cheirogaleids and lorisiforms share certain characteristics of carotid circulation and related cranial morphology that are unique within living and known fossil primates, these authorities concluded that lorises and dwarf lemurs form a clade that excludes the remaining Malagasy primates. There is no doubt that the lorisiforms are the closest relatives of the Malagasy lemuriforms, and that the two groups together form the suborder Strepsirrhini (i.e., the tooth-combed primates), but the idea that lorisiforms and cheirogaleids share a relationship that excludes other lemurs was initially considered a radical departure from traditional thinking. The phylogenetic position of *Daubentonia madagascariensis* (Aye-aye) (see Sterling et al., pp. 1975–78) was also considered problematic. Its bizarre morphology and unusual ecological specializations made phylogenetic placement based on morphology within the Strepsirrhini very difficult, and consequently at least two mutually exclusive hypotheses were proposed in the literature. Various authors considered *Daubentonia* to be either a specialized indriid (J. H. Schwartz and Tattersall 1985) or the monotypic sister group to all remaining strepsirrhines (Groves 1989). Conversely, molecular phylogenetic hypotheses were nearly unanimous in finding that living Malagasy primates constitute a clade (Dene et al. 1976; A. D. Yoder 1994; Porter et al. 1995).

Subsequent investigation of this question using phylogenomic methods has served to confirm and strengthen these early molecular phylogenetic studies, finding that all living Malagasy nonhuman primates, including the Aye-aye, constitute a clade with strong

statistical support (DelPero et al. 2006; Horvath et al. 2008; dos Reis et al. 2018). Fantastically, the same revolutions in genomic technologies have allowed for the inclusion of the subfossil lemur (see Godfrey and Jungers, pp. 1824–28) in phylogenetic analysis, conclusively finding that they are members of the same clade as the living lemurs (K. P. Karanth et al. 2005; Kistler et al. 2015), with a single colonization of Madagascar occurring sometime in the early Cenozoic (A. D. Yoder et al. 1996b; dos Reis et al. 2018; Figure 14.19). One important implication of this phylogenetic result that we emphasize here is that the spectacular array of lemuriform morphologies, behaviors, ecotypes, and physiologies all derive from a single ancestral primate type that colonized Madagascar via over-water dispersal. And as implausible as this colonization may seem, given the rigors of an assumed transoceanic dispersal event from Africa to Madagascar, recent and sophisticated climatological models that have reconstructed the likely direction and magnitude of Indian Ocean currents have provided credible mechanisms by which early strepsirrhines (and other terrestrial Malagasy vertebrates) could have been relatively rapidly transported from the west to the east across the Mozambique Channel (Ali and Huber 2010; see Samonds et al., pp. 73–78). Further, if patterns observed in the present, as described by Krause et al. (pp. 59–68), were also true for the early Cenozoic, ancestral lemurs might easily have been transported on large island rafts torn from the riverbanks of eastern Africa, perhaps aided by metabolic mechanisms of “emergency” torpor (Kappeler 2000a).

The only subsequent kink in this otherwise consistent story of lemur origins can be found in a recent reanalysis of the 20-million-year-old fossil primate *Propotto* from Africa (Gunnell et al. 2018). Based on a variety of morphological characteristics, the authors concluded that *Propotto* was actually a basal Aye-aye, implying that there were two rather than one lemuriform dispersal event from Africa to Madagascar. Given that essentially *all* published molecular-phylogenetic studies have identified *Daubentonia* as the basal-most lineage in the lemuriform radiation (e.g., Horvath et al. 2008; Matsui et al. 2009; dos Reis et al. 2018), this conclusion not only upends the idea that nonhuman Malagasy primates constitute a clade, it also has profound implications for the geological age of the radiation. If the early Miocene *Propotto* was indeed an ancestral