The Dwarf and Mouse Lemurs of Madagascar

The dwarf and mouse lemurs of Madagascar are two very species-rich lemur genera, yet there is a relative paucity of information on this primate family in published literature. In this first ever treatment of the Cheirogaleidae, international experts are brought together to review and integrate our current knowledge of the behavior, physiology, ecology, genetics, and biogeography of these species.

A wide range of direct and indirect research methods that are currently used to study these cryptic nocturnal solitary foragers is described. By uniting often disparate research on captive and free-ranging taxa and synthesizing recent methodological advances, this book provides new insights that will encourage further studies of this fascinating primate family.

This synthesis will provide an incentive for more integrative studies of the Cheirogaleidae in captivity and in the wild, enabling the impacts of deforestation and other factors to be identified and directions for future conservation efforts to be established.

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Biology, Behavior and Conservation Biogeography of the Cheirogaleidae

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Foreword

The group of primates of the subfamily Cheirogaleidae (Malagasy primates; family Lemuridae) are among the most interesting animals alive today. They originated approximately 25–30 million years ago; they are all Malagasy and are nocturnal in activity; they include the smallest of the living primates; they include the only known obligate hibernators within the primates; and, especially like the other nocturnal primate species, their taxonomy has been greatly expanded within the past two decades (Yoder *et al.*, Chapter 1; Groves, Chapter 2).

This book, *The Dwarf and Mouse Lemurs of Madagascar: Biology, Behavior and Conservation Biogeography of the Cheirogaleidae*, is edited by Shawn M. Lehman, Ute Radespiel, and Elke Zimmermann. It examines their evolution, taxonomy, and genetics; the methods used for studying captive and wild cheirogaleids; their behavior and ecology; the sensory ecology, communication system, and cognition of these animals; and their conservation biology. The book contains 27 chapters with an array of over 40 exceptional international authors, specializing in anthropology, biology, psychology, veterinary medicine, and primatology.

When research on the ecology and behavior of the Malagasy primates was just beginning, over 50 years ago, Jean-Jacques Petter and Arlette Petter-Rousseaux knew of only six species in three genera of cheirogaleids (Petter, 1962; Petter-Rousseaux, 1967). Now, over 30 species in 5 genera are recognized today. Changes have occurred because of "traditional" (morphological) taxonomic research. This has been related, since the mid-1980s, mainly to specific-mate recognition systems of the vocalizations of different nocturnal primate species. However, since around 2000, DNA sequencing has played a great role in recognizing different species (Yoder *et al.*, Chapter 1; Groves, Chapter 2).

Biologists have found that the molecular and morphological diversity related to biogeographic patterns is more complex in Cheirogaleidae than was previously thought. Related to a number of factors during their evolution, the family had initial genus-level divergence in the Oligocene–Miocene epochs, followed by a widespread Pliocene–Pleistocene species-level radiation. Louis, Jr. and Lei (Chapter 3) argue that there was a basal split within Cheirogaleidae at approximately 29 million years ago: with *Phaner* splitting at 28.17 million years ago, *Cheirogaleus* at 23.77 million years ago, *Allocebus* at 17.94 million years ago, and lastly *Mirza* from *Microcebus* at 14.81 million years ago. Andrews *et al.* (Chapter 4) argue that frugivory evolved convergently in Eocene stem primitive primates (strepsirrhines) and monkeys (haplorhines) from faunivorous ancestors. They assume that "the angiosperm evolutions model of primate evolution" (Sussman, 1991; Sussman *et al.*, 2013) provides a good context for the extensive euprimate radiations that occurred after 55 Ma. They also show that mouse lemurs have evolved small size only relatively recently (< 8 Ma), making this species an unsuitable model for a common primate ancestor.

Recent research by Herrera *et al.* (Chapter 5) shows that size differences in sympatric species of cheirogaleids enable them to avoid competition and exploit different resources. Discrete differences in female genital morphology indicate that sexual isolation also has occurred between sympatric species.

In the second part of the book, the authors show that these small primates can be used for the study of human disease. Here, Kästner *et al.* (Chapter 6) indicate that the smallest primates, *Microcebus* (the mouse lemurs), are an excellent model for research on human disease and modern imaging methods. The mainstay for short-term field procedures is anesthesia with the inhalation agents of isoflurane and sevoflurane. This allows induction and maintenance of anesthesia with stable physiologic conditions over several hours. *Microcebus murinus*, for example, is an exceptional model for Alzheimer's disease and bovine spongiform encephalopathy. This species displays most of the pathognomonic lesions observed in Alzheimer's disease (AD). Furthermore, its small size allows the maintenance of large breeding colonies and greater numbers for cognitive or behavioral tests (Verdier and Mestre-Francés, Chapter 7). Zimmermann *et al.* (Chapter 8) measure several life-history traits of *Microcebus* to assess the extent of intra- and interspecific variation and potential constraints. They find that a shortened annual cycle, of 8 months vs. 12 months, does not affect litter size, but leads to accelerated aging. In this genus, life-history patterns linked to a female's energy allocation to reproduction are species-specific and phylogenetically variable, whereas those related to aging are interspecifically invariant and phylogenetically constrained. In relationship to trapping, Deppe *et al.* (Chapter 9) assessed the effects of weather and lunar cycle on the activity pattern of brown mouse lemurs (*Microcebus rufus*). Trapping was highest during dryer, full moon nights, and trapping success increased with decreasing temperatures. Infectious diseases in wild primates are now receiving a great amount of research attention and mouse lemur parasitology is well positioned to become a new model in this research (Kessler *et al.*, Chapter 10). Zohdy and Durden (Chapter 11) provide a comprehensive overview of the known ectoparasites of the Cheirogaleidae. Understanding parasite–host associations has the potential to reveal novel ecological information about these lemurs, and their potential role as vectors of disease agents.

The third part of the book provides new data on the ecology and behavior of the Cheirogaleidae. There are new data on the morphology, behavior, ranging patterns, and habitat of the newly named and little known small species *Mirza zaza* (Margono *et al.*, Chapter 12). There is also a study of the mouse lemur, *Microcebus griseorufus*, that lives in the western reserve of Beza Mahafaly (Rasoazanabary and Godfrey, Chapter 13). This species lives in many habitats from xerophytic environments to more mesic forests, with little overlap in tree species composition. The mouse lemurs living in different forests are different in adult body mass, aspects of their cheiridial (foot and hand) morphology, and sleeping and feeding behavior. Although typically living in xerophytic forest habitats, they appear to do "well" in more mesic forests. The mouse lemurs have distinct and parallel seasonal shifts in both feeding and sleeping behavior. During the dry season, mouse lemurs feed more on gums and prefer tree holes for sleeping; during the rainy season, they rely more on insects and fruits and prefer open nests.

There is also a study of intra- and interspecific isotopic variation of the mouse lemurs (*Microcebus murinus* and *M. ravelobensis*) of northwestern Madagascar (Heck *et al.*, Chapter 14), showing that seasonal environmental changes influence the feeding ecology of these animals. Stable isotope ratios of carbon and nitrogen (δ13C and δ15N) offer a promising complementary methodological tool for diet. Isotope values for plants were influenced by the canopy effect, plant species, and study site. These factors influenced body mass, study site choice, and, to some extent, sex and seasonality. Seasonal changes can be related to dietary shift from a more omnivorous diet in the wet season to a more herbivorous diet in the dry season. Some degree of dietary plasticity may enable these species to avoid interspecific competition in times of food scarcity.

Finally, there is also a study of patterns of resource use in two sympatric mouse lemur species (the gray mouse lemur, *Microcebus murinus*, and the golden-brown mouse lemur, *M. ravelobensis*; Thorén *et al.*, Chapter 15). The lemurs live in the forest reserve of Ankarafantsika National Park, a dry deciduous forest located in northwestern Madagascar. The authors studied the food resources used by the *Microcebus* and found that: (1) food resources were typically shared by multiple individuals; (2) at least 5 of 14 foods were used by both species; (3) foods were used in succession (i.e., only one individual at a resource at a time); and (4) the majority of social encounters resulted in conflicts with decided outcomes, but aggressive behaviors were only observed in the minority of encounters. Basically, as in other primates (Sussman and Garber, 2011), the two species avoid competing over shared food resources by partitioning resources on a temporal scale. Studies like this help us understand the adaptive flexibility and possible environmental constraints of these animals.

Recent studies indicate that lepilemurids and cheirogaleids shared an ancestor in the late Eocene. It has been shown that the small size in cheirogaleids involved at least three episodes of parallel phyletic dwarfing, with the *Microcebus* lineage diverging in the late Miocene. These studies carry major implications for the evolutionary interpretations of these animals. Génin and Masters (Chapter 16) review the information and reinterpret it within the new phylogenetic framework for *M. murinus*. The suite of adaptations to environmental hypervariability and habitat fragmentation in *Microcebus*, such as the pleiotropic body size reduction by means of truncated ontogeny (progenesis), are among these changes.

The different species of *Cheirogaleus* are very flexible in the *modus operandi* and timing of hibernation. Even within species differences are considerable, depending on habitat and climatic parameters (Dausmann and Blanco, Chapter 17). In the dry forest, species hibernate in tree hollows with various insulation properties. In the rainforest, species retreat underground for hibernation. There are extensive consequences on hibernation parameters and patterns. Underground hibernacula and hibernation in well-insulated hollows in large trees cause energy expenditure and body temperature (T_b) bouts that are almost constant and spontaneous arousals can occur regularly. In thinner trees, insulation capacities are decreased, and energy expenditure and T_b fluctuate with the ambient temperatures (T_a) to various degrees. The colder the habitat, the greater the saving of energy through hibernation. Hibernation was originally adapted to, and runs best at, mostly constant ambient temperatures. It seems conceivable that hibernation in tree hollows could have been the original *modus operandi* in ancestral *Cheirogaleus*. This implies that hypometabolism in some species is truly independent of ambient temperatures, and fluctuating temperatures might be advantageous, allowing for extended, continuous bouts of hypometabolism. This would avoid interruptions by active arousals.

Part IV of this book focuses on the sensory ecology, communication, and cognition of the Cheirogaleidae. Valenta and Lehman (Chapter 18) show that the diminutive size, activity patterns, and distinct sensory ecology of the mouse lemur represent a unique frugivorous guild and make this animal an important seed disperser for numerous species of plants. Mouse lemurs rely heavily on olfaction and choose fruits based on the presence of certain micronutrients. New studies suggest that solitary foraging and crypsis are effective predator avoidance strategies for many nocturnal primates (Fichtel, Chapter 19). However, they also evolved specialized antipredator behaviors that are well adapted to the different hunting styles of their predators. Just as with other primates (Hart, 2000), the Cheirogaleidae employ specific tactics to reduce the risk of encounters with predators, such as predator-sensitive foraging, choosing safe sleeping sites, and vigilance. Tactics employed during or after encountering predators, such as alarm calling, fleeing, and confronting or mobbing predators, have also been described in some cheirogaleids. Picq (Chapter 20) summarizes the numerous behavioral tasks that have been specifically designed for mouse lemurs (*M. murinus*) in order to assess cognitive aging. These animals are good at numerous behavioral tasks: they easily master classical laboratory tests on cognition, possessing cognitive capacities. In fact, they far exceed common expectations for the species. They often age in a way that parallels aging patterns in humans and, thus, the neurobiological mechanisms underlying cognitive decline could be similar. For example, procedural memory is spared, executive function is especially vulnerable to the aging process, and declarative-like memory is only affected in a small set of the aged population. In time, these animals could provide a unique opportunity for understanding the mechanisms that drive cognitive impairment in humans.

Studying the acoustic divergence in communication of mouse lemurs, Zimmermann (Chapter 21) finds that calls used in mating and group reunion diverge most within and between populations and species, whereas calls used in the alarm and disturbance contexts show no species-specific variation. This study shows that for speciation and evolution a mixture of neutral and adaptive responses drives acoustic divergence in these species. Kessler *et al.* (Chapter 22) studied kin selection in mouse lemurs as a driving factor in the evolution of primate social complexity. They find that recent field studies on sleeping group associations, infant rearing behavior, and population genetics show that the key to the success of the mouse lemur radiation is likely to have been their flexibility. It appears that close maternal kin networks have been the foundation from which more complex social systems could evolve.

In the final section of the book, the subject of the conservation biology of the cheirogaleids is explored. Kamilar *et al.* (Chapter 23) studied the species diversity of six mouse lemur species. They found that climate, especially rainfall and temperature, plays a significant role in *Microcebus* distribution and in understanding their current biogeography. They also point out the possible future shifts and reduction in distribution related to current climate change. Lehman (Chapter 24) examined the edge effect on tree dendrometrics data (tree height, diameter at breast height, and canopy size), abiotic data (ambient temperature, percent humidity, wind speed, and light intensity), and mouse lemur densities in western dry forests. Edge effects are the changes in community structure that can occur between different populations living at the boundaries of two distinct habitats. He found that, contrary to previous studies, *M. murinus* had higher density estimates in edge habitats and *M. ravelobensis* had higher densities in interior habitats. He notes that the edge effect on mouse lemurs may differ markedly in eastern humid forests and western dry forests in Madagascar.

Steffens and Lehman (Chapter 25) studied the effects of plant dendrometrics, habitat diversity, and anthropogenic disturbance on two sympatric species of *Microcebus*. They found a significant, positive correlation between density and abundance for both primate species. Variations in the density of *M. murinus* were due to plant basal area, stem density, and the distance from continuous forest. Variations in *M. ravelobensis* density resulted from basal area, mean tree height, total disturbance, and the distance from continuous forest. The results indicate that the link between plant dendrometrics and *M. murinus* abundance and density may reflect sleeping site requirements and dietary preferences, whereas edge effects may explain abundance and density in *M. ravelobensis*. An understanding of animal density and abundance, in a heterogeneous landscape, is critical to understanding the dynamics of population biogeography. Out of 25 species of mouse lemur, one species, *Microcebus murinus*, occurs throughout large parts of southern to northwestern Madagascar. Radespiel (Chapter 26) shows that this species has a higher seasonal plasticity in feeding habits and, in northwestern Madagascar, they have a relatively higher ability to move about freely and migrate in areas of habitat disturbance or discontinuity. This would enable *M. murinus* to expand into new and unpredictable environments such as temporarily available and highly seasonal highland habitats.

Lehman *et al.* (Chapter 27) show that recent conservation assessments indicate high extinction risks for many cheirogaleids. Of the 32 species of cheirogaleids whose conservation status was assessed by the authors, 6 were assumed to be among the least threatened species, 6 were vulnerable, 16 were endangered, and 4 were assessed as critically endangered. Anthropogenic factors (for example, various forms of farming) were related to the problem of conservation of species with relatively small geographic ranges. Such things as additional spatial data on habitat breadth, abundance, and responses to varying kinds and intensities of anthropogenic disturbance are needed on all species. There were no major underlying biotic or abiotic correlates related to species living in or out of the currently protected animal area system in Madagascar. The authors recommend that further studies must be related to determining overall species richness, standardization of research methods, and how populations of each species respond to landscape patterns of forest fragmentation, forest loss, and edge effects.

This book brings the biology, behavior, and conservation biogeography of the Cheirogaleidae up to the standards of other research in primatology. Research on the evolution, taxonomy, and genetics; the methods used for studying captive and wild primates and their relationship to human biology and medicine; the natural behavior and ecology of the animals; their sensory ecology, communication system and cognition; and their conservation biology are all active areas of research in primate ecology and evolution. *The Dwarf and Mouse Lemurs of Madagascar: Biology, Behavior and Conservation Biogeography of the Cheirogaleidae* has added a great deal to our knowledge of these animals and of their primate relatives. The editors, Shawn M. Lehman, Ute Radespiel, and Elke Zimmermann, have done an exceptional job of collecting these papers.

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