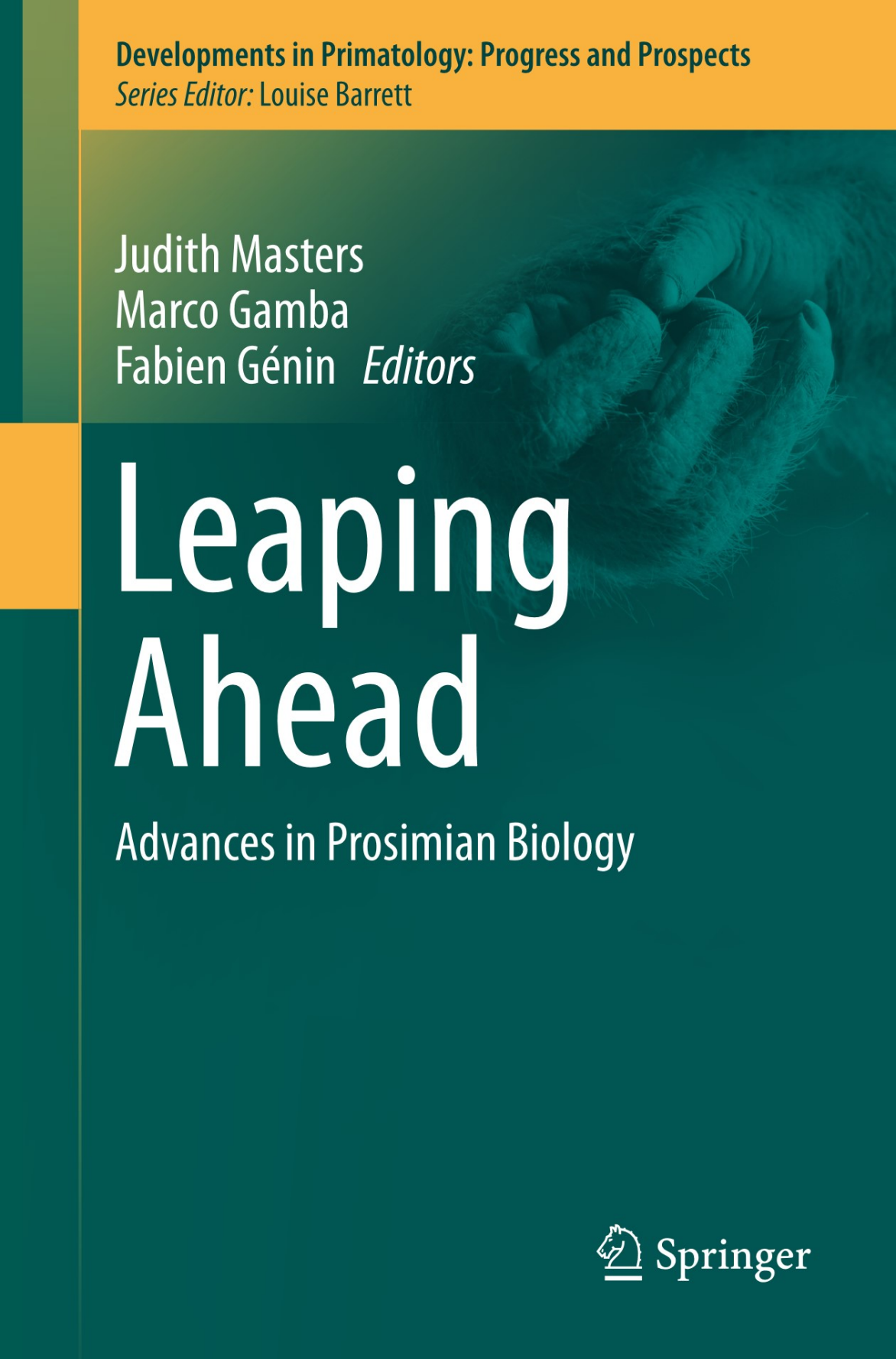
Developments in Primatology: Progress and Prospects
Series Editor: Louise Barrett



Judith Masters
Marco Gamba
Fabien Génin *Editors*

Leaping Ahead

Advances in Prosimian Biology

Springer

Developments in Primatology: Progress and Prospects

Series Editors: Louise Barrett and Russell Tuttle

For further volumes:
http://www.springer.com/series/5852

Judith Masters • Marco Gamba • Fabien Génin
Editors

Leaping Ahead

Advances in Prosimian Biology

Springer

Editors
Judith Masters
Department of Zoology
University of Fort Hare
Alice, South Africa

Fabien Génin
Department of Zoology
University of Fort Hare
Alice, South Africa

Marco Gamba
Dipartimento di Biologia Animale
e dell'Uomo
Università degli Studi di Torino
Torino, Italy

ISBN 978-1-4614-4510-4 ISBN 978-1-4614-4511-1 (eBook)
DOI 10.1007/978-1-4614-4511-1
Springer New York Heidelberg Dordrecht London

Library of Congress Control Number: 2012948133

Printed on acid-free paper

Springer is part of Springer Science+Business Media (www.springer.com)

Frontispiece

Participants in the Prosimians 2007 International Congress,
Ithala, KwaZulu-Natal, South Africa, 15–19 July 2007

We dedicate this volume to our colleagues Daniel Montagnon and Bjoern Siemers, whose premature deaths have left us and the field of prosimian biology much the poorer.

Foreword

Leaping Ahead takes its place in a series of collective and synthetic volumes updating current knowledge on prosimians. Initiated by Robert Martin, Gerald Doyle, and Alan Walker in 1974, and continued by Gerald Doyle and Robert Martin 5 years later, these volumes have become a recurrent necessity for the prosimian research community. It is no longer necessary to justify meetings or publications dedicated to prosimian studies: the gathering of papers synthesizing the latest contributions to the field provides researchers with an irreplaceable bibliographic tool which, complemented by publications in specialized international journals, is essential to all scientific disciplines.

In 1979, Gerald Doyle and Robert Martin questioned the practice of restricting these meetings to a fraction of primatologists, with the risk of seeing "prosimianology" become an autonomous discipline. This risk has not been realized, since prosimian researchers also frequent primatology meetings; but we can question the dichotomy between studies of so-called higher and prosimian primates. There are probably many reasons for this distinction. One of them is methodological: studying the biology and the sociology of nocturnal animals requires very different methods from those designed for analyzing and decoding the behavior of gregarious, diurnal animals. But other, more, profound reasons may also play a role. When Linnaeus proposed the term "Primates" in 1758 for a group formerly known as "Simia" or "Anthropoidea," he was implicitly placing them before the others, which seemed sensible at the time. A few decades later, in the same spirit, and basing his reasoning on the "degeneration" of the hand, Blainville created the "Secundates," "Tertiates," and "Quaternates" for the other mammalian orders. This nomenclature disappeared rapidly, but Linnaeus' Primates survived. This term could as well have been replaced by "Quadrumanes," created by Cuvier, but the notion of Primates is so deeply entrenched that no one would dare question it, despite the birth of Darwinism and modern theories which swept away the idea of linearity of evolution. This persistence is not fortuitous, and many people, including scientists, still regard primates as "primary" with an innate hierarchy of "higher" primates and prosimians.

There is also the fact that many primatological studies are undertaken to improve our understanding of the evolutionary and paleontological history of humans: research on so-called higher primates tends to focus on anatomical and behavioral characteristics associated with hominization, while prosimian research is often viewed as revealing ancient primate characteristics. A comprehensive study of primate evolution requires a synthesis of elements from the anthropological and zoological approaches to primatology, and *Leaping Ahead* reflects such a synthesis.

The book reveals the preoccupations of our time, and several chapters discuss the loss of biodiversity and habitat destruction, consequences of climate change, and overexploitation of forest ecosystems. The fields of phylogeny and systematics are also included, and the multiplicity of newly created taxa urges more in-depth research into prosimian diversity. Particular attention has been paid to species previously ignored because they are rare or localized, or because they were previously confused with other taxa. The field of paleontology is also advancing, allowing a more global vision of prosimians. Ecological studies produce new data on interspecific competition, dietary strategies, habitat use, social structures, ecophysiology, and much more. New technologies have been applied to several fields, while more classical methods have revealed unanticipated cerebral capacities in mouse lemurs. The study of vocalizations is undergoing renewal, providing behavioral data to support or challenge genetic taxonomic assignments. This broad diversity of approaches shows that prosimians still attract much interest among students and researchers and that their study allows scientists to ask essential questions, to which there are often unique answers.

Clapiers, France Pierre Charles-Dominique

Editors' Preface

The first international conference dedicated to prosimian primates was held in April, 1972 at the Institute of Archaeology of the University of London and was organized by Bob Martin, Alan Walker, and Gerry Doyle. The resultant publication of the conference proceedings (*Prosimian Biology*, Duckworth, London, 1974) became the "Bible" for prosimian primatologists working in the last decades of the twentieth century.

In June 1993, a conference dedicated to the nocturnal prosimians was held at Duke University, in Durham, NC. Kay Izard, Lon Alterman, and Gerry Doyle once again issued a volume of conference proceedings, entitled *Creatures of the Dark: The Nocturnal Prosimians* (Plenum Press, New York, 1995), that became a milestone in the development of prosimian studies.

In September 1995, the Duke meeting was followed by the International Conference on the Biology and Conservation of Prosimians, held at Chester Zoo in the UK. The proceedings were edited by Caroline Harcourt, Robin Crompton, and Anna Feistner and published as a supplement to *Folia Primatologica* in 1998. This volume served as a further focal point for prosimian biologists to reflect on the growth of their field, and it became as indispensable as the previous proceedings volumes had been.

A decade elapsed before a fourth conference was convened, and work on prosimians—particularly on the Malagasy lemuriforms—had blossomed in the interim. The Prosimians 2007 International Congress took place in mid-July, 2007, in Ithala Game Reserve, South Africa. The final program was comprised of 77 spoken presentations spread over four-and-a-half days and 26 posters. One hundred participants attended the conference, representing research and conservation institutions in 12 countries. Of particular note was the strong representation by participants from developing countries, who contributed one-third of the presentations. Prosimian

primates are found in the tropical and subtropical forests and woodlands of Africa, South-east Asia, and Madagascar, and the majority of countries in which they occur qualify as developing countries. For the conference to have a meaningful impact on the conservation and general understanding of prosimians, it was clear that a substantial percentage of the participants should be drawn from these habitat countries. Funds to make this possible were generously supplied by Conservation International, the University of Fort Hare, the Wenner-Gren Foundation, and the South African Department of Science and Technology. We are also indebted to Dr Mikhail Mostovski, who volunteered his skills in Web site design and management, and Patricia Birkett, who drew the logo.

This collected volume, inspired by the Ithala conference proceedings, is not simply an account of what transpired in July 2007. It presents a summary of the state and scope of prosimian research as we move into the second decade of the twenty-first century. The diverse chapters have been grouped into seven sections: systematics and evolution; general ecology; behavioral ecology; dietary ecology; physiological ecology; sensory ecology, communication and cognition; and prosimian conservation. Each chapter was thoroughly reviewed, and we acknowledge the following people who assisted with the review process:

Michelle Becker, Giovanna Bonodomo, Stefan Brudzynski, Robin Crompton, Frank Cuozzo, Massimiliano DelPero, Maarten de Wit, John Fleagle, Cristina Giacoma, Laurie Godfrey, Steven Goodman, Colin Groves, Sharon Gursky, Jean-Jacques Jaeger, David Lambert, Peter Lucas, Wolfgang Maier, Melchiorre Masali, Kate Meares, Nomakwezi Mzilikazi, Mike Perrin, Luca Pozzi, Michele Rasmussen, Kaye Reed, Marina Scheumann, Alain Schilling, Daniele Seglie, Myron Shekelle, Björn Siemers, Bruno Simmen, Viviana Sorrentino, Matt Sponheimer, Robert Sussman, Eleanor Weston, and Kirsten Wimberger. Unless otherwise stated, French translations of the summaries were provided by Fabien Génin, with help from Sébastien Couette. Gail Frank and David Masters performed many tasks as editorial assistants.

Alice, South Africa — Judith C. Masters
Torino, Italy — Marco Gamba
Alice, South Africa — Fabien G.S. Genin

Contents

Part VII Conservation of Prosimians

Contributors

Laura J. Alport Department of Anthropology, University of Texas at Austin, Austin, TX, USA

Haingoson Andriamialison Parc Botanique et Zoologique Tsimbazaza, Antananarivo, Madagascar

Tony B.D. Andrianaivo Département de Biologie Animale, Université d'Antananarivo, Antananarivo, Madagascar

Vonjy Nirina Andrianome Département des Eaux et Forêts, Ecole Supérieure des Sciences Agronomiques, Université d'Antananarivo, Antananarivo, Madagascar

Summer J. Arrigo-Nelson Department of Biological and Environmental Sciences, California University of Pennsylvania, California, PA, USA

Fabienne Aujard Mécanismes Adaptatifs et Evolution, UMR CNRS/MNHN 7179, Brunoy, France

Simon K. Bearder Nocturnal Primate Research Group, School of Social Sciences and Law, Oxford Brookes University, Oxford, UK

Michelle L. Becker Laboratory of Comparative Ethology, Eunice Kennedy Shriver National Institute of Child Health and Human Development NICHD/NIH, Poolesville, MD, USA

Lilia Bernede Applied Road Ecology Group, Environmental Futures Centre and Griffith School of Environment, Griffith University, Nathan, QLD, Australia

Karla Biebouw Nocturnal Primate Research Group, School of Social Sciences and Law, Oxford Brookes University, Oxford, UK

Kathryn Blumenfeld-Jones School of Human Evolution and Social Change, Arizona State University, Tempe, AZ, USA

David A. Burney National Tropical Botanical Garden, Kalaheo, HI, USA

Anne M. Burrows Department of Physical Therapy, Duquesne University, Pittsburgh, PA, USA

Department of Anthropology, University of Pittsburgh, Pittsburgh, PA, USA

Kierstin K. Catlett Institute of Human Origins, School of Human Evolution and Social Change, Arizona State University, Tempe, AZ, USA

Rebecca L. Collins Nocturnal Primate Research Group, School of Social Sciences and Law, Oxford Brookes University, Oxford, UK

Brooke E. Crowley Department of Geology, University of Cincinnati, Cincinnati, OH, USA

Department of Anthropology, University of Cincinnati, Cincinnati, OH, USA

Frank P. Cuozzo Department of Anthropology, University of North Dakota, Grand Forks, ND, USA

Deborah J. Curtis School of Human and Life Sciences, Roehampton University, London, UK

Nocturnal Primate Research Group, School of Social Sciences and Law, Oxford Brookes University, Oxford, UK

Melanie Dammhahn Abteilung Verhaltensökologie & Soziobiologie, Deutsches Primatenzentrum, Göttingen, Germany

Kathrin H. Dausmann Department of Ecology and Conservation, University of Hamburg, Hamburg, Germany

Robert Davies Nocturnal Primate Research Group, School of Social Sciences and Law, Oxford Brookes University, Oxford, UK

Catherine D. Depeine Laboratory of Comparative Ethology, Eunice Kennedy Shriver National Institute of Child Health and Human Development, Poolesville, MD, USA

Luke Dollar Department of Biology, Pfeiffer University, Misenheimer, NC, USA

Giuseppe Donati Nocturnal Primate Research Group, School of Social Sciences and Law, Oxford Brookes University, Oxford, UK

Claudia Fichtel Behavioral Ecology and Sociobiology Unit, German Primate Center, CRC "Evolution of Social Behavior," University of Göttingen, Göttingen, Germany

Marco Gamba Dipartimento di Biologia Animale e dell'Uomo, Università degli Studi di Torino, Torino, Italy

Jörg U. Ganzhorn Animal Ecology and Conservation, Hamburg University, Hamburg, Germany

Fabien Génin Department of Zoology and Entomology, University of Fort Hare, Private Bag, Alice, South Africa

Cristina Giacoma Dipartimento di Biologia Animale e dell'Uomo, Università degli Studi di Torino, Torino, Italy

Mark Gligor Institut für Anthropologie, Johannes-Gutenberg-Universität Mainz, Mainz, Germany

Laurie R. Godfrey Department of Anthropology, University of Massachusetts, Amherst, MA, USA

Asoka Gunawardene Department of Animal Science, Faculty of Agriculture, University of Ruhuna, Mapalana, Kamburupitiya, Sri Lanka

Sharon L. Gursky Department of Anthropology, Texas A&M University, College Station, TX, USA

Andreas Hapke Animal Ecology and Conservation, Hamburg University, Hamburg, Germany

Institut für Anthropologie, Johannes-Gutenberg-Universität Mainz, Mainz, Germany

Christopher P. Heesy Department of Anatomy, Arizona College of Osteopathic Medicine, Midwestern University, Glendale, AZ, USA

Roland Hilgartner Behavioral Ecology and Sociobiology Unit, German Primate Center, University of Göttingen, Göttingen, Germany

Department of Experimental Ecology, University of Ulm, Ulm, Germany

Christopher M. Holmes Wildlife Conservation Society, Soavimbahoaka, 101 Antananarivo, Madagascar

Shinichiro Ichino Unit of Behavioral Ecology and Sociobiology, German primate Center, Göttingen, Germany

Genome Diversity Section, Primate Research Institute, Kyoto University, Kanrin, Inuyama-city, Aichi, Japan

Mohammed Irfan-Ullah Ecoinformatics Centre, Ashoka Trust for Research in Ecology and the Environment (ATREE), Bengaluru, Karnataka, India

RMSI Pvt. Ltd, Noida, Uttar Pradesh, India

Mitchell T. Irwin Department of Anthropology, Northern Illinois University, DeKalb, IL, USA

Sarah M. Jaffe Nocturnal Primate Research Group, School of Social Sciences and Law, Oxford Brookes University, Oxford, UK

Steig E. Johnson Department of Anthropology, University of Calgary, Calgary, AB, Canada

Alison Jolly Department of Biology and Environmental Science, University of Sussex, School of Life Sciences, Falmer, Brighton, United Kingdom

William L. Jungers Department of Anatomical Sciences, School of Medicine, Stony Brook University, Health Sciences Drive, Stony Brook, NY, USA

Peter M. Kappeler Abteilung Verhaltensökologie & Soziobiologie, Deutsches Primatenzentrum, Göttingen, Germany

Abteilung Soziobiologie/Anthropologie, Universität Göttingen, Göttingen, Germany

Stephen J. King Department of Anthropology, University of Massachusetts, Amherst, MA, USA

Naoki Koyama The Center for African Area Studies, Kyoto University, Sakyo-ku, Kyoto, Japan

Shanthala Kumar Coimbatore, Tamil Nadu, India

Honnavalli N. Kumara Sálim Ali Centre for Ornithology and Natural History, Coimbatore, Tamil Nadu, India

National Institute of Advanced Studies, Bengaluru, Karnataka, India

Petra Lahann Conservation Department, ZSL London ZOO, Outer Circle, Regent's Park, London, UK

Judith Masters Department of Zoology and Entomology, University of Fort Hare, Alice, South Africa

Jules Medard Parc Botanique et Zoologique Tsimbazaza, Rue Fernand Kasanga, Tsimbazaza, Antananarivo, Madagascar

Anne S. Mertl-Millhollen Department of Anthropology, University of Oregon, Eugene, OR, USA

Daniel Montagnon Faculté de Médecine, Unité EA3428, Espèce Humaine et Primates: Variabilité et Évolution, Strasbourg, France

Magdalena N. Muchlinski Department of Anatomy and Neurobiology, College of Medicine, University of Kentucky, Lexington, KY, USA

Kathleen M. Muldoon Department of Anatomy, The Geisel School of Medicine at Dartmouth, Hanover, NH, USA

Department of Anthropology, Dartmouth College, Hanover, NH, USA

K. Anne-Isola Nekaris Nocturnal Primate Research Group, School of Social Sciences and Law, Oxford Brookes University, Oxford, UK

John D. Newman Laboratory of Comparative Ethology, Eunice Kennedy Shriver National Institute of Child Health and Human Development, National Institutes of Health, Poolesville, MD, USA

Luca Pozzi Department of Anthropology, Center for the Study of Human Origins, New York University, New York, NY, USA

Sahoby Marin Raharison École Normale Supérieur, Université d'Antananarivo, Antananarivo, Madagascar

Brigitte Raharivololona Animal Ecology and Conservation, Hamburg University, Hamburg, Germany

Département de Paléontologie et Anthropologie Biologique, Université d'Antananarivo, Antananarivo, Madagascar

Gilbert Rakotoarisoa Parc Botanique et Zoologique Tsimbazaza, Rue Fernand Kasanga, Tsimbazaza, Antananarivo, Madagascar

Jean-Baptiste Ramanamanjato QMM, Tolagnaro, Madagascar

Hajarimanitra Rambeloarivony Ecole Nomale Supérieure, Université d'Antananarivo, Antananarivo, Madagascar

Department of Zoology and Entomology, University of Fort Hare, Alice, South Africa

Marissa A. Ramsier Department of Anthropology, Humboldt State University, Arcata, CA, USA

Guy Hermas Randriatahina Département de Paléontologie et d'Anthropologie Biologique, Université d'Antananarivo, Antananarivo, Madagascar

Association Européene pour l 'Etude et la Conservation des Lemuriens (AEECL), Antananarivo, Madagascar

Hantanirina Rasamimanana Ecole Nomale Supérieure, Université d'Antananarivo, Antananarivo, Madagascar

Jonah H. Ratsimbazafy Durrell Wildlife Conservation Trust, Antananarivo, Madagascar

Emilienne Razafimahatratra Département de Biologie Animale, Université d'Antananarivo, Antananarivo, Madagascar

Josia Razafindramanana Nocturnal Primate Research Group, Department of Anthropology, School of Social Science and Law, Oxford Brookes University, Oxford, UK

Voahirana Razoliharisoa École Normale Supérieure, University of Antananarivo, Antananarivo, Madagascar

Ernest Refaly QMM, Tolagnaro, Madagascar

Jean-Jacques Roeder DEPE, UMR 7178, Strasbourg, France

Karen E. Samonds Department of Biological Sciences, Northern Illinois University, DeKalb, IL, USA

Michelle L. Sauther Department of Anthropology, University of Colorado, Boulder, CO, USA

Julia Schad Animal Ecology and Conservation, Hamburg University, Hamburg, Germany

Leibniz-Institute for Zoo and Wildlife Research, Berlin, Germany

Alain Schilling Achères la forêt, France

Jutta Schmid Department Experimental Ecology, Ulm, Germany

Gary T. Schwartz Institute of Human Origins, School of Human Evolution and Social Change, Arizona State University, Tempe, AZ, USA

Jeffrey H. Schwartz Departments of Anthropology and History and Philosophy of Science, University of Pittsburgh, Pittsburgh, PA, USA

Björn M. Siemers Sensory Ecology Group, Max-Planck Institute for Ornithology, Seewiesen, Germany

Mewa Singh Bio-Psychology Laboratory, Department of Psychology, University of Mysore, Mysore, Karnataka, India

Timothy D. Smith School of Physical Therapy, Slippery Rock University, Slippery Rock, PA, USA

Department of Anthropology, University of Pittsburgh, Pittsburgh, PA, USA

Takayo Soma The Center for African Area Studies, Kyoto University, Sakyo-ku, Kyoto, Japan

Simone Sommer Animal Ecology and Conservation, Hamburg University, Hamburg, Germany

Leibniz-Institute for Zoo and Wildlife Research, Berlin, Germany

Viviana Sorrentino Dipartimento di Biologia Animale e dell'Uomo, Università degli Studi di Torino, Torino, Italy

Nancy J. Stevens Department of Biomedical Sciences, Center for Ecology and Evolutionary Studies, Heritage College of Osteopathic Medicine, Ohio University, Athens, OH, USA

Ulrika Streicher Endangered Primate Rescue Center, Ninh Binh Province, Vietnam

Laurent Tarnaud Unité scientifique 104 du Muséum "Eco-anthropologie et ethnobiologie," Muséum National d'Histoire Naturelle, Paris Cedex 05, France

Ian Tattersall Division of Anthropology, American Museum of Natural History, New York, NY, USA

Stacey R. Tecot School of Anthropology, University of Arizona, Tucson, AZ, USA

Jérémy Terrien Mécanismes Adaptatifs et Evolution, UMR CNRS/MNHN 7179, Brunoy, France

Donald Raymond Tsaramanana École Normale Supérieur, Université d'Antananarivo, Antananarivo, Madagascar

Natalie Vasey Department of Anthropology, Portland State University, Portland, OR, USA

N. Sylviane M. Volampeno School of Biological and Conservation Sciences, University of KwaZulu-Natal, Scottsville, South Africa

Community Centred Conservation, Antananarivo, Madagascar

Angelina Wilson Nocturnal Primate Research Group, School of Social Sciences and Law, Oxford Brookes University, Oxford, UK

Patrica C. Wright Department of Anthropology, Stony Brook University, Stony Brook, NY, USA

Elke Zimmermann Institute of Zoology, Veterinary University, Hannover, Germany

Part I
Systematics and Evolution

Chapter 1
What's in a Name? Higher Level Taxonomy of the Prosimian Primates

Judith Masters, Marco Gamba, and Fabien Génin

Abstract The systematics and classification of the strepsirhine and tarsioid primates are contentious subjects. In compiling this volume, we have adopted a taxonomy that best fits our understanding of the evolution of these groups, and the spirit and intention inherent in systematic theory. In this chapter, we clarify and explain our choices regarding the title of this book and higher level taxonomic assignments.

Resume La systématique et la classification des Strepsirhines et des Tarsiers sont des sujets contentieux. En compilant ce volume, nous avons adopté une taxonomie qui suit de prêt notre compréhension de l'évolution de ces groupes, ainsi que l'esprit et la finalité de la théorie systématique. Dans ce chapitre, nous clarifions et expliquons ces choix, dans le contexte du titre donné à ce livre, et celui des niveaux taxonomiques plus élevés.

Introduction

We, the editors, unanimously support a cladistic approach to systematics, as we believe this is the best method currently available for understanding the complex and largely cryptic history of the subjects of this volume. Our use of the colloquial

J. Masters (✉) • F. Génin
Department of Zoology and Entomology, University of Fort Hare,
Private Bag X1314, Alice 5700, South Africa
e-mail: jdthmasters@gmail.com; FGenin@ufh.ac.za; fabien.genin@free.fr

M. Gamba
Dipartimento di Biologia Animale e dell'Uomo, Università degli Studi di Torino,
Via Accademia Albertina, 13, 10124 Torino, Italy
e-mail: marco.gamba@unito.it

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_1,

term "prosimians" in the title should, therefore, not be viewed as a reflection of closet gradistic tendencies. That being said, tarsiers and nocturnal strepsirhines share many aspects of their behavioral ecology, and researchers in the two fields have much to offer one another. Our volume includes two chapters on tarsiers.

Some of biology's most acrimonious battles have been fought over preferred methods of assessing evolutionary relatedness, but on one point systematists are unanimous: classifications should reflect phylogenetic relationships as closely as possible, or, at the very least, should not conflict with them. Phylogenetic relationships between strepsirhine taxa, both extant and fossil, have been the focus of much recent research, but taxonomic adjustments, much less so. This is problematic since as Simpson (1945, p. 3) pointed out "…the rapid advance of taxonomy makes it both inevitable and desirable that it should quickly become outmoded." We have, therefore, attempted to align the taxonomy employed in this book with current inferences regarding evolutionary relationships. In clarifying our taxonomic decisions, however, we have encountered several problems.

First, fossils are not generally included in molecular phylogenies, although extinct sister-groups are integral in assessments of higher taxonomic groupings. Much new fossil and subfossil evidence has come to light since the older taxonomies were devised, and needs to be accorded its appropriate influence.

Second, the use of several higher taxonomic names (e.g., Lemuroidea, Lemuriformes) is inconsistent and often idiosyncratic. For instance, Szalay and Delson's (1979) infraorder Lemuriformes comprises all living and recently extinct strepsirhines, whereas that of Martin (1990) includes extant and subfossil Malagasy strepsirhines plus Tertiary adapiforms, but not Afro-Asian lorisoids, and that of most molecular phylogeneticists, only Malagasy strepsirhines (Yoder et al. 1996; Roos et al. 2004; Horvath et al. 2008).

Third, despite the confidence placed by various authors in their chosen phylogenies (e.g., Roos et al. 2004; Horvath et al. 2008), consensus regarding relationships among some extant Malagasy families remains elusive.

Finally, although most evolutionary primatologists would claim to be cladistic in their thinking, they do not always follow cladistic principles; for example, "degree of divergence" is not a basis for taxonomic designation in the cladistic approach, although it was an important part of evolutionary systematics and classification (Simpson 1961; Mayr 1969). When authors implement this criterion, they are switching philosophical frameworks.

Subordinal Designation

Linnaeus (1758) coined the genus *Lemur* to include *L. catta*, *L. tardigradus* [actually a specimen of *Nycticebus* (Geoffroy Saint-Hilaire 1796)], and *L. volans* [consigned to *Cynocephalus* by Boddaert in 1768]. The first concentrated study of lemur diversity was undertaken by another of biology's great visionaries, Etienne Geoffroy Saint-Hilaire (1772–1844). Geoffroy (1796) focused on this group because they presented a perfect opportunity to test the idea that drove his scientific career:

"It seems that nature has restricted herself within certain limits, and has formed all living beings on only one unique plan, essentially the same in its principle, but which she has varied in a 1,000 ways in all its accessory parts." He was a staunch supporter of the nonfixity of species and pioneered the practice of identifying homologous characters in different taxa as well as laws of growth and allometry. Lemurs played a starring role in these insights.

In 1812, Geoffroy erected the family Strepsirrhini to comprise the genera *Indris*, *Lemur*, *Loris*, *Nycticebus*, *Galago*, and *Tarsius* (Geoffroy Saint-Hilaire 1812). In the preceding year, however, Johann Karl Wilhelm Illiger (1775–1813), the director of the zoological museum in Berlin, had erected the family Prosimii to house the lemurs, in his attempt to clarify Linnaeus' rather eccentric system. Illiger's (1811) arrangement was "professedly artificial" (Gray 1825): Prosimii contained the genera *Lichanotus* (for *Avahi* and *Indri*), *Lemur* and *Stenops* (for *Loris*), while the galagos were placed under the new generic epithet *Otolicnus* in the family Macrotarsi together with the tarsiers. The aye-aye had its own family, Leptodactyla.

Not only was Prosimii never intended to denote a natural group, the term has some unfortunate associations. Haeckel (1883) adopted a modified, more inclusive version of the taxon (Prosimiae) but argued for their exclusion from the order Primates on the grounds that they formed a ragbag collection of primitive groups whose closest affinities were to other mammal taxa. He saw aye-ayes as *in statu nascendi* to rodents, colugos as transitional to bats, macrotarsi (tarsiers and galagos) as having given rise to insectivores, and the short-footed forms (lemurs, avahis, and lorises) as forming the link between ancestral mammals and apes. Asian lorises he placed very close to humans. Prosimians, in their turn, had evolved from "Handed or Ape-footed Marsupials."

When Simpson reverted to Prosimii in his 1945 classification, he did not hold them in quite such a primitive light—he kept them within Primates—but he did see them as a similar ragbag group lacking any defining character, other than that they were nonanthropoid primates. Van Valen (1969) continued in this tradition: "The suborder Prosimiae is meant to include all primates not sufficiently evolved to warrant a separate suborder." Simons (1972, 1974) was appalled by the idea of demanding diagnostic traits for prosimians, as grouping the tarsiers and anthropoids together would compromise the diagnostic traits derived for anthropoids.

Prosimii has therefore always, and explicitly, been a wastebasket taxon. Simpson defended this as a good thing, a remarkable *volte face* in light of his systematic philosophy of "evolutionary classification." The contributing authors to this book have different priorities; all are committed to unraveling the history, biology, and behavior of the tarsioid and tooth-combed primates, and the basic requirement for such an investigation is a systematic scheme that reflects evolutionary history.

In 1918, Pocock reviewed the characters apparently uniting "prosimians" and concluded that tarsiers did not group with the "lemurs" (*sensu lato*) at all. His expression of this new set of relationships was to resurrect Geoffroy's Strepsirhini (this time with one r—a choice in line with classical etymology; I. Tattersall personal communication) and to erect Haplorhini to house "*Tarsius* and the Pithecoidea." Cladistic analyses (e.g., Kay et al. 1997) have generally supported the interpretation that the primary divergence between crown group primates took place in the late

Cretaceous/early Paleocene and yielded groups congruent with Strepsirhini and Haplorhini. Paleontologists familiar with the fossil group Adapiformes attest that this extinct group is the sister-taxon to the living tooth-combed primates by dint of carpal and tarsal articular features shared uniquely by these groups (Beard et al. 1988) and derived relative to the condition found in anthropoids (Covert and Williams 1994). These arguments led us to adopt the term Strepsirhini.

Strepsirhini and Haplorhini are not just fashionable replacements for prosimians and anthropoids. By definition, prosimians are evolutionarily older than anthropoids. In a cladistic system, as sister-taxa, strepsirhines and haplorhines must be of equivalent age.

Infraordinal Designation

When Gregory (1915) coined the terms commonly used today to denote infraorders within the Strepsirhini (Lemuriformes for Malagasy strepsirhines and Lorisiformes for Afro-Asian strepsirhines), his model of prosimian relationships was very different from that we infer from these terms today. First, he divided his "Suborder Lemuroidea" into three, not two, "major groups or series," the third being Tarsiiformes. Lemuriformes, in Gregory's scheme, included the families Adapidae; Chiromyidae or Daubentoniidae; Indrisidae (including the subfossils *Archaeolemur*, *Hadropithecus*, *Mesopropithecus*, and *Palaeopropithecus*), and Lemuridae. Cheirogaleids were included within Lemuridae, despite the fact that the adapids and true lemurids shared a basicranial morphology not found in Cheirogaleidae. *Megaladapis* was also included here. The Lorisiformes comprised a single family (Lorisidae) with two subfamilies (Lorisinae and Galaginae), while the series Tarsiiformes was made up of the Eocene family Microchoeridae and the living Tarsiidae.

Gregory (1915) accorded the three series equal status, i.e., no two series shared a closer relationship with one another than either did with the third group. His decision was based on his belief that the "members of the Lorisiformes combine the characters of the Lemuriformes and of the Tarsiiformes in a manner suggesting extensive parallelism within these groups" (p. 441). In other words, Gregory was unable to decide whether or not living strepsirhines form a clade. When authors (e.g., Martin 1990; Fleagle 1999) follow Gregory's taxonomy, do they share his systematic philosophy?

In our opinion, the complex similarities of the tooth-comb and its associated structures are good evidence that the lemuriforms and lorisiforms shared a common ancestor. However, if we retain them as infraorders and include the fossil infraorder Adapiformes within Strepsirhini where they belong, we are back in Gregory's position: the lemuriforms and lorisiforms are no longer sister-taxa defined by an exclusive synapomorphy. Szalay and Delson (1979) attempted to resolve this dilemma by placing all living strepsirhines in the Infraorder Lemuriformes, which had three superfamilies: Lemuroidea (lemurids, lepilemurids, and megaladapids), Indrioidea (living indris, *Mesopropithecus*, daubentoniids, archaeolemurids, and

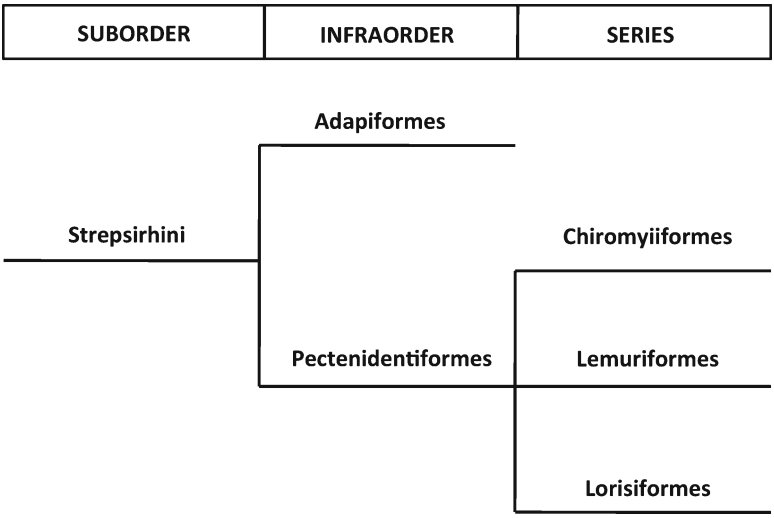


Fig. 1.1 Cladistic representation of higher level strepsirhine systematics

palaeopropithecids), and Lorisoidea (cheirogaleids and lorisids, *s.l.*). But this just pushes the problem one step down the hierarchy: indroids and lemuroids are clearly more closely related than either is to lorisoids. Martin (1990) and Fleagle (1999) included all the Malagasy forms under the superfamily Lemuroidea and the Afro-Asian taxa under Lorisoidea, but this can only be done at the expense of the taxonomy of the subfossil indroids. Martin (1990) placed all subfossil giant lemurs under family Megaladapidae, while Fleagle (1999) included them as genera within the living lemur families. However, the diversity of the subfossil indroids demands recognition of three families (Orlando et al. 2008), some of which are the sister-taxa to living lemur families. This means we need to retain the superfamily level within the Malagasy strepsirhine taxon.

The most sensible answer is to follow Gregory (1915) and Pocock (1918) in classifying the groups Lemuriformes and Lorisiformes at a taxonomic level below the infraorder but above the superfamily, i.e., as series comprising an infraorder that is the sister-taxon to Adapiformes. Simons (1974, p. 418) railed against such taxonomic adjustments as pedantic, puerile, and self-seeking—but the only alternative is to follow an outmoded classification that in no way reflects our understanding of phylogenetic relationships.

We have searched 250 years of systematic literature, and the only nomen proposed for an infraorder of tooth-combed primates is the Lemuriloriformes of Groves (2001). We applaud Groves' intention, but we find this term cumbersome, and indeed it has not been employed by other researchers since publication. The term Pectenidentiformes, from the Latin (pecten = comb, denti = teeth), has been nominated elsewhere (Masters et al. submitted). Figure 1.1 contains a cladistic diagram of this system.

Groves' (2001) tooth-combed infraorder explicitly did not include the daubentoniids. The recognition of the aye-ayes as requiring their own higher taxonomic grouping goes back to Illiger (1811), and Pocock (1918) placed them in their own suborder, Chiromyoidea. Groves gave them equivalent standing to the Lemuriloriformes, as Infraorder Chiromyiformes. A slew of molecular phylogenetic studies has placed *Daubentonia* as the basal divergence of the Malagasy clade (e.g., Roos et al. 2004; DelPero et al. 2006; Horvath et al. 2008), but much of its morphology argues otherwise (Groves 1974, 1989, 2001). From a cladistic viewpoint, the greatest challenge to *Daubentonia*'s classification is the fact that the lineage may never have had a tooth-comb (Luckett and Maier 1986; Groves 2001). Recently, Picone et al. (2011) have identified syntenic associations in *Daubentonia* chromosomes that are shared with other euarchintogliran mammals but not with any living primate. There is a clear conflict among data sets here, and Groves' retention of the group at a hierarchical level equivalent to the tooth-combed and adapiform lineages serves as an important record of this fact—lest our enchantment with nucleotide sequences leads us to believe that all the important questions have been answered.

Acknowledgments We thank Colin Groves for his encouragement in preparing this chapter and Barbara Picone and Ian Tattersall for their classical insights. The work was made possible by Grant number 2053615 awarded to J.C. Masters by the National Research Foundation, South Africa. Any opinion, findings, and conclusions or recommendations expressed in this material are those of the authors, and therefore the NRF does not accept any liability in regard thereto. This is A.P.I.E.S. publication No. 1.

References

Beard KC, Dagosto M, Gebo DL, Godinot M (1988) Interrelationships among primate higher taxa. Nature 331:712–714

Covert HH, Williams BA (1994) Recently recovered specimens of North American Eocene omomyids and adapids and their bearing on debates about anthropoid origins. In: Fleagle JG, Kay RF (eds) Anthropoid origins. Plenum, New York, pp 29–54

DelPero M, Masters JC, Pozzi L (2006) A composite molecular phylogeny of living lemuroid primates. Folia Primatol 77:434–445

Fleagle JG (1999) Primate adaptation and evolution, 2nd edn. Academic, New York

Geoffroy Saint-Hilaire E (1796) Mémoire sur les rapports naturels des makis *Lemur*, L. et. Description d'une espèce nouvelle de Mammifère. Mag Encycl 1:20–49

Geoffroy Saint-Hilaire E (1812) Tableau des Quadrumanes, ou des animaux composant le premier Ordre de la Classe des Mammifères. Ann Mus Hist Nat Paris 19:85–122, 156–170

Gray JE (1825) An outline of an attempt at the disposition of Mammalia into tribes and families, with a list of the genera apparently appertaining to each tribe. Ann Philos n.s.10:337–344

Gregory WK (1915) On the classification and phylogeny of the Lemuroidea. Bull Geol Soc Am 26:426–446

Groves C (1974) Taxonomy and phylogeny of the prosimians. In: Martin RD, Doyle GA, Walker AC (eds) Prosimian biology. Duckworth, London, pp 449–473

Groves CP (1989) A theory of human and primate evolution. Clarendon, Oxford

Groves C (2001) Primate taxonomy. Smithsonian Institution, Washington, DC

Haeckel E (1883) The history of creation: or the development of the earth and its inhabitants by the action of natural causes, 3rd edn. (transl. Lankester, ER). Kegan Paul, Trench and Co., London
Horvath JE, Weisrock DW, Embry SL, Fiorentino I, Balhoff JP, Kappeler P, Wray GA, Willard HF, Yoder AD (2008) Development and application of a phylogenomic toolkit: resolving the evolutionary history of Madagascar's lemurs. Genome Res 18:489–499
Illiger JKW (1811) Prodromus Systematis Mammalium et Avium. Sumptibus C. Salfeld, Berlin
Kay RF, Ross C, Williams BA (1997) Anthropoid origins. Science 275:797–804
Linnaeus C (1758) Systema naturae, 10th edn. Laurentii Salvii, Holmiae
Luckett WP, Maier W (1986) Developmental evidence for anterior tooth homologies in the aye aye, *Daubentonia*. Am J Phys Anthropol 69:233
Martin RD (1990) Primate origins and evolution. A phylogenetic reconstruction. Princeton University Press, Princeton
Mayr E (1969) Principles of systematic zoology. McGraw Hill, New York
Orlando L, Calvignac S, Schnebelen C, Douady CJ, Godfrey LR, Hänni C (2008) DNA from extinct giant lemurs links archaeolemurids to extant indriids. BMC Evol Biol 8:121. doi:10.1186/1471-2148-8-121
Picone B, Masters JC, Silvestro D, Sineo L, DelPero M (2011) A phylogenetic analysis of human syntenies revealed by chromosome painting in Euarchontoglires orders. J Mammal Evol 18:131–146
Pocock RI (1918) On the external characters of the lemurs and of *Tarsius*. Proc Zool Soc Lond 1918:19–53
Roos C, Schmitz J, Zischler H (2004) Primate jumping genes elucidate strepsirrhine phylogeny. Proc Natl Acad Sci USA 101:10650–10654
Simons EL (1972) Primate evolution: an introduction to man's place in nature. Macmillan, New York
Simons EL (1974) Notes on early Tertiary prosimians. In: Martin RD, Doyle GA, Walker AC (eds) Prosimian biology. Duckworth, London, pp 415–433
Simpson GG (1945) The principles of classification and a classification of the mammals. Bull Am Mus Nat Hist 85:1–350
Simpson GG (1961) Principles of animal taxonomy. Columbia University Press, New York
Szalay FS, Delson E (1979) Evolutionary history of the primates. Academic, New York
Van Valen L (1969) The classification of the primates. Am J Phys Anthropol 30:295–296
Yoder AD, Cartmill M, Ruvolo M, Smith K, Vilgalys R (1996) Ancient single origin of Malagasy primates. Proc Natl Acad Sci USA 93:5122–5126

Chapter 2
Species-Level Diversity Among Malagasy Lemurs

Ian Tattersall

Abstract The number of Malagasy lemur species recognized has skyrocketed over the past quarter-century, from 22 in 1982 to almost 100 today. This is largely a result of the wholesale application of phylogenetic species concepts and the elimination of subspecies from the lemur fauna. I argue that "silver-bullet" approaches to species recognition ignore real biological complexity, and that species are best recognized through weighing *all* available evidence including that furnished by morphology, molecules, behavior, communication, demography, and distributions. Only about 50 lemur species are fully justified by current evidence, although this is certainly a conservative estimate.

Resume Le nombre d'espèces de Lémuriens reconnus à Madagascar a explosé au cours du dernier quart de siècle, passant de 22 en 1982 à presque 100 aujourd'hui. Ceci découle de l'application sans limite du concept "d'espèce phylogénétique", et de l'élimination de toutes les sous-espèces de lémuriens. Je conteste cette approche réductrice de l'espèce, qui ignore la complexité du vivant, et j'affirme que les espèces sont mieux reconnues si *tous* les caractères identifiés sont pris en compte, combinant les approches morphologiques, moléculaires, comportementales (incluant les systèmes de communication), démographiques et géographiques. Une cinquantaine d'espèces de lémuriens seulement apparaît clairement justifiée, bien que cette estimation soit presque certainement conservatrice.

I. Tattersall (✉)
Division of Anthropology, American Museum of Natural History, New York, NY 10024, USA
e-mail: iant@amnh.org

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_2,

Introduction

Nobody doubts that Madagascar's lemur populations are coming under increasing pressure, and that a large part of the island's fauna has already disappeared (Godfrey et al. 2006). It is thus cause for celebration when any new and distinctive lemur population is located, but I still question whether more is always merrier for lemur species.

In 1982 I published (Tattersall 1982) a consensus classification of the lemurs for that time (Table 2.1). This consensus had endured in its essentials since Ernst

Table 2.1 Mittermeier et al. (2006, 2010) classifications of the Malagasy lemurs, annotated to show contrasts with Tattersall's (1982) classification

Tattersall (1982)	Mittermeier et al. (2006)	Mittermeier et al. (2010)
Family Cheirogaleidae		
Genus *Microcebus*		
		M. arnholdi
	M. berthae	*M. berthae*
		M. bongolavensis
		M. danfossi
	M. griseorufus	*M. griseorufus*
		M. jollyae
	M. lehilahytsara	*M. lehilahytsara*
		M. macarthurii
		M. mamiratra
		M. margotmarshae
		M. mittermeieri
M. murinus	*M. murinus*	*M. murinus*
	M. myoxinus	*M. myoxinus*
	M. ravelobensis	*M. ravelobensis*
M. rufus	*M. rufus*	*M. rufus*
	M. sambiranensis	*M. sambiranensis*
		M. simmonsi
	M. tavaratra	*M. tavaratra*
Genus *Allocebus*		
A. trichotis	*A. trichotis*	*A. trichotis*
Genus *Mirza*		
M. coquereli	*M. coquereli*	*M. coquereli*
	M. zaza	*M. zaza*
Genus *Cheirogaleus*		
	C. adipicaudatus	
	C. crossleyi	*C. crossleyi*
C. major	*C. major*	*C. major*
C. medius	*C. medius*	*C. medius*
	C. minusculus	*C. minusculus*
	C. ravus	
	C. sibreei	*C. sibreei*

(continued)

Table 2.1 (continued)

Tattersall (1982)	Mittermeier et al. (2006)	Mittermeier et al. (2010)
Genus *Phaner*		
P. furcifer	*P. furcifer*	*P. furcifer*
	P. electromontis	*P. electromontis*
	P. pallescens	*P. pallescens*
	P. parienti	*P. parienti*
Family Lepilemuridae		
Genus *Lepilemur*		
		L. aeeclis
		L. ahmansoni
	L. ankaranensis	*L. ankaranensis*
		L. ahmansonorum
		L. betsileo
	L. dorsalis[a]	*L. dorsalis*
	L. edwardsi[a]	*L. edwardsi*
		L. fleuretae
		L. grewcockorum
		L. hollandrum
		L. hubbardorum
		L. jamerosum
	L. leucopus[a]	*L. leucopus*
	L. microdon	*L. microdon*
		L. mittermeieri
		L. milanoii
L. mustelinus	*L. mustelinus*[a]	*L. mustelinus*
		L. otto
		L. petteri
		L. randrianasoloi
	L. ruficaudatus[a]	*L. ruficaudatus*
		L. sahamalazensis
		L. scottorum
	L. septentrionalis[a]	*L. septentrionalis*
		L. seali
		L. tymerlachsonorum
		L. wrighti
Family Lemuridae		
Genus *Hapalemur*		
	H. alaotrensis[a]	*H. alaotrensis*
	H. aureus	*H. aureus*
	H. gilberti	
H. griseus	*H. griseus*[a]	*H. griseus*
	H. meridionalis	*H. meridionalis*
	H. occidentalis[a]	*H. occidentalis*
Genus *Prolemur*[b]		
	P. simus	*P. simus*
Genus *Lemur*		
L. catta	*L. catta*	*L. catta*

(continued)

Table 2.1 (continued)

Tattersall (1982)	Mittermeier et al. (2006)	Mittermeier et al. (2010)
Genus *Eulemur*[b]		
	E. albifrons[a]	
	E. albocollaris[a]	*E. albocollaris*
		E. cinereiceps
	E. collaris[a]	*E. collaris*
E. coronatus	*E. coronatus*	*E. coronatus*
		E. flavifrons[a]
E. f. fulvus	*E. fulvus*[a]	*E. fulvus*
E. macaco	*E. macaco*	*E. macaco*
E. mongoz	*E. mongoz*	*E. mongoz*
E. rubriventer	*E. rubriventer*	*E. rubriventer*
		E. rufifrons
	E. rufus[a]	*E. rufus*
	E. sanfordi[a]	*E. sanfordi*
Genus *Varecia*		
V. v. variegata	*V. variegata*	*V. variegata*
V. v. Rubra	*V. rubra*	*V. rubra*
Family Indriidae		
Genus *Avahi*		
		A. betsileo
	A. cleesei	*A. cleesei*
A. laniger	*A. laniger*[a]	*A. laniger*
		A. meridionalis
		A. mooreorum
	A. occidentalis[a]	*A. occidentalis*
		A. peyrierasi
		A. ramanantsoavanai
	A. unicolor	*A. unicolor*
Genus *Propithecus*		
P.d. candidus	*P. candidus*[a]	*P. candidus*
	P. coquereli[a]	*P. coquereli*
	P. coronatus[a]	*P. coronatus*
	P. deckenii[a]	*P. deckenii*
P. d. diadema	*P. diadema*[a]	*P. diadema*
	P. edwardsi[a]	*P. edwardsi*
P. d. perrieri	*P. perrieri*[a]	*P. perrieri*
	P. tattersalli	*P. tattersalli*
P. v. verreauxi	*P. verreauxi*[a]	*P. verreauxi*
Genus *Indri*		
I. indri	*I. indri*	*I. indri*
Family Daubentoniidae		
Genus *Daubentonia*		
D. madagascariensis	*D. madagascariensis*	*D. madagascariensis*

Table enlarged and modified from Tattersall (2007)
[a]Recognized as subspecies in Tattersall (1982)
[b]Genus not recognized in Tattersall (1982)

Schwarz's (1931) revision recognized 22 living lemur species in Madagascar. Several were strongly polytypic (with a total of 38 species/subspecies) and most were at least mildly so. The only major debate in lemur species systematics was whether the discreetly colored nocturnal genus *Lepilemur* contained one polytypic species or several monotypic ones. I opted for a single *Lepilemur* species with six subspecies. So much for the lumper's fate. There are now 24 *Lepilemur* species, with no upper limit in sight. Lepilemurs are not alone; since 1982, the overall number of lemur species has skyrocketed. It had risen to 83 when Mittermeier et al. (2006) published the 2nd edition of their field guide and has now surpassed 100 (Mittermeier et al. 2010; see Table 2.1 for the state of play as this goes to press). Yet, remarkably, not many formerly unknown lemur populations have been discovered since 1982.

What *has* happened is that many previously known lemur communities are now considerably better known; and there is, without question, a lot more specific diversity than we suspected. Yet it is also true that much of the spectacular increase in species number has come at the price of the almost total elimination of subspecies, i.e., of morphologically and/or chromatically recognizable and geographically discrete intraspecific variants. By some reckonings there are only three polytypic lemur species in Madagascar today—and these are polytypic only by dint of containing subspecies for which I was unable to find adequate justification in 1982.

The Role of Local Populations

To anyone interested in evolutionary processes, this wholesale elimination of subspecies is disturbing, since subspecies are the indispensable cauldrons of innovation in evolution. Mechanisms of differentiation in primate populations are still poorly understood, but it is clearly routine for a widely distributed species to develop local variants in different parts of its range (Tattersall 1994). Indeed, across the spectrum of mammals, it is exceptional for local differentiation *not* to occur. It is also evident that natural selection drift must take place *within* local populations.

This is not to say that evolutionarily important triage takes place *only* at the intraspecific level, but it is differentiation *within* pre-existing species that potentiates the emergence of new, distinct lineages. Speciation is *not* simply a passive consequence of morphological divergence—although taxonomists would find it mightily convenient if it were, since it would make species recognition an easily quantifiable process. Some species undergo a huge amount of morphological differentiation without speciating, while in other cases one has to look closely to distinguish populations that have no evident reproductive interest in each other. The bottom line is that both speciation *and* morphological differentiation are essential for producing the patterns we see among living and fossil species, and both take place within local subunits of more widespread populations.

It might be argued that, in its splendid isolation, Madagascar's lemur fauna long ago achieved evolutionary equilibrium, and that its lack of subspecies reflects this. However, molecular estimates of divergence times among lemur populations argue

strongly against such a view. In fact, they indicate that the lemur fauna is actively diversifying—in which case the purported absence of subspecies on this huge landmass is curious indeed. Further, I question whether more is merrier in the lemur species department not only because the multiplication of lemur species has far outstripped the discovery of new lemur populations but also because the spectacular increase in lemur species has been effected largely—though not entirely—by the wholesale application by many lemurologists of a particularly fundamentalist interpretation of Cracraft's (1989) phylogenetic species concept.

Recognizing Species

By default, Cracraft's concept effectively eliminates subspecies as either biological or taxonomic units. Phylogenetic species are defined as the *minimal diagnosable units*—basically, any group you can recognize, even when presented with spotty evidence. But while in theory it simplifies matters for taxonomists, does this classificatory device really *mean* anything in terms of the way the luxuriant variety of nature is packaged? When we indulge in simple trait spotting, are we recognizing anything that is evolutionarily or biologically meaningful? The answer to these questions is no; and it is important because species are more than just the playthings of taxonomists. They are the primary actors in the evolutionary play. The adoption of the minimal diagnosability criterion has been justified on the basis of one arbitrary species definition; and any declarative definition of this kind must presuppose that species are straightforwardly definable entities. In one sense of course, they are. Species are the basic *kinds* of organisms, which corresponds to the intuitive way we interpret the world around us. Discontinuities are evident everywhere in nature, the larger ones corresponding neatly to the words—the discrete symbols—by which we categorize and explain our world. No one has any trouble telling a lion from a lobster from a mushroom. But as the categories get finer, the difficulties multiply, as witness the fact that there are at least 30 published definitions of species currently on offer.

In this regard we have not come very far since 1865, when Pierre Trémaux observed that "of definitions of species, there are as many as there are naturalists." Those definitions just keep piling up; and the crux of the problem is that species are not essentialist "kinds" defined by immutable sets of attributes. They are neither monothetic nor polythetic trait-based sets. Individuals of the same species resemble each other because they belong to the same population, not the other way around. Most importantly, it is they themselves, not taxonomists, who decide who's who.

At higher levels in the taxonomic hierarchy, morphology rules. Above the species level, potential reproductive compatibility ceases to be an issue—which is one reason why it is easier to demarcate genera than species, and so on up the line. But the unavoidable reality remains that, for sexually reproducing organisms, the boundaries between natural "kinds" are ultimately reproductive; and, sadly from the taxonomist's point of view, among close relatives those reproductive lines may not be clearly drawn. The manifold problems we have in species recognition stem from

the fact that speciation is an observed *result* rather than a unitary *mechanism*. Many different factors can affect reproductive choices or outcomes at the behavioral, anatomical, developmental, transcriptional or genetic level, and the resulting discontinuities may be expressed very differently. All are not equally irreversible. Additionally reproductive barriers may be absolute or permeable, complicating things further: a few instances of mating among sympatric or parapatric forms may be meaningless in the long term.

These limitations apply equally to cohesional and exclusionary approaches to identifying independent reproductive or historical units. To tidy-minded taxonomists, the inherent messiness in nature's packaging is a nasty inconvenience, so, rather than acknowledge this awkward truth—which would force them to deal with it, or at least admit that it is intractable—taxonomists have sought other, more clear-cut, ways of recognizing species. Which explains why species concepts based on gene exchange are currently in disfavor—and why the criterion of simple diagnosability exerts such siren attraction.

On a practical level, species definitions have also proliferated because systematists work with different kinds of data. Given that this is a reality that will not disappear, perhaps we should remove ourselves from abstract arguments of species definition and focus on the *roles* of species in nature. This inevitably brings us to Ghiselin's (1974) perceptive characterization—not definition—of species as *individuals*. In Ghiselin's perspective, species are populations that have embarked on independent evolutionary histories. Such populations compete on the ecological stage, and either flourish, persist, or go extinct. Whatever their fates, they can no longer cease by absorption into a larger entity.

This means that at fine degrees of evolutionary relationship, *no* single intellectual silver bullet can demonstrate infallibly what is and is not a species. One or two mtDNA base substitutions will no more indicate two species, than an occasional instance of hybridization between close relatives will indicate only one. So we have but one alternative: to look simultaneously at *all* the available evidence. This places alpha taxonomists in much the same position as judges trying pornography cases. Judges may never have developed a satisfactory definition of pornography, but they claim to know it when they see it, and their rulings are justified by weighing all the evidence presented. In the case of taxonomy, this means considering structural or transcriptional genetic information; karyology; size and external morphology; reproductive and activity rhythms; internal structure; vocalizations; olfactory signals; geographical and ecological distributions; behaviors in parapatry or sympatry; phylogenetic relationships; indeed, any information that throws light on the animals' own take on their population limits.

Implications for the Lemur Fauna

I recently reviewed the alpha systematics of Madagascar's lemurs (Tattersall 2007) and will not repeat the details here. I will, however, consider briefly a couple of cases, one diurnal and the other nocturnal.

Generally when diurnal forms spread and diversify, they form local populations that are distinguishable visually (Paterson 1980, 1985; Masters 1988; Masters and Spencer 1989). Several brown lemur populations that vary in coloration were described as separate species before being lumped by Schwarz (1931) into the species *Lemur fulvus*: a species now placed, with all "true" lemurs other than ringtails, in the genus *Eulemur.* Morphological and genetic information reconstruct *Eulemur* as a clade, with *E. fulvus* variants forming a subclade within it. Recent classifications (e.g., Mittermeier et al. 2006, 2010) have accorded the *fulvus* subspecies full species rank alongside the more established forms: *rubriventer*, *macaco*, *coronatus*, and *mongoz*. This has occurred despite indications that the *fulvus* radiation is "superimposed" phylogeographically on the older *Eulemur* one, and despite clear evidence of interfertility with the odd exception of the parapatric, and karyotypically distinct, *albocollaris* and *collaris.*

While visually differentiated and diagnosable, the *fulvus/albifrons/rufus/sanfordi* group appears to be a single entity. While each component is potentially a new species, there is as yet no evidence that the components have diverged irreversibly along their own historical trajectories. The appropriate tests of how the animals perceive their population limits have not been done. Happily, nothing prevents us from using these or any other infraspecific taxa as units of historical and biogeographic analysis; and indeed, if we insist on regarding all subspecies as full species, we limit our opportunities to study speciation processes.

Another example to mention briefly is the nocturnal genus *Microcebus*, in which for many years just two species were recognized: a gray, long-eared western form and a reddish, shorter-eared eastern one. Today the count is around 15 species, and rising (Table 2.1). While it has been clear for some time that systematic complexity among the cryptically colored mouse lemurs was greater than the two-species division suggests, it is less clear how many species there actually are. Many new species have been recognized principally on mtDNA criteria and, as elsewhere in the expanding lemur fauna, new species descriptions follow a stereotypical pattern, whereby a nondifferential description is made on the basis of external features of individuals obtained at a particular location, followed by a differential diagnosis based principally or purely on mtDNA characterizations and genetic distances derived therefrom.

Using sophisticated techniques, researchers have identified a set of molecular characters that seem—on limited sampling—to differentiate populations of mouse lemurs around Madagascar. But is that the same as identifying species? Quite honestly, no. It's a good start; but without supporting evidence it is impossible to tell whether we have a large set of species, or a smaller set of species that varies geographically in a continuous manner, or a species divided into discrete local populations. Although many localities have been sampled, we do not know how these molecular variants sort over the wider distributions of the taxa involved. More significantly, local samples tend to be small, and may consist of closely related individuals. Without resort to biological information, we cannot conclude that these variants are indicative of speciation rather than of intraspecific diversification by locale.

There are clearly more *Microcebus* species in the Malagasy forests than we once believed. The venerable *M. murinus* occurs in sympatry with several recently proposed or resurrected species such as *M. ravelobensis*, *M. berthae*, and *M. myoxinus*,

from which it does seem to be ecologically differentiated (Schmid and Kappeler 1994; Zimmermann et al. 1998). Information of this kind provides far firmer justification for species distinction. A similar argument applies to *M. rufus* and *M. lehilahytsara*, and likely in other cases too. So I am not arguing here against mouse lemur species diversity, but rather that claims for species identity require more justification than simply the simple possession of an mtDNA marker or two. Species are much more than containers for genetic or chromatic novelties.

A Plea

I hope I have not sounded unduly negative. It has been gratifying over past decades to see so many new discoveries in lemur diversity through the efforts of so many colleagues. On current evidence it appears (Tattersall 2007) that at least 50 lemur species—an almost 50% increase on the number recorded in 1982—may legitimately be recognized. More species are undoubtedly out there; but it is of little benefit to rush to recognize more than the full span of evidence will support. Much more needs to be learned and placed on record; and I hope that this volume replete with evidence of the vigor of ongoing lemur studies, will help inspire the collection of the data we need, and encourage more collaboration: gone is the time when molecular, morphological, demographic, ecological, communication, and behavioral studies could be carried out in isolation. For each local population, we need data on all these aspects if we are properly to understand the structure of diversity among Madagascar's lemurs.

Finally, at a time when lemur populations are under such pressure, every new piece of demographic information should be recognized as valuable by everybody. This includes journal editors, whether or not a new species is demonstrably involved—a factor that now seems to ease the route to publication. Rather than simply cataloging new genetic or morphological variants by allocating them reflexively to new species, we should be thinking more about the wider *roles* of the subjects of our study in the complex ecological and historical webs of which they form part. This would much better serve a mature and comprehensive appreciation of lemur diversity.

Acknowledgments My appreciation to Judith Masters for her energy and initiative in maintaining the important tradition of reviewing the state of lemur biology each decade and for her temperate commentary on this piece. Thanks also to Stephen Nash for (among many other things) keeping score on the roster of lemur species.

References

Cracraft J (1989) Speciation and its ontology. In: Otte D, Endler J (eds) Speciation and its consequences. Sinauer Associates, Sunderland, MA, pp 28–59

Ghiselin MT (1974) A radical solution to the species problem. Syst Zool 23:536–544

Godfrey LR, Jungers WL, Schwartz GT (2006) Ecology and extinction of Madagascar's subfossil lemurs. In: Gould L, Sauther ML (eds) Lemurs: ecology and adaptation. Springer, New York, pp 41–64

Masters J (1988) Speciation in the greater galagos (Prosimii: Galaginae): review and synthesis. Biol J Linn Soc 34:149–174

Masters JC, Spencer HG (1989) Why we need a new species concept. Syst Zool 38:270–279

Mittermeier RA, Konstant WR, Hawkins F, Louis EE, Langrand O, Ratsimbazafy J, Rasoloarison R, Ganzhorn JU, Rajaobelina S, Tattersall I, Meyers DM, Nash SD (2006) Lemurs of Madagascar, 2nd edn. Conservation International, Washington, DC

Mittermeier RA, Louis EE, Richardson M, Schwitzer C, Langrand O, Rylands AB, Hawkins F, Rajaobelina S, Ratsimbazafy J, Rasoloarison R, Roos C, Kappeler PM, Mackinnon J, Nash SD (2010) Lemurs of Madagascar, 3rd edn. Conservation International, Washington, DC

Paterson HEH (1980) A comment on "mate recognition systems". Evolution 34:330–331

Paterson HEH (1985) The recognition concept of species. In: Vrba ES (ed) Species and speciation. Transvaal Museum, Pretoria, pp 21–29

Schmid J, Kappeler PM (1994) Sympatric mouse lemurs (*Microcebus* spp.) in western Madagascar. Folia Primatol 63:162–170

Schwarz E (1931) A revision of the genera and species of Madagascar Lemuridae. Proc Zool Soc Lond 1931:399–428

Tattersall I (1982) The primates of Madagascar. Columbia University Press, New York

Tattersall I (1994) How does evolution work? Evol Anthropol 3:2–3

Tattersall I (2007) Madagascar's lemurs: cryptic diversity or taxonomic inflation? Evol Anthropol 16:12–23

Trémaux P (1865) Origine et Transformations de I'Homme et des Autres Etres. Hachette, Paris

Zimmermann E, Cepok S, Rakotoarison N, Zietemann V, Radespiel U (1998) Sympatric mouse lemurs in North-West Madagascar: a new rufous mouse lemur species (*Microcebus ravelobensis*). Folia Primatol 69:106–114

Chapter 3
Strepsirhine Divergence Dates Estimated from Mitochondrial Gene Sequences, and the Status of *Daubentonia madagascariensis*

Daniel Montagnon

Abstract Given the paucity of Cenozoic fossils on Madagascar, divergence times for strepsirhines must be calculated from nucleotide sequences. I used four mitochondrial genes (cytochrome *b*, ND3, ND4, and ND4L) from representatives of all extant lemur families, Lorisidae and Galagidae, to derive Bayesian molecular clock estimates of major clade divergences. Divergence of the Lemuriformes (excluding *Daubentonia*) ranged from 31 to 38 million years ago (Mya); when *Daubentonia* was included, this date was pushed back to 52–53 Mya. The divergence of living Strepsirhini was estimated at 58–59 Mya. These dates are appreciably younger than those reported in most previous studies. Divergence dates for Lemuriformes excluding *Daubentonia* fall within a 25–42 Mya window when the continental crust was emergent along the Davie Fracture Zone, affording a potential dispersal route between Africa and Madagascar. Despite lemuriform monophyly, multiple colonization events cannot be excluded. Regardless of the gene used, *Daubentonia* emerged substantially earlier than the other lemuriform families. Coalescence simulations revealed an early duplication of the four genes, probably of the whole mitochondrial genome, which led on one hand to *Daubentonia* and on the other to the remaining Lemuriformes. This supports the uniqueness of this genus, already demonstrated cytologically and morphologically.

Resume Etant donnée la rareté des fossiles Cénozoïque à Madagascar, les dates de divergence des Strepsirhiniens doivent être estimées à l'aide de séquences nucléotidiques. Nous avons utilisé quatre gènes mitochondriaux (cytochrome *b*, ND3, ND4 et ND4L) de représentants de toutes les familles de Lémuriens, Lorisidae et Galagidae pour estimer les dates de divergence des principaux clades, en utilisant

D. Montagnon (✉)
Faculté de Médecine, Unité EA3428, Espèce Humaine et Primates: Variabilité et Évolution, 11 rue Humann, 67000 Strasbourg, France
e-mail: daniel.montagnon@wanadoo.fr

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_3,

la méthode d'analyse Bayésienne. La divergence estimée pour les Lémuriformes, si *Daubentonia* est exclus, est de 31 à 38 million d'années (MA); et 52 à 53 MA si *Daubentonia* est inclus. La divergence estimée pour les Strepsirhiniens est de 58 à 59 MA. Ces divergences sont notablement plus récentes que celles reportées par la plupart des études antérieures. Les dates de divergence estimées pour les Lémuriformes, à l'exclusion de *Daubentonia*, se trouvent comprises dans une fenêtre temporelle (42 – 25 MA) au cours de laquelle il existait un pont de terre émergée, au niveau de la zone de fracture de Davie, entre l'Afrique et Madagascar, voie de dispersion possible pour les Lémuriformes. Malgré la monophylie des Lémuriformes, de multiples colonisations de Madagascar ne peuvent pas être exclues. Quel que soit les gènes utilisés, *Daubentonia* émerge sensiblement plus tôt que les autres familles de Lémuriformes. Des simulations par coalescence pour les quatre gènes indiquent une duplication primitive, sans doute de l'ensemble du génome mitochondrial, conduisant d'une part à *Daubentonia*, et d'autre part aux autres Lémuriformes. Ceci renforce le caractère unique de ce genre, déjà démontré par des études cytologiques et morphologiques.

Introduction

Groves (2001) divided the Strepsirhini into three infraorders: the Chiromyiformes (with one living representative, *Daubentonia madagascariensis*), the Lemuriformes, and the Lorisiformes. The first two groups are found only in Madagascar while the third comprises Afro-Asian taxa. The biogeographical origin of the extant terrestrial and freshwater vertebrate fauna of Madagascar remains unresolved (Wallace 1892; Masters et al. 2006) because of a paucity of fossils. To date, only subfossil lemurs have been recovered in Madagascar, dated between 26,000 and a few hundred years old (Godfrey and Jungers 2003). Molecular clock estimates imply a Cenozoic origin for most Malagasy vertebrate groups, when Madagascar was already isolated (Rabinowitz et al. 1983; Yoder et al. 1996). The presence of mammals on the island has been explained by various hypotheses, including Gondwanan vicariance (Arnason et al. 1998), temporary land bridges between Africa and Madagascar (McCall 1997), and the use of vegetation rafts to cross the Mozambique Channel (Kappeler 2000). Strepsirhine monophyly is widely accepted and supported by morphological (Charles-Dominique and Martin 1970), chromosomal (Dutrillaux 1988), and molecular (Porter et al. 1995; Yoder 1997) data. Using the nuclear gene IRBP, Poux and Douzery (2004) estimated the divergence date at 13.8–14.2 million years ago (Mya) for Lorisiformes, 26.5–27.2 Mya for Lemuroidea, 39.6–40.7 Mya for Lemuriformes, 45.4–46.7 for the Strepsirhini, and 56.7–58.4 for the Haplorhini. Using jumping genes, Roos et al. (2004) dated the main strepsirhine divergence at 61 Mya (range 50–80), followed by the Chiromyiformes/Lemuriformes divergence at 58 Mya (range 47–76), and the Lemuriformes radiation into megaladapids (lepilemurids), cheirogaleids, and indriids–lemurids at 43 Mya (range 35–56). Finally, the indriid/lemurid separation was estimated at 40 Mya (range 37–60). Yoder et al.

(1996) estimated the Lemuriformes/Lorisiformes divergence at 62 Mya, with Malagasy primates reaching Madagascar and beginning their radiation 54 Mya (earliest Eocene). Using a multigene analysis including mitochondrial and nuclear genes, Yoder and Yang (2004) estimated the age of the Lemuriformes clade at 62–65 Mya, with a divergence between cheirogaleids and lemurids at 8–12 Mya. Differences in the estimates demonstrate the difficulty with which they are calculated. This is mainly due to the fact that different genes have different evolutionary rates (Glazko and Nei 2003). In this study, I used four mitochondrial genes: cytochrome *b* and three NADH subunits (ND3, ND4, and ND4L) singly and combined to perform a Bayesian molecular clock estimate using a large suite of strepsirhine taxa. I also investigated the status of *Daubentonia madagascariensis*, the strangest living lemur. I compared my estimated divergence dates with geological events with the aim of providing a credible explanation for the lemuriform colonization of Madagascar.

Materials and Methods

Data Sources

A single sequence for each of the 68 lemuriform species and subspecies was downloaded from the EMBL database (11 Indriidae, 21 Cheirogaleidae, 22 Lemuridae, 13 Megaladapidae, and 1 Daubentoniidae); homologous sequences were also downloaded for 8 Lorisidae, 9 Galagidae, 1 *Tarsius*, 1 Cebidae, 13 Cercopithecidae, 6 Tupaiidae, 1 *Rattus*, 4 *Mus*, 3 *Canis*, 2 *Felis,* and 3 Monotremata taxa. EMBL accession numbers for sequences used in this study are available upon request. Sequences were aligned using CLUSTAL-X (Thompson et al. 1997). The final cytochrome *b* (cyt *b*) sequence was 1,134 base pairs (bp), the last six base pairs being deleted because of ambiguities. For the ND genes, whole sequences were used, yielding a concatenated sequence of 2,022 bp. For all genes, base composition, proportion of invariable sites, gamma distribution shape parameter, and the transition/transversion ratio (Table 3.1) were computed using TREE-PUZZLE (Schmidt et al. 2002).

Phylogenetic Reconstructions

I assessed the best substitution model for each gene using MODELTEST (Posada and Crandall 1998). Neighbor-joining (NJ) trees were reconstructed in MEGA (Kumar et al. 2004) and Maximum Likelihood (ML) and Maximum Parsimony (MP) trees in PHYLIP (Felsenstein 2005). Three Monotremata species served as outgroups. The most credible tree among NJ, ML, and MP reconstructions was determined using the Kishino–Hasegawa (KH), Shimodaira–Hasegawa (SH), and pRELL statistical tests in the PAML package (Yang 1997).

Table 3.1 Main characteristics of cytochrome *b* and ND sequences

Characteristics	Cytochrome *b*	ND3 + ND4 + ND4L
Total number of sequences	69	61
Sequence size (bp)	1,134	2,022
Percentage A	29.3	31.9
Percentage C	29.2	26.6
Percentage G	12.7	10.9
Percentage T	28.8	30.5
Proportion of invariable sites (I)	39.18	38.04
Gamma distribution shape parameter (G)	0.7487	1.0511
Ti/Tv[a]	6.27	7.09
Substitution model	GTR + I + G[b]	GTR + I + G
Most credible tree	ML[c]	MP[d]
Prior distribution for molecular evolution rate at ingroup root node	2 CP[e] : 0.6369 4 CP : 0.9366	2 CP : 0.5601 4 CP : 0.6921

[a]Transition/transversion ratio
[b]General time reversible model + Invariants proportion + Gamma distribution shape parameter
[c]Maximum Likelihood
[d]Maximum Parsimony
[e]Calibration points

Divergence Date Estimations

I estimated model parameters using BASEML (Yang 1997), and used ESTBRANCHES to estimate branch lengths and to generate a variance–covariance matrix by approximating the likelihood surface with a multivariate normal distribution based on branch length estimates (Thorne et al. 1998). I performed a Bayesian Markov Chain Monte Carlo (MCMC) procedure using the MULTIDIVTIME software to estimate the posterior distribution of substitution rates and divergence times (Thorne et al. 1998; Kishino et al. 2001). The MULTIDIVTIME analysis was run at least twice and the MCMC parameters were adjusted when results from two runs differed significantly. Two analyses were performed. The first included two primate calibration points (CP): the split between Cercopithecoidea and Hominoidea at 25–30 Mya and that between *Gorilla* and *Pan-Homo* at 14–17 Mya (Raaum et al. 2005), and the second used the same two primate calibration points plus two nonprimate points: the split between *Felis* and *Canis* at 45–65 Mya (Flynn 1996) and that between *Mus* and *Rattus* at 8.8–14 Mya (Chevret and Dobigny 2005).

Coalescence Studies

These were performed using the three Monotremata outgroups and representatives of Daubentoniidae, Indriidae, Lemuridae, Cheirogaleidae, Megaladapidae,

Galagidae, Lorisidae, Cebidae, Cercopithecidae, Hominoidea, and Scandentia as well as representatives of the Dermoptera, Suina, Ruminantia, Cetacea, Hippopotamidae, and Tylopoda. A species tree was constructed for each gene (cyt *b*, ND3, ND4, and ND4L) using GENETREE software (Page 2000) and a heuristic search with a random starting tree and a deep coalescence process. The data were analyzed in MESQUITE (Maddison and Maddison 2007) using the CONTAINED ASSOCIATES option which displays gene trees within species trees. Such analysis helps track the evolution of gene copies and duplication events.

Results

Sequence Characteristics

For all genes, the Tamura-Nei (TN93) model was used in TREE-PUZZLE. As there were differences in the gamma distribution shape parameter, in the transition/transversion ratio and in the most credible tree under the same substitution model (Table 3.1), I did not combine cyt *b* and the ND genes in a single analysis.

Divergence Date Estimations

The two- and four-calibration point (CP) analyses yielded similar divergence dates, but different topologies. With two CPs, *Daubentonia* was reconstructed as the sister group to Cercopithecidae + Hominoidea, while it shifted to its more common position at the base of the Lemuriformes with four CPs. The initial Strepsirhini divergence was dated as Paleocene (59 Mya) and the common Lemuriformes ancestor as 38.2 Mya (excluding *Daubentonia*) or 50.5 Mya (including *Daubentonia*). Diversification within the Indriidae, Cheirogaleidae, and Lemuridae apparently began not long (5–8 My) after the initial divergence of the families, but for the Megaladapidae this occurred more than 13 My after divergence. The split between Lorisidae and Galagidae is dated at 44.4 Mya using two CPs and 50.4 Mya using four. The Lorisiformes/Lemuriformes divergence is estimated at 59 Mya (Fig. 3.1).

Using the ND3, ND4, and ND4L genes and two and four CPs, the divergence estimates for Lemuriformes families are within the range obtained for cyt *b*. The split between Lorisidae and Galagidae is dated a little later, at 30 Mya. A common ancestor for Lemuriformes excluding Daubentoniidae was estimated at 45 Mya, and at 53 Mya if Daubentoniidae is included (Fig. 3.2).

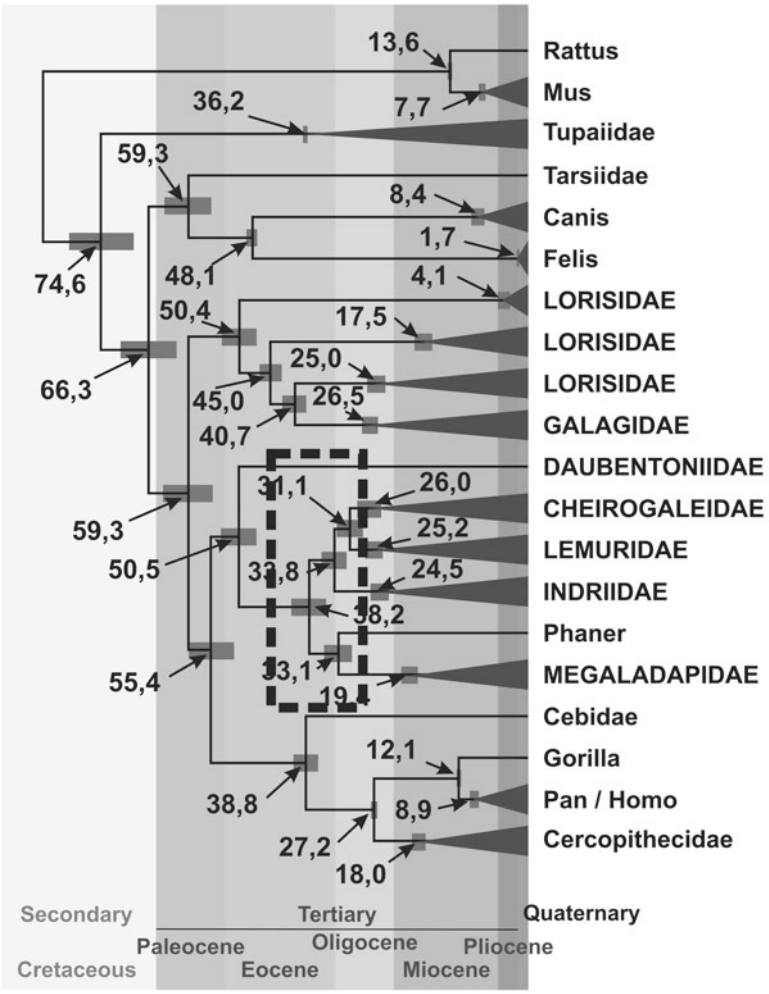


Fig. 3.1 Divergence dates estimated using the cytochrome *b* gene and four calibration points. *Light gray box* indicates the standard deviation for the divergence date; *dark gray triangle* indicates the earliest divergence date for a family. The *dashed rectangle* indicates the time window during which subaerial land was present along the Davie Fracture Zone

Coalescence Studies

In most molecular phylogenetic reconstructions, *D. madagascariensis* forms the basal divergence of the Malagasy clade. For each of cyt *b* (Fig. 3.3), ND3, and ND4, copies unique to *Daubentonia* were identified as well as a duplication in the Cercopithecidae + Hominoidea clade. In the case of ND4L, the only gene duplication occurred in Cebidae, the sister group of the Cercopithecidae + Hominoidea in this study.

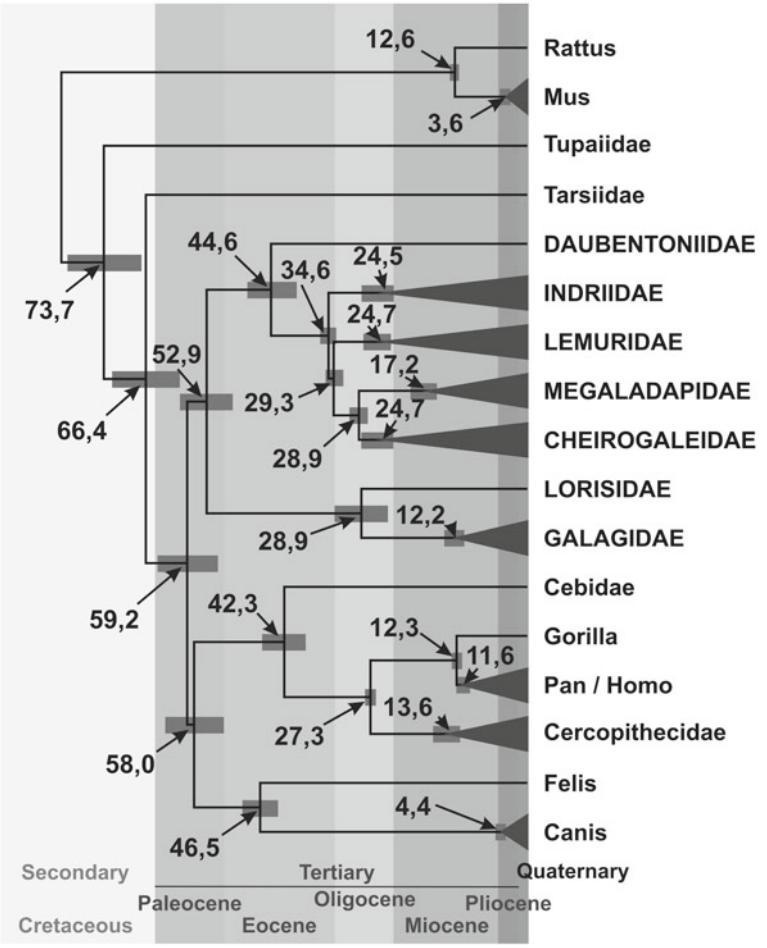


Fig. 3.2 Estimation of divergence dates using the concatenated ND gene sequences and four calibration points

Discussion

While Madagascar essentially lacks a Cenozoic fossil record, Eocene beds in North America and Eurasia contain a large radiation of lemur-like primates that may include the ancestors of living lemurs (Godinot 1998). The hypothesis currently favored for the mammalian colonization of Madagascar is by sweepstakes dispersal on rafts of vegetation, with the possible assistance of torpor (Albignac 1972; Racey and Sephenson 1996), but terrestrial mammals have colonized few isolated islands (Lawlor 1986). A range of divergence dates has been proposed for Malagasy mammals [50 Mya for Tenrecidae from proto-insectivores (Eisenberg 1981), 33–27 Mya for Malagasy carnivores (Wayne et al. 1989), 30–16 Mya for nesomyine rodents

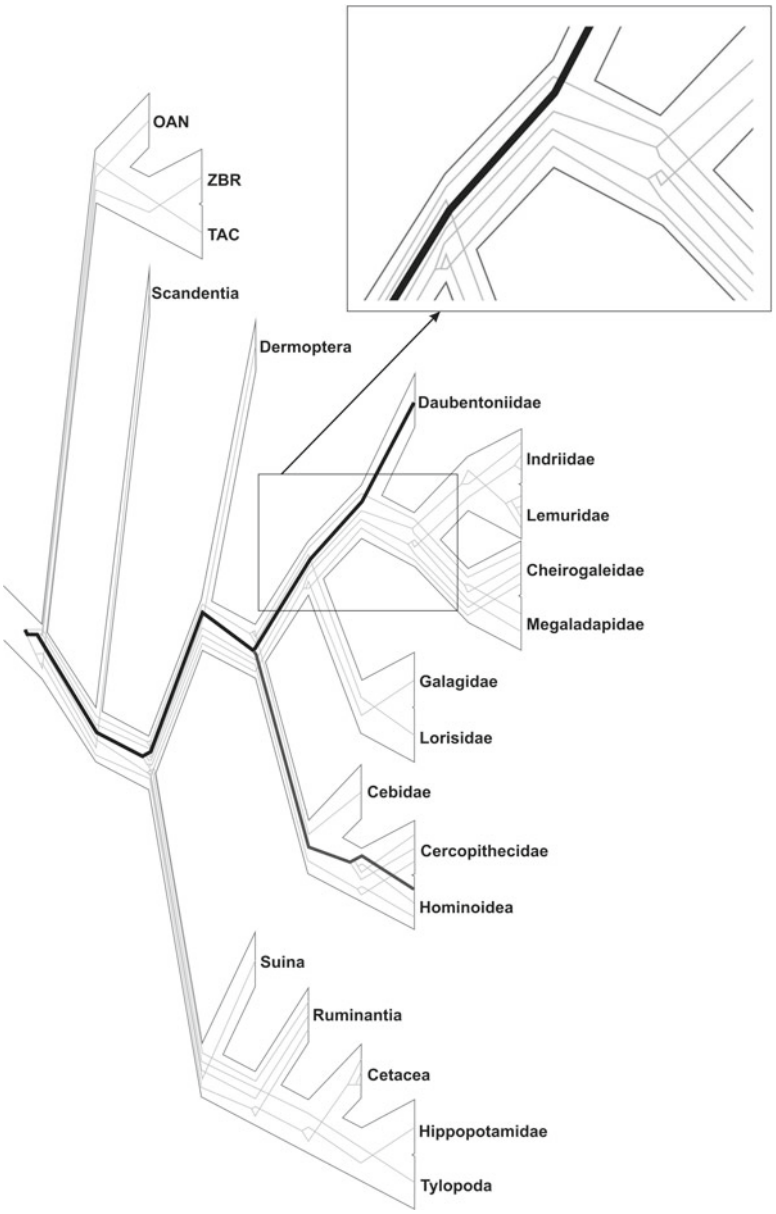


Fig. 3.3 Coalescence study using cytochrome *b* sequences. OAN, *Ornithorhynchus anatinus*; TAC, *Tachyglossus aculeatus*; ZBR, *Zaglossus bruijni*

(Eisenberg 1981; Catzeflis et al. 1993), >40 Mya for the Malagasy aardvark (MacPhee 1994), and <7 Mya for the Malagasy hippopotamus (Faure and Guérin 1990)]. Except for the hippopotamus, all these dates fall within a 45–26 Mya

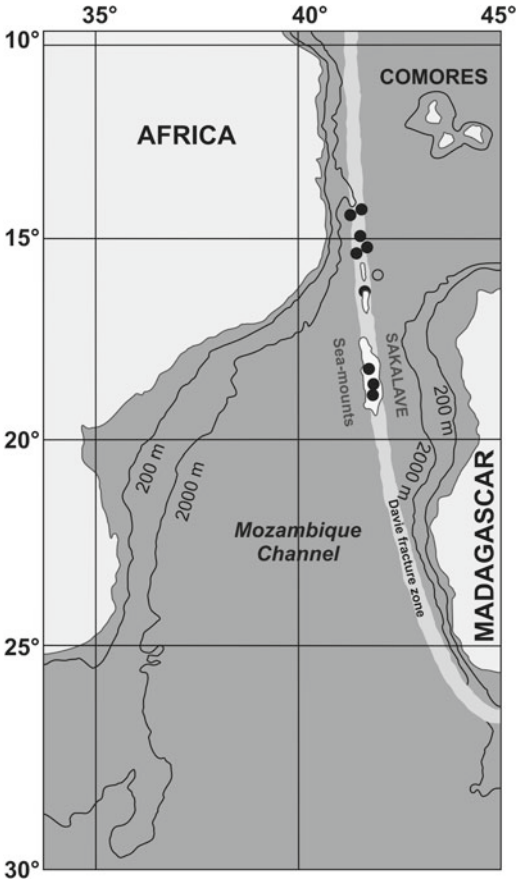


Fig. 3.4 Geographical position of the Davie Fracture Zone after McCall (1997)

window during which patches of dry land were probably present in the Mozambique Channel (McCall 1997). With the early Miocene subsidence of this land, groups like Old World monkeys, felids, and canids, which diverged or arrived in Africa later in the Miocene, would have been unable to cross the Mozambique Channel (Wayne et al. 1989; Martin 1993). The emergent land was associated with the Davie Fracture Zone (DFZ; Fig. 3.4): DFZ core samples suggest a marine sedimentary environment from the lower Miocene (26 Mya) and prior to this, between the mid-Eocene (45 Mya) and lower Miocene (26 Mya), episodic subaerial exposure of some sections (Leclaire et al. 1989; Bassias 1992).

The coincidence of these geological events and my molecular divergence dates may indicate that ancestral Malagasy mammals colonized Madagascar in this way, and that multiple colonization events cannot be excluded. Terrestrial colonization is more credible than transoceanic rafting because only micro-mammals can use rafts. These dates are also in agreement with a Late Eocene lemuriform divergence.

A second point of debate is the position of *Daubentonia madagascariensis*, considered either as the sister group of all other Lemuriformes (Yoder et al. 2003) or of Strepsirhini on the basis of morphology (Groves 1989) and analyses of the mitochondrial genome (Adkins and Honeycutt 1994; Arnason et al. 1998). Aye-ayes have unusual morphological specializations (e.g., continuously growing rodent-like incisors, clawed digits, and an elongated middle finger). Despite the fact that mtDNA CO I sequences placed *D. madagascariensis* at the base of the strepsirhine clade (Adkins and Honeycutt 1994), nuclear DNA studies placed it securely with the other Malagasy primates (e.g., Porter et al. 1995). My coalescence simulations using four mitochondrial genes clearly indicate the existence of an ancestral duplication of these genes, after which one gene copy leads to the *Daubentonia* lineage and the other to all the other Lemuriformes (Fig. 3.3). A second duplication event is reflected in the Cebidae, in the case of the ND4L gene, and in the Cercopithecidae + Hominoidea, in the case of the three other genes. These results confirm the genetic uniqueness of *D. madagascariensis*.

Conclusion

I provide a new estimate of strepsirhine divergence dates using mitochondrial genes. These dates are more recent than those determined by most other authors, especially for Lemuriformes. The lemuriform divergence dates reported here (excluding *Daubentonia madagascariensis*) are compatible with multiple colonizations of Madagascar via a land bridge hypothesized to have existed along the DFZ 45–25 Mya. Megaladapidae appears to be the last lemuriform family to have diverged (during the Miocene), while Indriidae, Cheirogaleidae, and Lemuridae started their diversification approximately 10 Mya earlier (during the Oligocene). The uniqueness of *Daubentonia madagascariensis* is confirmed by coalescence simulations, and the connection between this species and other living lemuriforms is very ancient.

References

Adkins RM, Honeycutt RL (1994) Evolution of the primate cytochrome *c* oxidase subunit II gene. J Mol Evol 38:215–231

Albignac R (1972) The Carnivora of Madagascar. In: Battistini R, Vindard R (eds) Biogeography and ecology in Madagascar. Junk, The Hague, pp 667–682

Arnason U, Gullberg A, Janke A (1998) Molecular timing of primate divergences as estimated by two nonprimate calibration points. J Mol Evol 47:718–727

Bassias Y (1992) Petrological and geochemical investigations of rocks from the Davie Fracture Zone (Mozambique Channel) and some tectonic implications. J Afr Earth Sci 15:321–339

Catzeflis FM, Dickerman AW, Michaux J, Kirsch JAW (1993) DNA hybridisation and rodent phylogeny. Springer, Berlin

Charles-Dominique P, Martin RD (1970) Evolution of lorises and lemurs. Nature 227:257–260

Chevret P, Dobigny G (2005) Systematics and evolution of the subfamily Gerbillinae (Mammalia, Rodentia, Muridae). Mol Phylogenet Evol 35:674–688
Dutrillaux B (1988) Chromosome evolution in primates. Folia Primatol 50:134–135
Eisenberg JF (1981) The mammalian radiations. Athlone Press, London
Faure M, Guérin C (1990) *Hippopotamus laloumena* nov. sp., la troisième espèce d'hippopotame holocéne de Madagascar. C R Acad Sci II 310:1299–1305
Felsenstein J (2005) PHYLIP (Phylogeny Inference Package) version 3.6. University of Washington, Seattle
Flynn JJ (1996) Phylogeny and rates of evolution: morphological, taxic and molecular. In: Gittleman JL (ed) Carnivore behavior, ecology, and evolution, vol 2. Cornell University Press, Ithaca, NY, pp 542–581
Glazko GV, Nei M (2003) Estimation of divergence times for major lineages of primate species. Mol Biol Evol 20:424–434
Godfrey LR, Jungers WL (2003) The extinct sloth lemurs of Madagascar. Evol Anthropol 12:252–263
Godinot M (1998) A summary of adapiform systematics and phylogeny. Folia Primatol 69:218–249
Groves CP (1989) A theory of human and primate evolution. Oxford University Press, Oxford
Groves CP (2001) Primate taxonomy. Smithsonian Institution, Washington, DC
Kappeler PM (2000) Lemur origins: rafting by groups of hibernators? Folia Primatol 71:422–425
Kishino H, Thorne JL, Bruno WJ (2001) Performance of a divergence time estimation method under a probabilistic model of rate evolution. Mol Biol Evol 18:352–361
Kumar S, Tamura K, Nei M (2004) MEGA3: integrated software for Molecular Evolutionary Genetics Analysis and sequence alignment. Brief Bioinform 5:150–163
Lawlor TE (1986) Comparative biogeography of mammals on islands. Biol J Linn Soc 28:99–125
Leclaire L, Bassias Y, Clocchiatti M, Segoufin J (1989) La Ride de Davie dans le Canal de Mozambique: approche stratigraphique et géodynamique. C R Acad Sci II 308:1077–1082
MacPhee RDE (1994) Morphology, adaptations and relationships of *Plesiorycteropus* and a diagnosis of a new order of eutherian mammals. Bull Am Mus Nat Hist 220:210–214
Maddison WP, Maddison DR (2007) Mesquite: a modular system for evolutionary analysis. Version 1.06. http://mesquiteproject.org
Martin RD (1993) Primate origins: plugging the gaps. Nature 363:223–234
Masters JC, de Wit MJ, Asher RJ (2006) Reconciling the origins of Africa India and Madagascar with vertebrate dispersal scenarios. Folia Primatol 77:399–418
McCall RA (1997) Implications of recent geological investigations of the Mozambique Channel for the mammalian colonization of Madagascar. Proc R Soc Lond B 264:663–665
Page RDM (2000) Extracting species trees from complex gene trees: reconciled trees and vertebrate phylogeny. Mol Biol Evol 14:89–106
Posada D, Crandall KA (1998) Modeltest: testing the model of DNA substitution. Bioinformatics 14(9):817–818
Porter CA, Sampaio I, Schneider H, Schneider MPC, Czelusniak J, Goodman M (1995) Evidence on primate phylogeny from ε-globin gene sequences and flanking regions. J Mol Evol 40:30–55
Poux C, Douzery EJP (2004) Primate phylogeny, evolutionary rate variations, and divergence times: a contribution from the nuclear gene IRBP. Am J Phys Anthropol 124:1–16
Raaum RL, Sterner KN, Noviello CM, Stewart C-B, Disotell TR (2005) Catarrhine primate divergence dates estimated from complete mitochondrial genomes: concordance with fossil and nuclear DNA evidence. J Hum Evol 48:237–257
Rabinowitz P, Coffin M, Falvey D (1983) The separation of Madagascar and Africa. Science 220:67–69
Racey PA, Sephenson PI (1996) Reproductive and energetic differentiation of the Tenrecidae of Madagascar. In: Lourenço WR (ed) Biogéographie de Madagascar. Editions de l'ORSTOM, Paris, pp 307–319

Roos C, Schmitz J, Zischler H (2004) Primate jumping genes elucidate strepsirhine phylogeny. Proc Natl Acad Sci USA 101:10650–10654

Schmidt HA, Strimmer K, Vingron M, von Haeseler A (2002) TREE-PUZZLE: maximum likelihood phylogenetic analysis using quartets and parallel computing. Bioinformatics 18:502–504

Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG (1997) The CLUSTAL_X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Res 25:4876–4882

Thorne JL, Kishino H, Painter IS (1998) Estimating the rate of evolution of the rate of molecular evolution. Mol Biol Evol 15:1647–1657

Wallace AR (1892) Island life. MacMillan, London

Wayne RK, Benveniste RE, Janczewski DN, O'Brien SJ (1989) Molecular and biochemical evolution of the Carnivora. In: Gittleman JL (ed) Carnivore behavior, ecology, and evolution, vol 1. Cornell University Press, Ithaca, NY, pp 465–494

Yang Z (1997) PAML: a program for package for phylogenetic analysis by maximum likelihood. Comput Appl Biosci 15:555–556

Yoder AD (1997) Back to the future: a synthesis of strepsirhine systematics. Evol Anthropol 6:11–22

Yoder AD, Burns MM, Zehr S, Delefosse T, Veron G, Goodman SM, Flynn JJ (2003) Single origin of Malagasy Carnivora from an African ancestor. Nature 421:734–737

Yoder AD, Vilgalys R, Ruvolo M (1996) Molecular evolutionary dynamics of cytochrome *b* in strepsirhine primates: the phylogenetic significance of third-position transversions. Mol Biol Evol 13:1339–1350

Yoder AD, Yang Z (2004) Divergence dates for Malagasy lemurs estimated from multiple gene loci: geological and evolutionary context. Mol Ecol 13:757–773

Chapter 4
Organismal Biology, Molecular Systematics, and Phylogenetic Reconstruction

Jeffrey H. Schwartz

Abstract DNA sequence data enjoys the singular position of being the arbiter of phylogenetic relationships; yet the justifications for this endeavor—the notions of continual molecular change, and that the degree of overall similarity reflects recency of divergence from a common, constantly changing ancestral sequence—was based on studies of bacteria not multicellular organisms. This is important because ca. 98% of a bacterial genome codes for metabolically active proteins, while a similar proportion in the metazoan genome is dedicated to the regulation of development. Consequently, random mutation in the metazoan genome would likely lead to organismal failure, not survival, which suggests that sequence similarity in this region reflects primitive retention (= nonchange). Further, since metazoan mtDNA and the ca. 2% coding region are involved in metabolic processes, demonstration of taxic similarity in these nucleotide sequences is likely to reflect similar physiological adaptation, not evolutionary history.

Resume Les données génétiques moléculaires bénéficient d'une singulière place d'arbitre des relations phylogénétiques ; et pourtant la justification de cette ambition—la notion de changement moléculaire continu, et celle selon laquelle le degré de similarité reflète l'ancienneté de la divergence d'une séquence ancestrale qui change continuellement—se fonde sur l'étude des bactéries, et non celle des organismes multicellulaires. Ce fait est important parce que 98% du génome bactérien code pour des protéines métaboliquement actives, alors que dans le génome des Métazoaires, une proportion similaire est dédiée à la régulation du développement. Ainsi, chez les Métazoaires, les mutations sont le plus souvent fatales, se qui suggère que les séquences similaires reflètent des rétentions primitives, et non des

J.H. Schwartz (✉)
Departments of Anthropology and History and Philosophy of Science,
University of Pittsburgh, Pittsburgh, PA 15260, USA
e-mail: jhs@pitt.edu

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_4,

changements. De plus, puisque l'ADN mitochondrial et 2% de l'ADN nucléaire sont impliqués dans le métabolisme, les séquences de nucléotides similaires reflètent des adaptations physiologiques, plutôt que l'histoire évolutive.

Introduction

Although molecular systematics began to crystallize as a discipline in the 1960s, it was not until the late 1980s that it became commonplace for hypotheses of phylogenetic relationship to be presented as definitive statements of relatedness that trumped those based on comparative morphology. Indeed, the widespread belief in the infallibility of molecular analyses in divining phylogenetic relationships is so strongly entrenched that an appreciation of the uncertainty of reconstructing an evolutionary history and pattern of relatedness is all but forgotten. Disappeared from the literature are the debates that during the 1970s and early 1980s filled the pages of journals such as *Systematic Zoology* (now *Systematic Biology*) and *Cladistics* about how one might in theory and in practice attempt to reconstruct an evolutionary past that, because of its singularity, cannot be proven. Consequently, the best one could do was adopt a hypothetico-deductive approach to phylogenetic reconstruction, generate alternative theories of relatedness, and then strive to falsify them (Kitts 1977; Popper 1962, 1968; Wiley 1975). The theory of relatedness that most consistently resisted falsification became the working hypothesis until other data led to its demise.

The debates over how to generate and test theories of relatedness ensued from Hennig's (1966) ideation of phylogenetic systematics known as cladistics. In contrast to the tradition of determining closeness of relatedness on the basis of overall degrees of similarity, a cladistic analysis emphasized the hierarchical nature of shared, derived characters (Eldredge and Cracraft 1980). Thus while two taxa (A and B) may share more features than either does with a third (C), a broad comparison could demonstrate that most features A and B share are present in many other taxa, whereas most features A or B and C share are unique to this pair alone. The theory is that more uniquely shared features indicate more recent common ancestry, while more widely shared features have been retained from a more distant common ancestor. That is, while the demonstration of greater overall similarity between A and B might be real, it need not be phylogenetically significant in terms of closeness of relationship because most of these shared features could be primitive retentions.

A cladistic approach also forces one to confront situations in which more than one hypothesis of relationship emerges. In a broad comparison of taxa, one might not only demonstrate that A and B exclusively share certain features, suggesting that these taxa are closely related but also that A and C exclusively share other features, also implying a close relationship. Since there is only one evolutionary history, only one set of uniquely shared features, and thus only one theory of relationship can be correct; but it is only upon embracing one of the competing theories of relationship that one can deem the other similarities phylogenetically irrelevant

and interpret them as either primitive retentions or homoplasies (i.e., parallelisms, convergences, and reversals) (Schwartz 2008).

A Brief Historical Overview of Molecular Systematics

Nuttall (1904) was among the first to infer evolutionary relatedness among an array of animals from relative degrees of immunological reactivity between blood sera and antisera, but this approach lay fallow until Zuckerkandl and Pauling (1962) cross-reacted hemoglobin from a fish, chicken, horse, gorilla, and human with the antihemoglobins produced in host organisms. The question of including fish along with free oxygen-breathing vertebrates notwithstanding, hemoglobin/antihemoglobin cross-reactions yielded a familiar sequence of apparent increasing similarity (fish (chicken (horse (gorilla, human)))).

Of longer lasting importance, however, was Zuckerkandl and Pauling's interpretation of this pattern of similarity, which they declared "can be understood at once if it is *assumed* [emphasis added] that in the course of time the hemoglobin-chain genes duplicate, [and] that the descendants of the duplicate genes 'mutate away' from each other" (p. 233). Consequently, "over-all similarity must be an expression of evolutionary history" with descendants "mutating away" and becoming "gradually more different from each other" (p. 233). Lineages that diverged earlier were more different because they had more time over which to accumulate molecular change, while more recently diverged lineages had had less time for molecular differences to accrue. Zuckerandl and Pauling concluded that the taxa showing the greatest degree of molecular similarity are the most closely related, with greater degrees of dissimilarity indicating increasingly distant relationships. Crucial here are the assumptions that lineages exist and are in constant states of gradual change.

But these assumptions do not derive from the data themselves; for, as with the discovery of fossils [including the recently found "intermediates" between primitive and crown-clade flatfish (Friedman 2008)], demonstrations of similarity or dissimilarity provide only static data points that by themselves reveal nothing about evolutionary tempo or mode. Rather, by 1962, the gradualism of the modern evolutionary synthesis had become the only way in which to conceive evolutionary change: typically ploddingly slow but always in constant motion. Indeed, in defense of their brainchild, the founders of the synthesis aggressively squelched alternative models, such as Goldschmidt's (1940) systemic mutations and Schindewolf's (1993) stepwise leaps, or ignored them altogether, such as Waddington's (1940) epigenetic landscapes. But like nineteenth century saltationism, these alternatives conceived evolution in terms of alterations early in development, which led to the conclusion that evolutionarily significant change must be rapid, and the emergent novelty functional. Consequently, when Zuckerkandl and Pauling sought an evolutionary model to explain their observations of similarity and dissimilarity, the only one available was the constant gradualism of the synthesis, which seemed to have been validated by earlier work on bacterial genomes.

Is a Bacterial Model Appropriate?

Arguably the most influential experiments during the formative years of DNA research were Jacob and Monod's (1959) studies of the effects of glucose-rich and -depauperate environments on bacteria. Depending on the "environmental condition," bacteria responded or "adapted" by inducing different levels of lactose-metabolizing enzymes. The experiments demonstrated that bacterial genes are associated with regulatory sequences that bind proteins to activate or suppress gene transcription. The concept was extended to multicellular organisms, although their genomic organizations differ markedly from those of bacteria.

About 98% of a bacterial genome is coding (i.e., encodes inducible, metabolically active proteins, production of which is linked to the cell's nutritional status), while the remaining ca. 2% is not (i.e., represents promoter region) (Eisen 2000). MtDNA, because of endosymbiosis, is bacterial in nature and shares this distribution. In metazoans and plants, however, the situation is essentially reversed (Eisen 2000; Goff et al. 2002): ca. 2% of the genome codes for inducible proteins, while much of the remaining ca. 98% is intimately tied to the regulation of development and tissue differentiation. Because in the Darwinian paradigm evolution is adaptation writ large, bacterial genomic change is referred to interchangeably as adaptive and evolutionary (Lenski and Travisano 1994), while for mtDNA, change is typically referred to as evolutionary. The problem arises when extrapolating from bacteria to multicellular organisms.

If mutations were equally likely to occur at any point along a nucleotide sequence, the probability of a mutation affecting promoter and control regions or introns (which appear to have a regulatory function at least early on) in multicellular organisms would be much greater than that for coding regions (Schwartz and Maresca 2006). Coordination of the interplay between transcription factors and other regulatory molecules and promoter and control regions is crucial to proper development; so if mutations were unconstrained, mortality would be high (because embryos would not be viable) and morphological novelty should appear in virtually every generation (Schwartz and Maresca 2006). However, as Victorian evolutionists including Darwin knew, like tends to beget like. Indeed, because developmental regulation is so highly constrained (Gerhart and Kirschner 1997), we expect the vast majority of a multicellular organism's DNA to remain stable and unchanged—which, of course, is precisely the effect that myriad heat shock proteins and other housekeeping molecules have while maintaining DNA homeostasis (Maresca and Schwartz 2006). Consequently, rather than reflecting the recent divergence of taxa (and thus a shared predivergent lineage that underwent continual molecular change), molecular similarities between taxa are plausibly interpreted as the absence of change, or, in cladistic terminology, primitive retentions (Schwartz 2005).

Adaptation Versus Evolution

When bacteria and mitochondria respond to changes in their environment, they are adapting, not evolving; thus if bacterial and mtDNA sequence similarity is not the result of primitive retention, it is more likely due to similar cellular adaptation than phylogenetic propinquity. Since most of a bacterium's genome encodes inducible proteins, most of its DNA reflects a direct relationship between "genes" and proteins. In contrast, a small fraction of a multicellular organism's genome is geared to responding to environmental circumstances, while the majority is involved in the regulation of development, which, of course, does not apply to bacteria. Consequently, if one does turn to molecular data for the determination of phylogenetic relationships of multicellular organisms, it would be more appropriate to focus on the details of signaling pathways—because they produce the organism—than on DNA sequences. Indeed, even though fruit flies and mice, for example, differ in the number of orthologous homeobox genes affecting segmentation and spatial positioning of appendages (Duboule and Dollé 1989), there is abundant evidence that differences between invertebrates (fruit flies and other insects) and vertebrates (e.g., zebrafish, frogs, mice, and humans) are due less to specific gene differences than to different ways—in time and space—in which the same developmental molecules are recruited and interact (Duboule and Dollé 1989; Stern et al. 2006). Once an evolutionary novelty, such as the arthropod body plan or the vertebrate tooth-bearing jaw, is established, modification of the underlying signaling pathway—not of the DNA sequences—produces different versions of the basic organization (Hulsey et al. 2006; Ronshaugen et al. 2002).

Conclusion

Although the assumptions upon which molecular systematics rests have been elevated to the level of scientific truth, increasing understanding of the molecular basis of multicellular organismal development makes more obvious the need to revisit them. The generally accepted notion of DNA as the blueprint of life, while a catchy phrase, not only relies too heavily on the linear bacterial organization of DNA into genes for specific proteins but also fails to recognize alternative intron splicing and the importance of epigenetic events (e.g., maternally induced DNA methylation, the role of RNA in "reintroducing" DNA nucleotide sequences not present in the P_1 generation but present in earlier generations) in development (Lolle et al. 2005; Rassoulzadegan et al. 2006; Stotz 2006).

The forgoing discussion also provides reason to return to morphologically based systematics because of the tightly constrained linkage between molecular signaling pathways and morphology. Developmentally there is a hierarchy of instructional information from gene regulatory networks (GRNs) fundamental to establishing basic body plans to differentiation gene batteries (DGBs) involved in the terminal differentiation of tissues and structures (Davidson and Erwin 2006). Different levels

of diversification of GRNs underlie taxic diversity, from major clades to subclades and the species that form them, which would require the alteration of signaling pathways. The DGBs provide the between-individual variability that typifies all species and result from different intensities of expression of extant signaling pathways.

As a systematist who began his career investigating the phylogenetic relationships of prosimians from the perspective of morphology and development, I look forward to a rejuvenated return to the concerns of organismal biology.

Acknowledgments I thank Judith Masters for the opportunity to share these views, Bruno Maresca for inspiring me toward them, and two reviewers for offering suggestions for their clarification.

References

Davidson EH, Erwin DH (2006) Gene regulatory networks and the evolution of animal body plans. Science 311:796–800

Duboule D, Dollé P (1989) The structural and functional organization of the murine HOX gene family resembles that of *Drosophila* homeotic genes. EMBO J 8:1497–1505

Eisen JA (2000) Assessing evolutionary relationships among microbes from whole-genome analysis. Curr Opin Microbiol 3:475–480

Eldredge N, Cracraft J (1980) Phylogenetic patterns and the evolutionary process: method and theory in comparative biology. Columbia University Press, New York

Friedman M (2008) The evolutionary origin of flatfish asymmetry. Nature 454:209–212

Gerhart J, Kirschner M (1997) Cells, embryos, and evolution: toward a cellular and developmental understanding of phenotypic variation and evolutionary adaptability. Blackwell, Malden, MA

Goff SA et al (2002) A draft sequence of the rice genome (*Oryza sativa* L. ssp. *japonica*). Science 296:92–100

Goldschmidt RB (1940) The material basis of evolution. Yale University Press, New Haven

Hennig W (1966) Phylogenetic systematics. University of Chicago Press, Chicago

Hulsey CD, Fraser GJ, Streelman JT (2006) Evolution and development of complex biomechanical systems: 300 million years of fish jaws. Zebrafish 2:243–257

Jacob F, Monod J (1959) Genes of structure and genes of regulation in the biosynthesis of proteins. C R Hebd Seances Acad Sci 249:1282–1284

Kitts DB (1977) Genes of structure and genes of regulation in the biosynthesis of proteins. Syst Zool 26:185–194

Lenski RE, Travisano M (1994) Dynamics of adaptation and diversification: a 10,000-generation of experiment with bacterial populations. Proc Natl Acad Sci USA 91:6808–6814

Lolle SJ, Victor JL, Young JM, Pruitt RE (2005) Genome-wide non-Mendelian inheritance of extra-genomic information in *Arabidopsis*. Nature 434:505–509

Maresca B, Schwartz JH (2006) Sudden origins: a general mechanism of evolution based on stress protein concentration and rapid environmental change. Anat Rec B New Anat 2898:38–46

Nuttall GHF (1904) Blood immunity and blood relationship. Cambridge University Press, Cambridge

Popper KR (1962) Conjectures and refutations: the growth of scientific knowledge. Routledge and Kegan Paul, London

Popper KR (1968) The logic of scientific discovery. Harper Torchbooks, New York

Rassoulzadegan M, Grandjean V, Gounon P, Vincent S, Gillot I, Cuzin F (2006) RNA-mediated non-Mendelian inheritance of an epigenetic change in the mouse. Nature 441:469–474

Ronshaugen M, McGinnis N, McGinnis SW (2002) Hox protein mutation and macroevolution of the insect body plan. Nature 415:914–917

Schindewolf O (1993) Basic questions in paleontology: geologic time, organic evolution, and biological systematics (trans: Schaefer J). University of Chicago Press, Chicago

Schwartz JH (2005) The Red Ape: Orangutans and Human Origins. Westview Press, Boulder, CO

Schwartz JH (2008) Cladistics. In: Regal B (ed) Icons of evolution. Greenwood Press, Westport, CT, pp 517–544

Schwartz JH, Maresca B (2006) Do molecular clocks run at all? A critique of molecular systematics. Biol Theory 1:1–15

Stern CD, Charité J, Deschamps J, Duboule D, Durston AJ, Kmita M, Nicolas J-F, Palmeirem I, Smith JC, Wolpert L (2006) Head-tail patterning of the vertebrate embryo: one, two or many unresolved problems? Int J Dev Biol 50:3–15

Stotz K (2006) With 'genes' like that, who needs an environment? Postgenomics's argument for the 'Ontogeny of Information'. Philos Sci 73:905–917

Waddington CH (1940) Organisers and genes. Cambridge University Press, Cambridge

Wiley EO (1975) Karl R. Popper, systematics, and classification: a reply to Walter Bock and other evolutionary taxonomists. Syst Zool 24:233–243

Zuckerkandl E, Pauling L (1962) Molecular disease, evolution, and genic heterogeneity. In: Kasha M, Pullman B (eds) Horizons in biochemistry. Academic, New York, pp 189–225

Chapter 5
Is Temporal Plasticity in Lemurs a Strategy for Dealing with Unpredictable or Predictable, Seasonal Environments?

Deborah J. Curtis and Giuseppe Donati

Abstract Madagascar is unique among tropical regions, in that its diverse habitats pose numerous challenges to the animals inhabiting them, with different degrees of environmental unpredictability, seasonality, frequent droughts, and cyclones. We review the temporal strategies that two groups of lemurs, the lemurids and the cheirolgaleids, have evolved to deal with these factors and that are rare and unique, respectively, among primates. These strategies, cathemerality (day/night activity) and torpor/hibernation, may be the key to their broad distribution within Madagascar and their success in all habitat types on the island, as these lemurs can respond rapidly to abiotic and biotic variation and avoid the time and seasonal constraints placed on other primates.

Resume Madagascar est unique, dans le monde tropical, du fait de sa diversité d'habitats qui pose de nombreux problèmes aux animaux, comme différents niveaux d'imprévisibilité et de saisonnalité, ainsi que de fréquentes sécheresses et cyclones. Nous passons en revue les stratégies temporelles, rares (cathéméralité = activité diurne et nocturne) ou même uniques (torpeur et hibernation) chez les primates, et rencontrées dans deux groupes de lémuriens, les Lémuridés et les Cheirogaleidés, en réponse à ces conditions environnementales. Ces stratégies pourraient être la

D.J. Curtis (✉)
School of Human and Life Sciences, Roehampton University,
Holybourne Avenue, London SW15 4JD, UK

Nocturnal Primate Research Group, School of Social Sciences and Law,
Oxford Brookes University, Oxford OX3 0BP, UK
e-mail: curtis@scimedtrans.co.uk

G. Donati
Nocturnal Primate Research Group, School of Social Sciences and Law,
Oxford Brookes University, Oxford OX3 0BP, UK
e-mail: gdonati@brookes.ac.uk

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_5,

raison de leur large distribution à Madadagascar et leur succès dans tous les habitats de l'île, dans la mesure où ces lémuriens sont capables de répondre rapidement aux variations abiotiques et abiotiques et ainsi éviter les contraintes temporelles et saisonnières qui affectent les autres primates.

Unpredictability and Seasonality on Madagascar

Madagascar has been called a small continent because of its varied topography and regional climatic differences (Martin 1972). The island also exhibits numerous distinctive features when compared with other tropical regions. One of these is the unpredictability of its environment, with variability in rainfall patterns and food availability, and the occurrence of droughts and cyclones (Ganzhorn et al. 1999; Wright 1999; Dewar and Richard 2007). Dewar and Richard (2007) have shown that rainfall is highly unpredictable: the east is subjected to high intra-annual variation in precipitation and low seasonality and the north, south, west, and center exhibit high interannual variation in rainfall and greater seasonality. The west shows a north–south gradient, characterized by a decrease in annual rainfall and an increase in intra- and interannual variation in precipitation. These conditions have probably prevailed since the Indian Ocean monsoon system started to affect Madagascar approximately 5 Mya (Wells 2003). This unpredictability is likely to have played a central role in the evolution of some of the unusual temporal strategies seen in lemurs but absent or very rare in other primates, i.e., hibernation/torpor and cathemerality (Fietz and Dausmann 2006; Curtis et al. 2006).

In contrast to its unpredictable environment, Madagascar does not exhibit extreme seasonality in comparison with other tropical regions (Dewar and Richard 2007). However, seasonality underlies hibernation/torpor and variation in cathemeral activity in all types of environment in Madagascar (Fietz and Dausmann 2006; Curtis et al. 2006). Seasonal changes affect many aspects of lemur behavior, and underlying this is photoperiodic change. Photoperiod exhibits little interannual variation and is therefore highly predictable and provides a seasonal cueing mechanism that is present even if the environment itself is aseasonal (e.g., rainfall). These cues trigger the temporal strategies that lemurs have evolved for dealing with lean, bottleneck periods in all habitat types on Madagascar with respect to timing of reproduction (all lemurs except *Daubentonia*; van Horn 1980; Sterling 1994), torpor/hibernation (cheirogaleids; Fietz and Dausmann 2006), and activity rhythms (lemurids; Curtis et al. 2006). Analyses of hair growth, body fat, and metabolism have also demonstrated that captive lemurids show physiological adaptations for energetic optimization to different photoperiodic conditions (Pereira et al. 1999). The physiological mechanism involves the transduction of the light–dark ratio into an internal endocrine signal that coordinates seasonal responses (Halle and Stensteth 2000).

In this chapter, we review temporal programs in lemurs and examine the potential roles that seasonality, photoperiod, and unpredictability may have played in their evolution.

Temporal Programs

Time acts as a constraint on many primates. This is particularly true at high latitudes, where variation in day length is greater and seasonality in the availability of resources is more marked. Most primates are constrained by their anatomical and physiological adaptations to either a diurnal or a nocturnal lifestyle and compensate for short days or short nights, respectively, through behavioral flexibility. For example, diurnal baboons (*Papio hamadryas ursinus*) adapt their time budgets and group sizes to a latitudinal gradient in the Southern Hemisphere (Hill et al. 2003). Time spent feeding, moving, grooming, and resting are all positive functions of day length. The same holds true in the Northern Hemisphere for Japanese macaques (*Macaca fuscata*; Agetsuma and Nakagawa 1998). A clear constraint due to annual variation in night length is also evident in nocturnal galagos (*Galago moholi*) in South Africa (Curtis et al. 2006). Thus, the oscillation in the day/night cycle represents a significant bottleneck for primates unable to extend their activity into the "opposite" phase of the 24-h cycle or escape into torpor or hibernation.

Cathemerality

This term describes a rhythm in which activity occurs during both the light and the dark portions of the 24-h cycle (Tattersall 1987). It is common in many mammals, but rare in primates, and has thus far only been documented in lemurids (*Eulemur* spp., *Hapalemur* spp., *Lemur catta*) and some South American populations of *Aotus* (Cebidae) (Curtis et al. 2006; Donati et al., in press). Cathemeral lemurs cope with the different challenges posed by night and day through visual morphological characteristics that are intermediate between those found in diurnal and nocturnal primates (Curtis et al. 2006). The adaptive value of cathemerality has been linked to thermoregulation, predator avoidance, avoidance of interspecific competition, and temporal availability, quality and digestibility of food (Curtis et al. 2006; Donati et al. 2007). Three different cathemeral modes have been described (Rasmussen 1999): in Mode A, activity alternates on a seasonal basis between the day (austral summer) and night (austral winter); Mode B is an alternation between mainly diurnal (austral summer) and 24-h activity (austral winter); and Mode C describes year-round 24-h activity.

Cathemerality, seasonality, and photoperiod. Photoperiod provides the main cues for onset and cessation of activity (triggers: sunrise/sunset), as well as for seasonal changes in activity (trigger: light-dark ratio). Unlike genetically determined diurnal and nocturnal activity rhythms, cathemerality in primates results from modulation of the endogenous nocturnal activity cycle by external factors (e.g., light intensity) that either stimulate or inhibit activity at certain times of the 24-h period (Erkert 1989). There is some indication that the austral equinoxes (L:D 12:12) trigger the changes in ratios of nocturnal to diurnal activity in cathemerality (Kappeler and

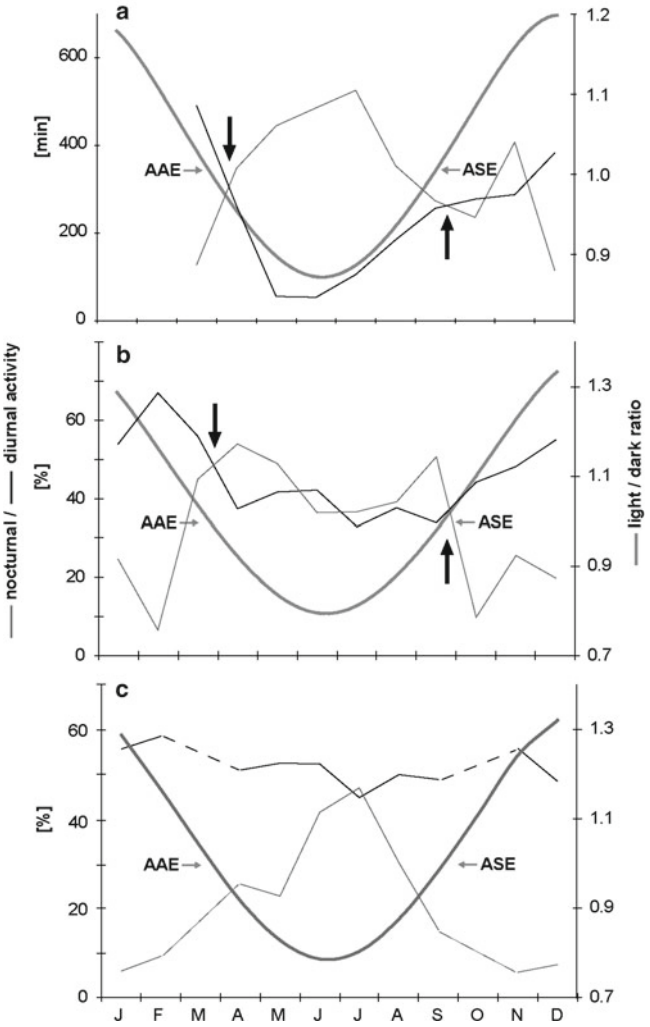


Fig. 5.1 Mean monthly nocturnal and diurnal activity compared with annual changes in the light/dark ratio (Thomas and Curtis 2001) at (**a**) Anjamena, north-western Madagascar (16°03′S; 45°55′E) for *Eulemur mongoz* (no data for January and February), (**b**) Sainte Luce, south-eastern Madagascar (24°45′S; 47°11′E) for *E. collaris*, and (**c**) Berenty, southern Madagascar (25°03′S; 46°18′E) for *E. fulvus* × *E. collaris* hybrids (no data for March and October) (Curtis et al. 1999; Donati et al. 2007, 2009). *Black arrows* indicate when the seasonal shift in activity occurs, just after the equinoxes (*AAE* austral autumnal equinox, *ASE* austral spring equinox). In (**a**) and (**b**) the shift applies to both nocturnal and diurnal activity, while in (**c**) this only applies to nocturnal activity. Because we have no data for the months of the equinoxes, however, we have not inserted arrows in (**c**)

Erkert 2003; Curtis et al. 2006). Figure 5.1 shows how at different latitudes and in very different environments, seasonal changes in activity may be linked to the equinoxes. In more predictable, seasonally dry forest in the west, *E. mongoz* shifts

its activity from being predominantly diurnal during the austral summer to predominantly nocturnal during the austral winter (Fig. 5.1a; Mode A); in the less seasonal and more unpredictable littoral forest in the south-east, *E. collaris* exhibits a shift from mainly diurnal activity in the austral summer to 24-h activity in the austral winter (Fig. 5.1b; Mode B) and in seasonally dry gallery forest in the more unpredictable south, *E. fulvus* × *E. collaris* hybrids exhibit no shift in diurnal activity but a similar trend for nocturnal activity (Fig. 5.1c; Mode B) (Curtis et al. 1999; Donati et al. 2007, 2009). Photoperiod thus provides a reliable cue for temporal activity shifts in cathemeral lemurs in both seasonal and less seasonal habitats.

Cathemerality and unpredictability. In highly predictable environments, a genetically fixed temporal program is probably adaptive, while extreme variability and unpredictability demand rapid and variable responses to environmental fluctuations (Halle and Stensteth 2000). The plasticity observed in the temporal programs of cathemeral lemurs may thus be an adaptation for coping with unpredictable environments. Although the long-term data do not yet exist to assess the advantages of cathemerality in the face of interannual variation, we present two examples of how it allows lemurs to respond to intra-annual variation.

In the fairly predictable seasonally dry forests of west Madagascar, Figure 5.1a shows that there is a shift back to more nocturnal activity in November for Eulemur mongoz, when the overall trend indicates a shift towards more diurnal activity. This coincides with when canopy cover is lowest in density, the infants are first moving about independently and the nesting season for raptors. While the raptors' nesting season is predictable from one year to the next, this nevertheless demonstrates the capacity to shift into a different temporal phase in the short-term (Curtis et al., 1999).

Figure 5.1b represents the activity rhythm shown by *Eulemur collaris* in the more unpredictable environment of the littoral forests in south-eastern Madagascar. The mid-year decrease in nocturnal activity coincided with unusually high levels of rainfall in July 2000 (≈800 mm) as compared with the average rainfall (≈200 mm) for 2001 and 2002. Donati et al. (2007) demonstrated that, once the effects of moonlight and day length (the two proximate factors that most influenced their activity) had been removed, the availability of ripe fruits was a good predictor of variation in activity rhythm. *E. collaris* responded to bottlenecks in fruit availability by increasing nocturnal activity, extending their diurnal activity when ripe fruit was abundant. There was no correlation between rainfall and fruit availability.

Torpor and Hibernation

Compared with other primates, lemurs have evolved different solutions to overcome energy shortages and time constraints during lean periods. One of these is to reduce energy expenditure through torpor or hibernation, both of which involve a reduction in basal metabolic rate (but not necessarily a drop in body temperature, Dausmann et al. 2004), with the former lasting several hours and the latter, weeks (Geiser and Ruf 1995).

Torpor and hibernation are common strategies in small mammals and birds living in highly seasonal or unpredictable climatic conditions (Geiser and Ruf 1995), but among primates, they only occur in the cheirogaleids *Microcebus* and *Cheirogaleus* (Fietz and Dausmann 2006). The mouse lemurs, *Microcebus* spp., are known to use torpor not only for saving energy but also to reduce water requirements during the dry season (Ganzhorn et al. 2003). They have been shown to enter torpor in response to food restriction in captivity under both short and long photoperiods, but torpor was more prevalent at low ambient temperatures and under a short photoperiod (Génin and Perret 2003). In *M. murinus*, seasonal fattening, hypothermia, and daily torpor are directly triggered by photoperiod (Aujard et al. 1998; Génin and Perret 2000; Schmid 2001), while the seasonality of reproduction is controlled by a circannual endogenous rhythm (Perret and Aujard 2001). Dramatic climatic differences are evident between the western deciduous forests and the eastern rainforests, but shorter day length is probably associated with torpor in *Microcebus* spp. all over Madagascar (Atsalis 1999). A similar role is played by photoperiodic cues in synchronizing the annual cycle of hibernation in *Cheirogaleus* (Fietz and Dausmann 2006).

Conclusions

The unusual temporal programs we see in lemurs appear to constitute a successful strategy for dealing both with seasonality and with unpredictability. Given the extreme variability in different types of environments in Madagascar, exhibiting a variety of combinations of seasonality and aseasonality with intra- and interannual predictability and unpredictability, these temporal programs may well have contributed towards the radiation of these groups of lemurs across Madagascar. Lemurids and cheirogaleids are not constrained by photoperiodic changes but use these to trigger shifts in activity and hibernation/torpor, respectively, in both seasonal and less seasonal habitats. They also have the capacity to respond rapidly to abiotic and biotic variation and to thus cope with unpredictability and catastrophic events.

Acknowledgments We would like to thank Judith Masters and everyone else involved for organizing such a wonderful conference and Elke Zimmermann and Ute Radespiel for the invitation to participate in their symposium. Financial support was provided by Roehampton University for DJC to attend the Prosimians 2007 conference.

References

Agetsuma N, Nakagawa N (1998) Effects of habitat differences on feeding behaviors of Japanese monkeys: comparison between Yakushima and Kinkazan. Primates 39:275–289

Atsalis S (1999) Diet of the brown mouse lemur (*Microcebus rufus*) in Ranomafana National Park Madagascar. Int J Primatol 20:193–229

Aujard F, Perret M, Vannier G (1998) Thermoregulatory responses to variations of photoperiod and ambient temperature in the male lesser mouse lemur: a primitive or an advanced adaptive character. J Comp Physiol B 168:540–548

Curtis DJ, Zaramody A, Martin RD (1999) Cathemerality in the mongoose lemur, *Eulemur mongoz*. Am J Primatol 47:279–298

Curtis DJ, Donati G, Rasmussen MA (2006) Cathemerality. Folia Primatol 77:1–194

Dausmann KH, Glos J, Ganzhorn JU, Heldmaier G (2004) Hibernation in a tropical primate. Nature 429:825–826

Dewar RE, Richard AF (2007) Evolution in the hypervariable environment of Madagascar. Proc Natl Acad Sci USA 104:13723–13727

Donati G, Bollen A, Borgognini-Tarli SM, Ganzhorn JU (2007) Feeding over the 24-hour cycle: dietary flexibility of cathemeral collared lemurs (*Eulemur collaris*). Behav Ecol Sociobiol 61:1237–1251

Donati G, Baldi N, Morelli V, Ganzhorn JU, Borgognini-Tarli SM (2009) Proximate and ultimate determinants of cathemeral activity in brown lemurs. Anim Behav 77:317–325

Donati G, Santini L, Razafindramanana J, Boitani L, Borgognini-Tarli SM (in press) (Un-)expected nocturnal activity in "diurnal" *Lemur catta* supports cathemerality as one of the key adaptations of lemur radiation. Am J Phys Anthropol

Erkert HG (1989) Lighting requirements of nocturnal primates in captivity: a chronobiological approach. Zoo Biol 8:179–191

Fietz J, Dausmann KH (2006) Big is beautiful – fat storage and hibernation as a strategy to cope with marked seasonality in the fat-tailed dwarf lemur (*Cheirogaleus medius*). In: Gould L, Sauther ML (eds) Lemurs – ecology and adaptation. Springer, New York, pp 97–110

Ganzhorn JU, Wright PC, Ratsimbazafy J (1999) Primate communities: Madagascar. In: Fleagle JG, Janson CH, Reed KE (eds) Primate communities. Cambridge University Press, Cambridge, pp 75–89

Ganzhorn JU, Klaus S, Ortmann S, Schmid J (2003) Adaptations to seasonality: some primate and nonprimate examples. In: Kappeler PM, Pereira ME (eds) Primate life histories and socioecology. University of Chicago Press, Chicago, pp 132–148

Geiser F, Ruf T (1995) Hibernation versus daily torpor in mammals and birds: physiological variables and classification of torpor patterns. Physiol Zool 68:935–966

Génin F, Perret M (2000) Photoperiod-induced changes in energy balance in grey mouse lemurs. Physiol Behav 71:315–321

Génin F, Perret M (2003) Daily hypothermia in captive grey mouse lemurs (*Microcebus murinus*): effects of photoperiod and food restriction. J Comp Physiol B 136:71–81

Halle S, Stensteth NC (2000) Activity patterns in small mammals: an ecological approach. Springer, Berlin

Hill RA, Barrett L, Gaynor D, Weingrill T, Dixon P, Payne H, Henzi SP (2003) Daylength, latitude and behavioural (in)flexibility in baboons. Behav Ecol Sociobiol 53:278–286

Kappeler PM, Erkert HG (2003) On the move around the clock: correlates and determinants of cathemeral activity in wild redfronted lemurs *(Eulemur fulvus rufus)*. Behav Ecol Sociobiol 54:359–369

Martin RD (1972) Adaptive radiation and behaviour of the Malagasy lemurs. Philos Trans R Soc Lond B Boil Sci 264:295–352

Pereira ME, Strohecker RA, Cavigelli SA, Hughes CL, Pearson DD (1999) Metabolic strategy and social behavior in Lemuridae. In: Rakotosimamanana B, Rasamimanana H, Ganzhorn JU, Goodman SM (eds) New directions in lemur studies. Kluwer/Plenum, New York, pp 93–118

Perret M, Aujard F (2001) Regulation by photoperiod of seasonal changes in body mass and reproductive function in gray mouse lemurs (*Microcebus murinus*): differential responses by sex. Int J Primatol 22:5–24

Rasmussen MA (1999) Ecological influences on activity cycle in two cathemeral primates, *Eulemur mongoz* (mongoose lemur) and *Eulemur fulvus fulvus* (common brown lemur). Unpublished PhD thesis, Duke University, Durham, NC

Schmid J (2001) Daily torpor in free-ranging gray mouse lemurs (*Microcebus murinus*) in Madagascar. Int J Primatol 22:1021–1031

Sterling EJ (1994) Evidence for nonseasonal reproduction in wild aye- ayes (*Daubentonia madagascariensis*). Folia Primatol 62:46–53

Tattersall I (1987) Cathemeral activity in primates: a definition. Folia Primatol 49:200–202

Thomas RM, Curtis DJ (2001) A novel software application for the study of photoperiodic cueing mechanisms underlying circadian and circannual rhythms and lunar-periodic modulations. Folia Primatol 72:187. http://www.psgb.org/Software/index.html

Van Horn RN (1980) Seasonal reproductive patterns in primates. Prog Reprod Biol 5:181–221

Wells NA (2003) Some hypotheses on the Mesozoic and Cenozoic paleoenvironmental history of Madagascar. In: Goodman SM, Benstead JP (eds) The natural history of Madagascar. University of Chicago Press, Chicago, pp 16–34

Wright PC (1999) Lemur traits and Madagascar ecology: coping with an island environment. Yearb Phys Anthropol 42:31–72

Part II
General Ecology

Chapter 6
Life History Variation in Madagascar's Giant Extinct Lemurs

Laurie R. Godfrey, Gary T. Schwartz, William L. Jungers, Kierstin K. Catlett, Karen E. Samonds, Stephen J. King, Kathleen M. Muldoon, Mitchell T. Irwin, and David A. Burney

Abstract **Parmi** les lémuriens **existants**, la reproduction **lente** n'est pas nécessairement liée au ralentissement du développement dentaire ou à l'acquisition tardive de l'indépendance. La variation du développement dentaire **est indépendante** de la

L.R. Godfrey (✉)
Department of Anthropology, University of Massachusetts, 240 Hicks Way, Amherst, MA 01003, USA
e-mail: lgodfrey@anthro.umass.edu

G.T. Schwartz • K.K. Catlett
Institute of Human Origins, School of Human Evolution and Social Change, Arizona State University, Tempe, AZ 85287, USA
e-mail: garys.iho@asu.edu; kierstin.catlett@asu.edu

W.L. Jungers
Department of Anatomical Sciences, School of Medicine, Stony Brook University, Health Sciences Drive, Stony Brook, NY 11794, USA
e-mail: william.jungers@stonybrook.edu

K.E. Samonds
Department of Biological Sciences, Northern Illinois University, DeKalb, IL 60115, USA
e-mail: k.samonds@uq.edu.au

M.T. Irwin
Department of Anthropology, Northern Illinois University, DeKalb, IL 60115, USA
e-mail: m.irwin@uq.edu.au

S.J. King
Department of Anthropology, University of Massachusetts, 240 Hicks Way, Amherst, MA 01003, USA
e-mail: sking@anthro.umass.edu

K.M. Muldoon
Department of Anatomy, The Geisel School of Medicine at Dartmouth, Hanover, NH 03755, USA

Department of Anthropology, Dartmouth College, Hanover, NH 03755, USA
e-mail: kathleen.m.muldoon@dartmouth.edu

D.A. Burney
National Tropical Botanical Garden, 3530 Papalina Road, Kalaheo, HI 96741, USA
e-mail: dburney@ntbg.org

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_6,

taille **du corps** des adultes. Les lémuriens existants diffèrent des anthropoïdes de même taille dans leurs modèles de croissance et développement (maturation dentaire précoce, petite taille à la naissance, sevrage précoce). Nos études sur la microstructure dentaire, la chronologie, et le changement du relief topographique des dents nous ont permis de tirer des conclusions sur les histoires de vie de lémuriens disparus. Le développement dentaire de *Hadropithecus stenognathus* est semblable à celui des Hominoïdes, tandis que le développement dentaire extrêmement rapide en a caractérisé d'autres, même de corps plus grand comme *Palaeopropithecus*. L'âge du sevrage est très varié selon les espèces. Nous avons estimé l'intervalle entre des naissances successives de lémuriens géants, d'une manière conservatrice, à deux ou trois ans. Cette diversité est corrélée aux conditions environnementales. Certains Lémuriens disparus ont montré des convergences saisissantes avec les anthropoïdes de grande taille, en particulier des grands intervalles entre les naissances et des sevrages tardifs. C'étaient aussi les lémuriens avec le plus grand cerveau par rapport à la taille de leur corps.

Resume Chez les lémuriens actuels, la reproduction différée n'est pas nécessairement liée au ralentissement du développement dentaire ou à l'acquisition tardive de l'indépendance, et la variation en développement dentaire ne dépend pas de la taille corporelle des adultes. Les lémuriens actuels ont des croissances et des développements différents des anthropoïdes de tailles similaires (maturation dentaire précoce, petite taille à la naissance, sevrage précoce). Nos études sur la microstructure, la chronologie, et le changement du relief topographique des dents nous ont permis d'inférer les systèmes d'histoire de vie de lémuriens éteints. Le développement dentaire de *Hadropithecus stenognathus* ressemble à celui des Hominoïdes, tandis que celui de plus grands animaux, comme *Palaeopropithecus*, est beaucoup plus rapide. L'âge du sevrage est très varié. L'intervalle entre des naissances successives peut être estimé à deux ou trois ans. Cette diversité est corrélée aux conditions environnementales. Certains Lémuriens éteints montrent des convergences avec les grands anthropoïdes, en particulier de longs intervalles entre les naissances et un sevrage tardif. Ce sont aussi les lémuriens qui ont les capacités crâniennes les plus grandes, par rapport à leur tailles corporelles.

Introduction

Among extant lemur species, slow reproduction is not necessarily linked to slow dental development or to late acquisition of independence, and variation in the pace of dental development is independent of variation in adult body size. Sifakas, for example, have accelerated dental development, but a slow rate of reproduction resembling that of Old World monkeys (Richard et al. 2002). Nevertheless, sifakas and other lemurs have life history profiles that differ from those of anthropoids in several ways. First, fetal energy deposition rates are low in lemurs (Tilden 2008); neonates are small relative to like-sized anthropoids. Second, dental development is

often accelerated. Many lemur species are dentally precocious at birth, some (such as sifakas) extraordinarily so, and the molar crowns continue to form rapidly postnatally so that dental maturation is achieved early. Third, weaning occurs relatively early. Pronounced synchrony in the timing of weaning of several species occurs at some sites, coincident with the onset of the resource-rich rainy season (Wright 1999). Fourth, infant and juvenile mortality are relatively high, and female fertility remains high until death (Pochron et al. 2004). Finally, lemurs display minimal sexual dimorphism in growth (Leigh and Terranova 1998), and adults have relatively small brains (Godfrey et al. 2006a). Despite these generalities across species, lemurs are variable in the timing of reproduction, with some living species very anthropoid-like and others quite distinct.

Ross (1998) inferred slow life history profiles for giant extinct lemurs by analogy with extant large-bodied primates. However, mounting evidence shows that giant lemurs varied dramatically in their patterns of growth and development and consequently in life history parameters (Godfrey et al. 2002). In this chapter we ask: which (if any) of the giant lemurs were similar to anthropoids?

Estimating Reproductive Rates in Extinct Species

This aspect of paleontology is fraught with simplifying assumptions. Johnson (2002) regressed reproductive rates on log body masses for extant species representing nine mammalian families or superfamilies (including lemurs) and used these relationships to estimate reproductive rates for their extinct relatives using body mass estimates from the literature. His data for living lemurs showed a nonsignificant correlation between reproductive rate and log mass ($r=0.28$, $p=0.46$, $N=9$), and body mass may not be a good predictor of reproductive rate in lemurs. Indeed, Barrickman et al. (2008) suggest that brain size may be a better predictor of life history parameters.

We measured extinct lemur adult brain sizes (Godfrey et al. 2006a) and reconstructed their body masses using postcranial dimensions (Jungers et al. 2008). We then sought to derive reproductive rates independently of brain or body size estimates to assess (a) whether adult brain or body size predicts reproductive rate better in giant lemurs; (b) whether reproduction was slowest in the largest lemurs; and (c) the degree to which extinct lemurs resembled anthropoids in their life histories. To do this we used chronologies of dental development (Table 6.1) according to methods described elsewhere (Schwartz et al. 2002, 2005; Godfrey et al. 2006b, Catlett et al. 2010). Admittedly, certain aspects of the life history profiles of extinct species may be intractable. Infant mortality and lifespan are difficult to assess (but see Godfrey et al. 2002), but traits like molar crown formation time (CFT) can be measured accurately in fossils. We can also determine, for fossils with pristine dentition, the state of dental development at birth, the age at crown and root completion, and the approximate age at eruption of each molar. Using reconstructed rates of dental development together with occlusal wear, we can estimate weaning age. Gestation length can be estimated using prenatal developmental data. For example, if we assume that, among close relatives, M1 crown formation begins at roughly the same

Table 6.1 Life history parameters of extinct lemurs

Species	Body mass (kg)	Brain size (cc)	Gestation length (years)	Age at weaning (years)	IBI minimum (years)	IBI with seasonality (years)	Maximum reproductive rate (offspring/year)	Reproductive rate with seasonality
Archaeolemur majori	18.2	93	0.48	1.67	2.15	3.00	0.47	0.33
Hadropithecus stenognathus	35.4	106	0.52	3.04	3.56	4.00	0.28	0.25
Megaladapis edwardsi	85.1	136	0.68	1.04	1.72	2.00	0.58	0.50
Mesopropithecus globiceps	11.3	41	0.58	0.55	1.13	2.00	0.93	0.50
Palaeopropithecus ingens	41.5	80	0.88	0.50	1.38	2.00	0.72	0.50

For explanation of the methods we used to generate these numbers, see text and Catlett et al. (2010)

time relative to other prenatal events, we can use the relationship between gestation length and the timing of M1 initiation in living relatives to estimate gestation times in extinct species. Minimum interbirth intervals can be estimated by summing estimates for gestation length and weaning age, and maximum birth rates by taking the inverse of the minimum interbirth interval (assuming rare or nonexistent twinning). Assuming seasonality, a minimum interbirth interval is the number of whole years that accommodates gestation length and weaning age, and the maximum birth rate is the inverse of that number.

Results

Several generalizations can be drawn from our analyses. First, like extant lemurs, extinct lemurs initiated molar crown formation well before birth (Godfrey et al. 2006b). From this alone we infer that gestation was long (and must have exceeded 9 months in at least one species, *Palaeopropithecus ingens*, Schwartz et al. 2002). Age at weaning was variable among giant lemurs, conservatively estimated at 2 years for some species and 3 for others.

Figure 6.1 shows a principal component analysis of the correlation matrix for six life history parameters (body mass, brain volume, reproductive rate, interbirth interval, gestation length, and weaning age, all log transformed) in 32 anthropoid species (representing Atelidae, Cebidae, Cercopithecidae, Hylobatidae, and Hominidae) and 5 giant lemurs (*Mesopropithecus globiceps*, *Palaeopropithecus ingens*, *Archaeolemur majori*, *Hadropithecus stenognathus*, and *Megaladapis edwardsi*). Comparisons with extant lemurs are made elsewhere (Catlett et al. 2010). The first two axes comprise 93% of the variance. The first axis (85.2%) describes variation negatively correlated with reproductive rate and positively correlated with all other variables. The second axis (7.7%) describes variation positively correlated with gestation length and body mass but negatively correlated with brain size and weaning age. Large-bodied hominoids fall in the lower right portion of the graph. Two of the five extinct lemurs (*Archaeolemur* and *Hadropithecus*, Archaeolemuridae) resemble these species because they (1) weaned their young late and (2) had relatively large brains for their body mass.

Estimated maximum reproductive rates for the largest-bodied extinct lemurs in our analysis (*Palaeopropithecus ingens* and *Megaladapis edwardsi*) were not well predicted by their body masses (Fig. 6.2). Similar-sized anthropoids have lower reproductive rates, signaling slower life histories. In predicting reproductive rates, the residuals for extinct lemurs were significantly higher when log body mass (rather than log brain size) was selected as the explanatory variable. A paired *t*-test comparing giant lemur residuals from the two regressions was highly significant ($t = 7.3$, $df = 4$, $p < 0.002$). When log brain and log body mass were both entered into a multiple regression as possible explanatory variables ($F = 65.1$, $df = 2, 34$, $p < 0.001$, adjusted $R^2 = 0.78$), only log brain size was significant ($t = -3.5$, $p = 0.001$). Among giant lemurs, the species with the slowest life histories and longest apparent interbirth intervals are not the largest bodied but those with the relatively largest brains.

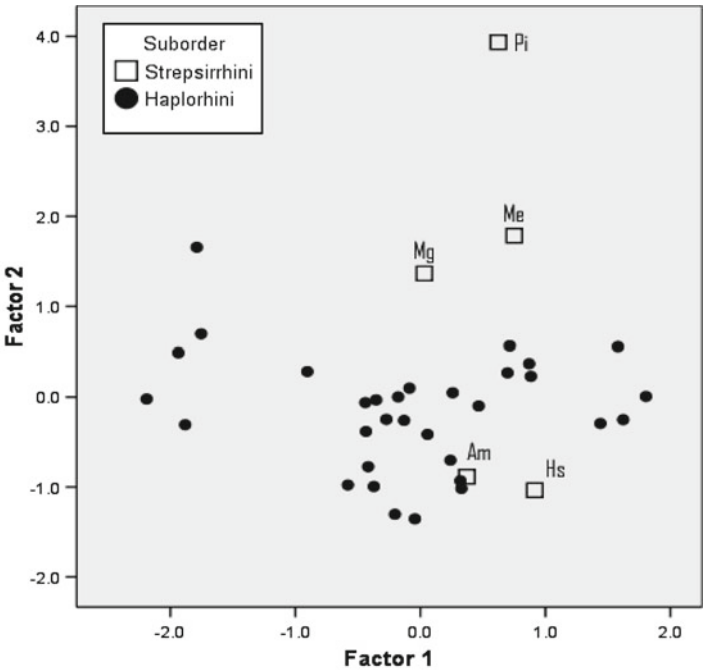


Fig. 6.1 Principal component analysis of life history characteristics of giant lemurs (*open squares*) and representative haplorhines (*solid circles*). Data sources available on request. Am = *Archaeolemur majori*; Hs = *Hadropithecus stenognathus*; Me = *Megaladapis edwardsi*; Mg = *Mesopropithecus globiceps*; Pi = *Palaeopropithecus ingens*. The two haplorhines that lie closest to *Archaeolemur majori* are *Papio hamadryas* and *Theropithecus gelada*. The haplorhines with the most negative scores on Factor 2 are *Cebus apella* and *C. capucinus*

Our reproductive rates estimated for extinct lemurs are maxima derived under assumptions of reproductive seasonality and nonseasonality and do not take into account infant mortality, which may have been high. We have no simple way of estimating which extinct lemurs would have been worst affected by infant mortality or how much such mortality would have lowered their reproductive rates. Even without this consideration, our estimated rates are low, not relative to large-bodied anthropoids but to other large-bodied mammals (Johnson 2002). In our statistical comparisons, we conservatively assumed no seasonality for *Archaeolemur* and *Hadropithecus* and seasonality for *Megaladapis*, *Palaeopropithecus*, and *Mesopropithecus* (thus reducing the inferred differences among taxa). Even the largest-bodied extant lemurs have seasonal reproduction; the only exceptions are species like *Hapalemur* that specialize on resources that are ubiquitous during the dry season or like *Daubentonia* that extract resources generally not available to other lemurs. Similar specializations probably characterized the Archaeolemuridae (Godfrey et al. 2008) which apparently had the slowest (and most anthropoid-like) reproductive rates.

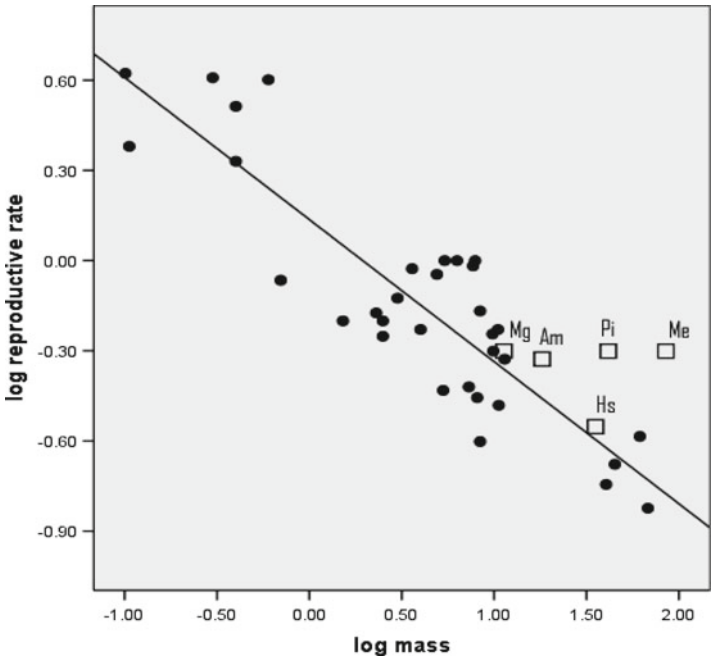


Fig. 6.2 Log reproductive rate (*Y*) vs. Log body mass (*X*) for extant haplorhine primates (*solid circles*) and extinct lemurs (*open squares*). The least squares fit for haplorhines only is shown. Note that all of the extinct lemurs fall above the line. $R^2 = 0.775$. Am = *Archaeolemur majori*; Hs = *Hadropithecus stenognathus*; Me = *Megaladapis edwardsi*; Mg = *Mesopropithecus globiceps*; Pi = *Palaeopropithecus ingens*

Discussion

It is, perhaps, unsurprising that the slowest reproduction was found among the most highly encephalized extinct lemurs. Among primates, adult brain size predicts life history variables like life expectancy, the duration of "immaturity" (i.e., gestation length + age at first reproduction), and interbirth interval better than does adult body mass (Sacher 1959; Harvey and Clutton-Brock 1985; Allman 1995; Barrickman et al. 2008). Protracted dental development is correlated with large brain size and late weaning (Godfrey et al. 2001). *Archaeolemur* spp. have been reconstructed as generalists with the capacity for hard object processing, somewhat like *Cebus* or *Daubentonia* (Godfrey et al. 2004, 2005). It is therefore interesting that *Cebus* and *Daubentonia* have similar dental morphology (bunodont molars endowed with very thick enamel) coupled with similarly high degrees of encephalization (Stephan et al. 1981, 1988; Gibson 1986; Sterling 1994; Godfrey et al. 2006a), and slow acquisition of foraging independence (Feistner and Ashbourne 1994; Godfrey et al. 2006a).

The most enigmatic extinct lemur is the remarkably anthropoid-like *Hadropithecus stenognathus*, a close relative of *Archaeolemur*. Microwear analysis using SEM (Rafferty et al. 2002), low magnification stereomicroscopy (Godfrey et al. 2004), and confocal microscopy (Scott et al. 2009) indicated that *Hadropithecus* was at least facultatively a hard object feeder. However, the heavy pitting on its enamel surfaces may reflect exogenous grit or dust. Stable isotope analysis demonstrates that, in southern Madagascar, *Hadropithecus* consumed CAM or C4 plants, while sympatric *Archaeolemur* relied heavily on C3 plants (Burney et al. 2004; Godfrey et al. 2005; Ryan et al. 2008; Crowley et al. 2011). Further research on plant material properties and stable isotopes may elucidate further details about the diet of *Hadropithecus* and how it relates to this species' pace of dental development.

Acknowledgments This chapter is dedicated to the late Dr. Gisèle Randria, Professor in the Département de Paléontologie et d'Anthropologie Biologique, Université d'Antananarivo, Madagascar, whose untimely death left a hiatus in a vibrant program. Our research was conducted under collaborative agreements with her department, as well as with the Académie Malgache, and supported by grants NSF BCS-0721233 to Patricia C. Wright, LRG, and Jukka Jernvall, NSF BCS-0237338 to LRG, NSF BCS-0503988 to GTS, and NSF BCS-0129185 to DAB, LRG and WLJ.

References

Allman J (1995) Brain and life span in catarrhine primates. In: Butler R, Brody J (eds) Delaying the onset of late-life dysfunction. Springer, New York, pp 221–241

Barrickman NJ, Bastian ML, Isler K, van Schaik CP (2008) Life history costs and benefits of encephalization: a comparative test using data from long-term studies of primates in the wild. J Hum Evol 54:568–590

Burney DA, Burney LP, Godfrey LR, Jungers WL, Goodman SM, Wright HT, Jull AJT (2004) A chronology for late prehistoric Madagascar. J Hum Evol 47:25–63

Catlett KK, Schwartz GT, Godfrey LR, Jungers WL (2010) "Life history space": a multivariate analysis of life history variation in extinct and extant Malagasy lemurs. Am J Phys Anthropol 143:391–404

Crowley BE, Godfrey LR, Irwin MT (2011) A glance to the past: subfossils, stable isotopes, seed dispersal, and lemur species loss in southern Madagascar. Am J Primatol 73:25–37

Feistner ATC, Ashbourne CJ (1994) Infant development in a captive-bred aye-aye (*Daubentonia madagascariensis*) over the first year of life. Folia Primatol 62:74–92

Gibson K (1986) Cognition, brain size and the extraction of embedded food resources. In: Else J, Lee P (eds) Primate ontogeny, cognition, and social behavior. Cambridge University Press, New York, pp 93–103

Godfrey LR, Samonds KE, Jungers WL, Sutherland MR (2001) Teeth, brains, and primate life histories. Am J Phys Anthropol 114:192–214

Godfrey LR, Petto AJ, Sutherland MR (2002) Dental ontogeny and life history strategies: the case of the giant extinct indroids of Madagascar. In: Plavcan JM, Kay R, Jungers WL, van Schaik C (eds) Reconstructing behavior in the primate fossil record. Kluwer/Plenum, New York, pp 113–157

Godfrey LR, Semprebon GM, Jungers WL, Sutherland MR, Simons EL, Solounias N (2004) Dental use wear in extinct lemurs: evidence of diet and niche differentiation. J Hum Evol 47:145–169

Godfrey LR, Semprebon GM, Schwartz GT, Burney DA, Jungers WL, Flanagan EK, Cuozzo FP, King SJ (2005) New insights into old lemurs: the trophic adaptations of the Archaeolemuridae. Int J Primatol 26:825–854

Godfrey LR, Jungers WL, Schwartz GT (2006a) Ecology and extinction of Madagascar's subfossil lemurs. In: Gould L, Sauther M (eds) Lemurs: ecology and adaptation. Springer, New York, pp 41–64

Godfrey LR, Schwartz GT, Samonds KE, Jungers WL, Catlett KK (2006b) The secrets of lemur teeth. Evol Anthropol 15:142–154

Godfrey LR, Jungers WL, Schwartz GT, Irwin MT (2008) Ghosts and orphans: Madagascar's vanishing ecosystems. In: Fleagle JG, Gilbert CC (eds) Elwyn Simons, a search for origins. Springer, New York, pp 361–395

Harvey P, Clutton-Brock T (1985) Life history variation in primates. Evolution 39:559–581

Johnson CN (2002) Determinants of loss of mammal species during the Late Quaternary 'megafauna' extinctions: life history and ecology, but not body size. Proc R Soc Lond B 269:2221–2227

Jungers WL, Demes B, Godfrey LR (2008) How big were the "giant" extinct lemurs of Madagascar? In: Fleagle JG, Gilbert CC (eds) Elwyn Simons, a search for origins. Springer, New York, pp 343–360

Leigh SR, Terranova CJ (1998) Comparative perspectives on bimaturism, ontogeny, and dimorphism in lemurid primates. Int J Primatol 19:723–749

Pochron ST, Tucker WT, Wright PC (2004) Demography, life history, and social structure in *Propithecus diadema edwardsi* from 1986–2000 in Ranomafana National Park, Madagascar. Am J Phys Anthropol 125:61–72

Rafferty KL, Teaford MF, Jungers WL (2002) Molar microwear of subfossil lemurs: improving the resolution of dietary inferences. J Hum Evol 43:645–657

Richard AF, Dewar RE, Schwartz M, Ratsirarson J (2002) Life in the slow lane? Demography and life histories of male and female sifaka (*Propithecus verreauxi verreauxi*). J Zool 256:421–436

Ross C (1998) Primate life histories. Evol Anthropol 6:54–63

Ryan TM, Burney DA, Godfrey LR, Göhlich U, Jungers WL, Vasey N, Ramilisonina, Walker A, Weber GW (2008) A reconstruction of the Vienna skull of *Hadropithecus stenognathus*. Proc Natl Acad Sci USA 105:10698–10701

Sacher G (1959) Relation of lifespan to brain weight and body weight in mammals. In: Wolstenholme G, O'Connor M (eds) CIBA foundation symposium on the lifespan of animals. Little, Brown, and Co., Boston, pp 115–133

Schwartz GT, Samonds KE, Godfrey LR, Jungers WL, Simons EL (2002) Dental microstructure and life history in subfossil Malagasy lemurs. Proc Natl Acad Sci USA 99:6124–6129

Schwartz GT, Mahoney P, Godfrey LR, Cuozzo FP, Jungers WL, Randria GFN (2005) Dental development in *Megaladapis edwardsi* (Primates, Lemuriformes): implications for understanding life history variation in subfossil lemurs. J Hum Evol 49:702–742

Scott JR, Godfrey LR, Jungers WL, Scott RS, Simons EL, Teaford MF, Ungar PS, Walker A (2009) Dental microwear texture analysis of two families of subfossil lemurs from Madagascar. J Hum Evol 56:405–416

Stephan H, Frahm H, Baron G (1981) New and revised data on volumes of brain structures in insectivores and primates. Folia Primatol 35:1–29

Stephan H, Baron G, Frahm H (1988) Comparative size of brains and brain components. In: Steklis HD, Erwin J (eds) Comparative primate biology, vol 4, Neurosciences. Alan R. Liss, New York, pp 1–38

Sterling EJ (1994) Aye-ayes: specialists on structurally defended resources. Folia Primatol 62:142–154

Tilden C (2008) Low fetal energy deposition rates in lemurs: another energy conservation strategy. In: Fleagle JG, Gilbert CG (eds) Elwyn Simons, a search for origins. Springer, New York, pp 311–318

Wright PC (1999) Lemur traits and Madagascar ecology: coping with an island environment. Yearb Phys Anthropol 42:31–72

Chapter 7
Population Genetics, Parasitism, and Long-Term Population Dynamics of *Microcebus murinus* in Littoral Forest Fragments of South-Eastern Madagascar

Jörg U. Ganzhorn, Andreas Hapke, Petra Lahann, Brigitte Raharivololona, Jean-Baptiste Ramanamanjato, Ernest Refaly, Jutta Schmid, Julia Schad, and Simone Sommer

Abstract Habitat fragmentation is a major threat for lemur conservation, as it reduces population sizes to levels that are nonviable in the long term. Alternatively, isolated populations may have great importance for conservation, as some are well

J.U. Ganzhorn (✉)
Animal Ecology and Conservation, Hamburg University,
Martin-Luther-King Platz 3, 20146 Hamburg, Germany
e-mail: ganzhorn@zoologie.uni-hamburg.de

A. Hapke
Institut für Anthropologie, Johannes-Gutenberg-Universität Mainz,
Colonel-Kleinmann-Weg 2, 55099 Mainz, Germany
e-mail: ahapke@uni-mainz.de

P. Lahann
Conservation Department, ZSL London ZOO, Outer Circle, Regent's Park, London, NW1 4RY, UK
petra.lahann@gmail.com

B. Raharivololona
Animal Ecology and Conservation, Hamburg University,
Martin-Luther-King Platz 3, 20146 Hamburg, Germany

Département de Paléontologie et Anthropologie Biologique,
Université d'Antananarivo, BP 906 Antananarivo 101, Madagascar
e-mail: brie536@hotmail.com

J.-B. Ramanamanjato • E. Refaly
QMM, BP 225 Tolagnaro (614), Madagascar
e-mail: jeanbaptiste.ramanamanjato@riotinto.com; refaly_ernest@hotmail.com

J. Schmid
Department Experimental Ecology, Albert-Einstein Allee 11, 89069 Ulm, Germany
e-mail: jutta.schmid@uni-ulm.de

J. Schad • S. Sommer
Animal Ecology and Conservation, Hamburg University, Martin-Luther-King Platz 3,
20146 Hamburg, Germany

Leibniz-Institute for Zoo and Wildlife Research, Alfred-Kowalke Str. 17 10315 Berlin, Germany
e-mail: jschad@web.de; SOMMER@izw-berlin.de

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_7,

protected and some lemurs do well even in small areas. Hence, knowing which characteristics indicate a population under threat is of paramount importance for conservation action. We studied *Microcebus murinus* populations confined to forest fragments of different sizes and states of degradation in south-eastern Madagascar to investigate relationships between population size, population dynamics, genetic diversity of coding and noncoding DNA, and infection rates by gut parasites. Population sizes decreased with decreasing fragment size and with increasing degradation. Population dynamics sampled over 9 years (equivalent to 9 generations in the littoral forest fragments) suggested a constant decline over time but several populations recovered unexpectedly, indicating substantial fluctuations in population size rather than a systematic trend. Sex ratios and parasite loads did not differ significantly between populations living in fragments of different size and degradation. Genetic diversity of noncoding DNA decreased with declining population size, but the diversity of the major histocompatibility complex, selected for high variability to act against parasites, did not differ between populations.

Resume La fragmentation des habitats est une sérieuse menace à considérer pour la conservation des lémuriens, parce qu'elle réduit la taille des populations à des niveaux qui ne sont pas viables à long terme. Alternativement, des populations isolées peuvent avoir une grande importance pour la conservation, car certaines sont bien protégées, et certains lémuriens survivent bien, même sur des surfaces limitées. Ainsi, ils est extrêmement important pour les actions de conservation d'identifier des caractéristiques propres aux populations menacées. Nous avons étudié des populations de *Microcebus murinus* confinées à des fragments forestiers de différentes tailles et niveaux de dégradation, dans le sud-est de Madagascar, afin de mettre en relation la taille et la dynamique des populations, la diversité génétique de L'ADN codant et non-codant, et la charge parasitaire intestinale. La taille des population diminue avec la taille des fragments et les niveaux croissants de dégradation. Les populations suivies pendant neuf ans (neuf générations dans la forêt littorale) indique un déclin continu, mais plusieurs populations ont recouvré des densités étonnamment élevées, qui indique des fluctuations plutôt qu'une tendance systématique. Le sex ratio et la charge parasitaire ne variant pas significativement d'un fragment à l'autre. La diversité génétique diminue avec la taille des populations, mais pas la diversité du système d'histo-compatibilité, sélectionnée pour la résistance antiparasite.

Introduction

The importance of interactions between population size, parasitism, and genetic constitution for the long-term survival of lemur populations is poorly understood. Degraded habitat conditions may result in population declines (Ratsimbazafy et al. 2002), sex ratios skewed in favor of males (Perret 1990; Bayart et al. 2005; Foltz and Roeder 2008), increased parasite load owing to poor body condition, invasion by new vectors such as rats (Duplantier and Duchemin 2003), and reduced genetic

variation, all increasing the risk of extinction (Garner et al. 2005; Sommer 2005). While all these factors have been described in different populations, we do not have a standard measure to estimate the state of a lemur population under degraded environmental conditions. To understand lemur responses to habitat changes better, we compiled data on the factors listed above over nine generations for populations of gray mouse lemurs (*Microcebus murinus*) living in forest fragments of different size and degradation.

Methods

Study Sites

This contribution includes data collected between 1998 and 2006 in the forest fragments of Mandena, Tolagnaro region (Fort Dauphin, Madagascar; Fig. 7.1). The results derive from different studies, not all of which cover the entire study period. Some data are pooled from sites with similar characteristics to increase sample sizes. Vegetation features, assessment of degradation state, and background information on the sites are described in Ganzhorn et al. (2007) We distinguished large/small and nondegraded/degraded forest fragments as listed in Table 7.1.

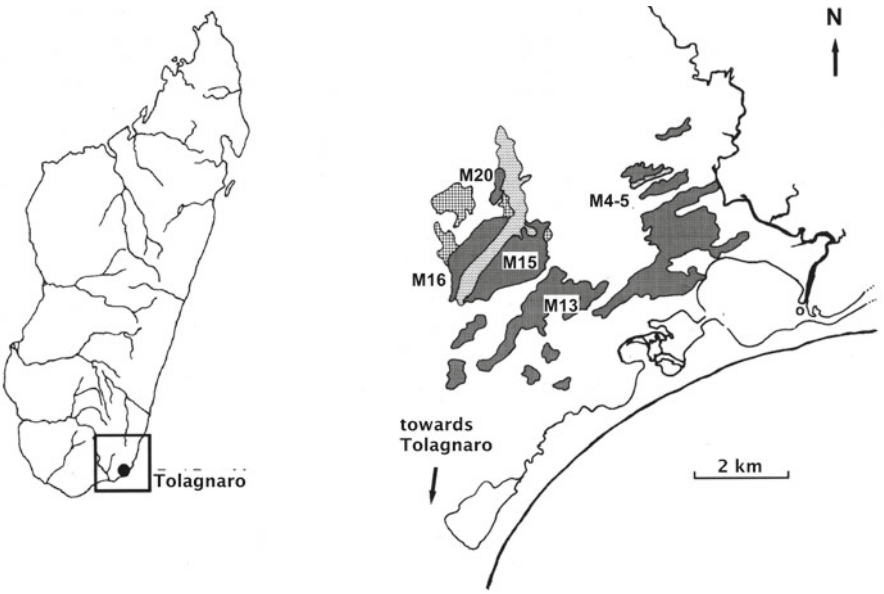


Fig. 7.1 Location of study sites in the Tolagnaro region. The forest remnants are numbered and shown as *dark shading*. *Eucalyptus* plantations are crosshatched. Swamps with bordering *Melaleuca* (introduced) are marked with *curved lines* (modified from Ramanamanjato and Ganzhorn 2001)

Table 7.1 Characteristics of forest fragments of the Mandena region (Ganzhorn et al. 2007)

Size category	Degradation	Fragment	Size (ha)	Canopy cover
Large	Low	M15/M16	95+53	51–70%
	High	M13	109	≤20%
Small	Low	M4/M5	36+18	51–70%
	High	M20	6–40	<50%

Population Estimates

We walked transects at about 1 km/h at night. Population densities were calculated as the number of animals sighted divided by the length of the transect times twice the average distance perpendicular to the trail at which the lemurs were seen (Ganzhorn et al. 2007). We set 80 Sherman traps at permanent trapping stations in the different forest fragments at least once per year between 1998 and 2006, as indicated in Fig. 7.2. Traps were baited with banana and set at about 1.5 m height in trees for four consecutive nights at 25 m intervals along parallel transects spaced 25 m apart. The trapping grids covered an area of 2.25 ha (for details see Ramanamanjato and Ganzhorn 2001).

Intestinal Parasites

Feces of adult *M. murinus* were screened for nematode eggs/g of feces by counting four McMaster chambers for each sample and by using a flotation-dilution of potassium iodide with a specific weight of 1.5 g/ml. Nematodes were assigned to morphotypes based on morphological characteristics and size. We estimated parasite load per individual based on the total number of intestinal parasites, the number of different nematode morphotypes, fecal egg counts (FEC) of nematodes ($FEC_{nematodes}$), and FEC of all helminths. ($FEC_{helminthes}$) (for details see Schad et al. 2005; Raharivololona et al. 2007)

Population genetics

Noncoding markers: We used the hypervariable region I of the mitochondrial D-loop as a genetic marker. To evaluate the influence of different sample sizes on the detection of haplotypes, we used FSTAT version 2.9.3 to calculate the allelic richness index for the number of haplotypes in each sample based on only eight individuals. This was the lowest number of animals caught in any fragment (for details see Hapke et al. 2007).

Coding markers (MHC): We examined a highly variable 171-bp fragment of exon 2 of the MHC class II DRB gene which includes both nonantigen binding sites and antigen binding and recognition sites (for details see Schad et al. 2005).

Results and Conclusions

Population Estimates

Estimated population sizes ranged from approximately 100 adults in the small fragments to >500 adults in the large fragments (Table 7.2). Sex ratios were skewed in all fragments, although there was no systematic skew associated with degradation or population size. Populations fluctuated independently in most forest fragments (Fig. 7.2), a pattern also detected during transect walks. Only the trapping results from M16 and M13 covaried ($r_s = 0.78$, $p = 0.008$, $n = 10$). For sites where trapping and transect surveys were conducted, the number of animals caught per 100 trap-nights (y) was significantly correlated with the number of animals seen per 1 km of transect (x) as follows: $y = 0.36x - 0.32$ ($R^2 = 0.77$, $p = 0.009$, $n = 7$). No population showed a significant decline or increase over the 9-year period.

Parasites

Effect of Degradation

Large fragments (M15/M16 [less degraded]–M13 [degraded]): The number of nematode morphotypes and $FEC_{nematodes}$ were significantly higher in the less degraded fragment M15/M16 than in the degraded fragment M13. For the total intestinal parasite count and FEC for all helminthes, the situation was reversed (Table 7.3).

Table 7.2 Population characteristics of *M. murinus* in different littoral forest fragments

Size category	Degradation	Estimated population size	Male:Female sex ratio (sample size)
Large	Low	420–2,400[a]	1.32
			$N = 178$
	High	350–1,170[a]	0.60
			$N = 69$
Small	Low	80[b]	0.58
			$N = 52$
	High	40–110[a]	1.56
			$N = 92$

[a]Based on transect walks (Ganzhorn et al. 2007)
[b]Based on trapping study

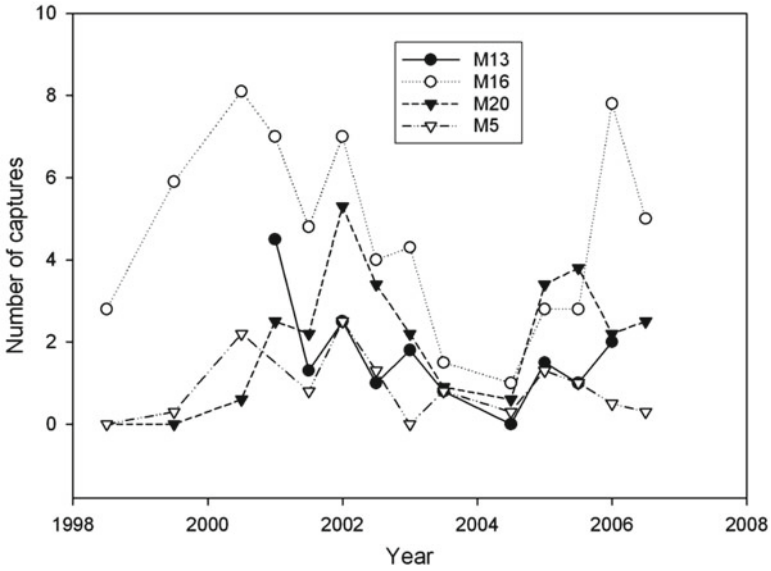


Fig. 7.2 Numbers of *M. murinus* individuals caught per 100 trap-nights in different forest fragments. *Points* directly above the years represent captures at the end of the hot (reproductive) season (April/May), while *marks* between years represent captures at the end of the cold (hibernation/torpor) season

Table 7.3 Number of nematode morphotypes per individual (NNI), log transformed fecal egg count (FEC) of all nematodes, number of all intestinal parasite morphotypes (NHI), and log FEC of all helminth morphotypes (All FEC)

Size category	Degradation	NNI 1998–2003[a]	FEC 1998–2003[a]	NHI 2003–2005[b]	All FEC 2003–2005[b]
Large	Low	1	1.9	1	2.2
	M15+M16	0–3	0.4–2.5	0–2	0–3.3
		(30)	(30)	(63)	(63)
	High	1	1.1	2	3.0
	M13	0–2	0–1.6	1–3	2.2–3.5
		(19)	(19)	(14)	(14)
Small	Low	2	1.9	2	3.8
	M4+M5	0–3	1.7–2.4	1–5	3.0–4.2
		(18)	(18)	(9)	(9)
	High	1	1.6	2	3.0
	M20	0–2	0–2.2	1–3	2.3–3.6
		(15)	(15)	(15)	(15)

Values are medians and quartiles; sample size in brackets
[a]Schad et al. (2005)
[b]Raharivololona et al. (2007)

Small fragments (M20 [degraded]–M4/M5 [less degraded]): The number of nematode morphotypes was significantly higher in the less degraded fragment (M4/M5) than in the degraded fragment M20 ($p = 0.03$) but total parasite count did not

Table 7.4 Haplotypes of the hypervariable region I of the mt D-loop, allelic richness index for haplotypes in each sample of eight individuals, and number of MHC class II DRB-exon 2 alleles in *M. murinus* populations

Size category	Degradation	D-loop[a]	D-Loop: Allelic richness[a]	MHC[b]
Large	Low	3	3	11
	M15 + M16	(104)		(136)
	High	2	2	7
	M13	(22)		(29)
Small	Low	1	1	9
	M4 + M5	(27)		(37)
	High	2	2	8
	M20	(16)		(26)

[a]Hapke et al. (2007)
[b]Schad et al. (2005)

differ. $FEC_{nematodes}$ did not differ between fragments but $FEC_{helminthes}$ was significantly higher in M5 than in M20 ($p = 0.04$).

Effect of Fragment Size

Less degraded fragments (M15/16 [large]–M5 [small]): The total numbers of intestinal parasites, nematode morphotypes, and $FEC_{helminths}$ were higher in the small fragment than in the large fragment.

Degraded fragments (M13 [large]–M20 [small]): Neither the number of parasite species nor the number of helminth eggs found in the feces differed between degraded fragments of different size.

Since each treatment was represented only once, the effects of degradation and fragment size cannot be separated (Raharivololona and Ganzhorn 2009).

Population Genetics

Noncoding markers declined with decreasing fragment size, as expected under the scenario of genetic erosion. However, fragment size also declined in the direction of the postulated colonization history of *M. murinus* in the region (Table 7.4; Hapke et al. 2007). Thus, it is unclear whether the pattern of mitochondrial haplotypes reflects declining population sizes or not. In contrast, the number of alleles of the MHC class II DRB-exon 2 remained high even in small populations. Within the MHC alleles, the estimated rates of nonsynonymous and synonymous substitutions for antigen (ABS) and nonantigen (Non-ABS) binding sites differed significantly. ABS had many more nonsynonymous substitutions than the Non-ABS (Schad et al. 2005). The high substitution rates in the immunologically important parts of the molecule may be the result of positive selection for variation, while the Non-ABS are held constant.

Conclusions

At the population level, with respect to intestinal parasites, we found no consistent indicator of population threat from habitat fragmentation or degradation. At the genetic level, the variability of noncoding markers declined with declining population size, which could either be a consequence of genetic erosion or reflect fragment colonization history by *M. murinus* (Hapke et al. 2007, 2012). MHC coding markers were little affected by reduced population size, if at all. Thus, the noncoding markers used frequently in fragmentation studies to infer reduced population viability can be misleading for this function.

The lack of clear signals in *M. murinus* populations regarding habitat reduction and degradation could have several explanations. Either we did not investigate the right characteristics or all populations were still above the threshold at which size effects become apparent (which, for lemurs, seems to be around 30–40 adults; Ganzhorn et al. 2000), or the present state of habitat fragmentation and degradation was not perceived as such by the study animals.

Acknowledgments This study was conducted under the Accord de Collaboration between the Université d'Antananarivo (Département de Biologie Animale and Département d'Anthropologie et de Biologie Evolutive) and Hamburg University and forms part of the environmental project of QIT Madagascar Minerals (QMM). M. Vincelette and her environmental team provided excellent support in the field. The studies were supported by the DFG, DAAD, Margot Marsh Biodiversity Foundation, and QMM.

References

Bayart F, Simmen B, Hladik A (2005) Demography and body mass of Black Lemurs (*Eulemur macaco macaco*) at Ampasikely (Nosy Faly Peninsula), northwest Madagascar. Am J Primatol 67:299–312

Duplantier J-M, Duchemin J-B (2003) Human diseases and introduced small mammals. In: Goodman SM, Benstead J (eds) The natural history of Madagascar. University of Chicago Press, Chicago, pp 158–161

Foltz J, Roeder JJ (2008) Group size and group composition in Milne-Edwards' sifakas (*Propithecus edwardsi*) at Ialatsara Forest Station. Lemur News 13:24–28

Ganzhorn JU, Andrianasolo T, Andrianjazalahatra T, Donati G, Fietz J, Lahann P, Norscia I, Rakotondranary J, Rakotondratsima B, Ralsion J, Ramarokoto REAF, Randriamanga S, Rasarimanana S, Rakotosamimanana B, Ramanamanjato JB, Randria GFN, Rasolofoharivelo TM, Razanahoera-Rakotomalala MR, Schmid J, Sommer S (2007) Lemurs in evergreen littoral forest fragments. In: Ganzhorn JU, Goodman SM, Vincelette M (eds) Biodiversity, ecology, and conservation of littoral ecosystems in the region of Tolagnaro (Fort Dauphin), southeastern Madagascar. Smithsonian Institution, Washington, DC, pp 223–235

Ganzhorn JU, Goodman SM, Ramanamanjato J-B, Ralison J, Rakotondravony D, Rakotosamimanana B (2000) Effects of fragmentation and assessing minimum viable populations of lemurs in Madagascar. In: Rheinwald G (ed) Isolated vertebrate communities in the tropics. Museum Alexander Koenig, Bonn, pp 265–272

Garner A, Rachlow JL, Hicks JF (2005) Patterns of genetic diversity and its loss in mammalian populations. Conserv Biol 19:1215–1221

Hapke A, Rakotondravony D, Ramanamanjato JB, Ramilijaona O, Randria G, Zischler H (2007) Mitochondrial genetic data indicate a recent range expansion of gray mouse lemurs (*Microcebus murinus*) in the littoral forests of southeastern Madagascar. In: Ganzhorn JU, Goodman SM, Vincelette M (eds) Biodiversity, ecology, and conservation of littoral ecosystems in the region of Tolagnaro (Fort Dauphin), southeastern Madagascar. Smithsonian Institution, Washington, DC, pp 273–280

Hapke A, Andrianaivo TBD, Gligor M, Razafimahatratra E (2012) Range shifts of mouse lemurs in south-eastern Madagascar: evidence from mitochondrial genetic data. In: Masters J, Gamba M, Génin F (eds) Leaping ahead: advances in prosimian biology. Springer, New York

Perret M (1990) Influence of social factors on sex ratio at birth, maternal investment and young survival in a prosimian primate. Behav Ecol Sociobiol 27:447–454

Raharivololona BM, Rakotondravao, Ganzhorn JU (2007) Gastrointestinal parasites of small mammals in the littoral forest of Mandena. In: Ganzhorn JU, Goodman SM, Vincelette M (eds) Biodiversity, ecology, and conservation of littoral ecosystems in the region of Tolagnaro (Fort Dauphin), southeastern Madagascar. Smithsonian Institution, Washington, DC, pp 247–258

Raharivololona B, Ganzhorn JU (2009) Gastrointestinal parasite infection of the Gray Mouse Lemur (Microcebus murinus) in the littoral forest of Mandena, Madagascar: effects of forest fragmentation and degradation. Madagascar Conservation and Development 4:103–112

Ramanamanjato J-B, Ganzhorn JU (2001) Effects of forest fragmentation, introduced *Rattus rattus* and the role of exotic tree plantations and secondary vegetation for the conservation of an endemic rodent and a small lemur in littoral forests of southeastern Madagascar. Anim Conserv 4:175–183

Ratsimbazafy JH, Ramarosandratana HV, Zaonarivola RJ (2002) How do black-and-white ruffed lemurs still survive in a highly disturbed habitat? Lemur News 7:7–10

Schad J, Ganzhorn JU, Sommer S (2005) Parasite burden and constitution of the major histocompatibility complex in the Malagasy mouse lemur, *Microcebus murinus*. Evolution 59:439–450

Sommer S (2005) The importance of immune gene variability (MHC) in evolutionary ecology and conservation. Front Zool 2:16. doi:10.1186/1742-9994-2-16

Chapter 8
Range Shifts of Mouse Lemurs in South-Eastern Madagascar: Evidence from Mitochondrial Genetic Data

Andreas Hapke, Tony B.D. Andrianaivo, Mark Gligor, and Emilienne Razafimahatratra

Abstract The gray mouse lemur, *Microcebus murinus*, occurs mainly in dry forests in western Madagascar, but its distribution extends into humid littoral forests in the south-eastern Anosy Region. We sequenced the mitochondrial hypervariable region 1 for 282 *M. murinus* individuals from 13 south-eastern study sites. The spatial distribution of mitochondrial haplotypes and the varying genetic distances within two haplotype clades indicated a trend of decreasing genetic diversity towards the south-eastern margin of the range. Rufous mouse lemurs, *Microcebus* cf. *rufus*, have a complementary distribution in south-eastern Madagascar which does not overlap with that of *M. murinus*. Taken together, the spatial distribution of genetic diversity within *M. murinus* and the distinct ranges of the two species could indicate a recent expansion of gray mouse lemurs into littoral forests in south-eastern Madagascar.

A. Hapke (✉)
Animal Ecology and Conservation, Hamburg University,
Martin-Luther-King Platz 3, 20146 Hamburg, Germany

Institut für Anthropologie, Johannes-Gutenberg-Universität Mainz,
Colonel-Kleinmann-Weg 2, 55099 Mainz, Germany
e-mail: ahapke@uni-mainz.de

T.B.D. Andrianaivo • E. Razafimahatratra
Département de Biologie Animale, Université d'Antananarivo,
BP 906, Antananarivo 101, Madagascar
e-mail: barivelotony@yahoo.fr; remiarisoa@gmail.com

M. Gligor
Institut für Anthropologie, Johannes-Gutenberg-Universität Mainz,
Colonel-Kleinmann-Weg 2, 55099 Mainz, Germany
e-mail: MGligor@gmx.de

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_8,

Resume Le Microcèbe gris, *Microcebus murinus*, est surtout rencontré dans la forêt sèche de l'ouest de Madagascar, mais son aire de distribution s'étend à la forêt humide littorale du sud-est, dans la région de l'Anosy. Nous avons séquencé la région hypervariable 1 mitochondriale de 282 individus *M. murinus* capturés dans 13 sites du sud-est. La distribution spatiale des haplotypes mitochondriaux et la variation des distances génétiques au sein de deux clades d'haplotypes indiquent une tendance à une diminution de la diversité génétique à la limite sud-est de l'aire. Les microcèbes roux *M.* cf. *rufus* ont une aire de répartition au sud-est de Madagascar, qui ne recoupe pas celle de *M. murinus*. Considérés ensemble, la distribution spatiale de la diversité génétique de *M. murinus*, ainsi que les étendues distinctes des deux espèces indiqueraient une expansion récente de *M. murinus* dans la forêt littorale du sud-est de Madagascar.

Introduction

The Anosy Region in south-eastern Madagascar (Fig. 8.1) is a transition zone between widely different vegetation units: the eastern Malagasy rainforest belt and the southern dry spiny forest. The north–south oriented Anosy and Vohimena mountain chains form a climatic barrier, creating a steep ecological gradient between the spiny forest to the west and the humid east (Donque 1972; Ratsivalaka-Randriamanga 1985). Patches of littoral forest constitute a distinct vegetation type (Ratsivalaka-Randriamanga 1987; Lowry and Faber-Langendoen 1991). The Anosy and Vohimena mountains reach elevations of 1,900 and 1,300 m, respectively. South of the Anosy mountains, separated by lowlands approximately 20 m in elevation, are the smaller Lavasoa–Ambatotsirongorongo mountains, which reach 823 m in altitude. Small patches of humid forest are found around their summits.

Three mouse lemur species occur in south-eastern Madagascar. The dry spiny forest is inhabited by *Microcebus griseorufus* (Yoder et al. 2002). *M.* cf. *rufus* occurs in humid forests on the eastern flanks of the mountain ranges and in littoral forests (Martin 1972). We refer to it as *M.* cf. *rufus* since its taxonomy in south-eastern Madagascar is currently unclear (Weisrock et al. 2010). The habitats of the third species, *M. murinus*, are unusual with respect to the major part of its range. The species is widely distributed throughout the dry deciduous forests of western Madagascar (Rasoloarison et al. 2000). In south-eastern Madagascar, however, it occurs in gallery forest in the dry western part (Yoder et al. 2002) and in littoral forests in the humid eastern part of the region (Martin 1972).

In this chapter, we present data regarding the spatial distribution of genetic variation within *M. murinus* in south-eastern Madagascar and interpret it in the context of the regional biogeography of mouse lemurs.

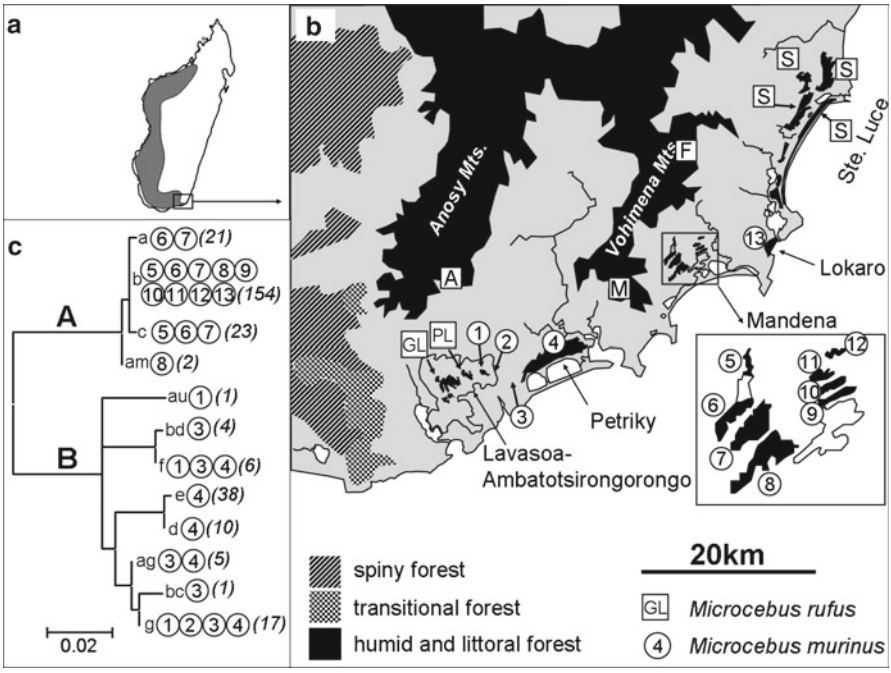


Fig. 8.1 (**a**) Simplified distribution of *Microcebus murinus*. (**b**) Study sites: GL: Grand Lavasoa, PL: Petit Lavasoa, 1: Ambatotsirongorongo, humid forests of Lavasoa-Ambatotsirongorongo Mts.; 2: Amporoforo, 3: Loharano, degraded bush; 4: Petriky, 5–12: Mandena, 13: Lokaro, S: Ste Luce littoral forests; A: Amboavola, M: Manantantely, F: Farafara, humid forests in Anosy and Vohimena Mts. (**c**) Phylogenetic tree reconstruction. *Capital letters*: clades; *lower case letters*: haplotypes; *numbers in circles*: sampling sites; *numbers in brackets*: number of individuals with respective haplotypes. Ingroup: 12*M. murinus* haplotypes. Outgroup (not shown): *M. griseorufus*

Methods

We present data from various field studies conducted between 1999 and 2006. We observed mouse lemurs at 22 sites in southern Madagascar (Fig. 8.1) in the Anosy and Vohimena mountains, the Lavasoa–Ambatotsirongorongo mountains and in littoral forests. At 13 of these sites we trapped a total of 282 *M. murinus* individuals. The sampling sites comprised the small and isolated littoral forest of Lokaro, eight fragments of littoral forest up to 150 ha in size at Mandena, the large littoral forest of Petriky (786 ha), degraded arboreous habitat around Loharano to the west of Petriky and at Amporoforo on the lower eastern flank of Ambatotsirongorongo mountain, and a humid forest patch at Ambatotsirongorongo's summit. The littoral forest fragments of Mandena included four western fragments, connected by different kinds of arboreous habitat, and four eastern fragments, isolated from one another by open heathland.

We trapped mouse lemurs using banana-baited Sherman traps. After anesthetizing the animals, we took small tissue samples from the ear for genetic analyses. We released all animals the afternoon after their capture at the capture locality. We isolated DNA from tissue samples using QIAamp DNA Mini Kits (Qiagen). We characterized all *M. murinus* individuals on the basis of a mitochondrial genetic locus, the hypervariable region 1 (HV1I), which we PCR-amplified and sequenced. For a more detailed description of laboratory methods see Hapke et al. (2007).

We calculated pairwise uncorrected *p*-distances among nonidentical haplotypes using Mega 3.0 (Kumar et al. 2004), and the allelic richness index as an estimator of the number of haplotypes independent of sample size, with FSTAT version 2.9.3 (Goudet 2002) based on a minimum sample size of 6. We used Tree-Puzzle 5.0 (Strimmer and von Haeseler 1996) to reconstruct a phylogenetic tree and applied the HKY substitution model (Hasegawa et al. 1985) with 10,000 puzzling steps and a sequence from *M. griseorufus* as the outgroup.

Results and Discussion

Phylogeography and Sex-Biased Dispersal

The 282 *M. murinus* individuals displayed 12 different haplotypes (NCBI Gen Bank accession numbers DQ865140–DQ865149, EU662698–662944, and EU730762–EU730787). The phylogenetic reconstruction (Fig. 8.1c) revealed two distinct, major haplotype clades which were supported by quartet puzzling values of 98 % and 96 %, respectively. We refer to them in the remainder of the text as clades A and B. Clade A contained four haplotypes, found exclusively in the littoral forests of Mandena and Lokaro. All other *M. murinus* haplotypes belonged to clade B and occurred in the littoral forest of Petriky and the three sites to the west of it. Such a pattern of geographic clustering of related haplotypes is typical for species with female philopatry and male-biased dispersal (e.g., Melnick and Hoelzer 1992; Perwitasari-Farajallah et al. 1999); several studies have demonstrated female philopatry and male-biased dispersal in *M. murinus* in northern and western Madagascar (e.g., Radespiel et al. 2003; Fredsted et al. 2004).

Several haplotypes of both clades were shared among several sampling sites. For example, haplotype b occurred in 154 individuals at all sampling sites in Mandena and Lokaro. The largest geographic distances between sites with shared haplotypes were 10 km (Ambatotsirongorongo–Petriky) and 12 km (Mandena–Lokaro). The presence of many shared haplotypes between geographically distinct subpopulations is not expected under female philopatry. A potential explanation could be anthropogenic fragmentation of formerly continuous forests and the populations therein. Such a scenario, however, generates the expectation of different randomly selected haplotypes in the resulting fragments and not the predominance of one haplotype in all fragments as in Mandena. A more likely explanation involves population movement, e.g., a range expansion.

Table 8.1 *Microcebus murinus* capture sites, sample sizes, and numbers of observed haplotypes

Study site	Site no.	Habitat	Number of individuals	Number of haplotypes	Allelic richness
Ambatotsirongorongo	1	Humid forest	6	3	3
Amporoforo	2	Degraded bush	3	1	n.a.
Loharano	3	Degraded bush	17	5	4.4
Petriky	4	Littoral forest	56	5	3.2
MandenaWest-M20	5	Littoral forest	16	2	2.0
Mandena-West-M16	6	Littoral forest	79	3	2.7
Mandena-West-M15	7	Littoral forest	25	3	2.4
Mandena-West-M13	8	Littoral forest	22	2	1.7
Mandena-East-M4	9	Littoral forest	11	1	1
Mandena-East-M5	10	Littoral forest	16	1	1
Mandena-East-M6	11	Littoral forest	14	1	1
Mandena-East-M7	12	Littoral forest	9	1	1
Lokaro	13	Littoral forest	8	1	1

Spatial Distribution of Sequence Diversity

Clade B comprised eight different haplotypes, which we detected within 82 individuals from 4 different sampling sites, while 200 individuals from 9 different sites at Mandena and Lokaro contained only the 4 haplotypes of clade A (Table 8.1). Five different haplotypes each occurred at Loharano and Petriky. In the western fragments of Mandena littoral forest, there were up to three different haplotypes per site. In the eastern four fragments and at Lokaro there was only a single haplotype. The allelic richness index (Table 8.1) estimates how many haplotypes would be expected per site within a sample size of six individuals. Its trend is very similar to the absolute number of haplotypes, which indicates that different sample sizes did not have a strong influence on the differences between sites.

Divergences between haplotypes decreased from west to east with a maximum *p*-distance of 0.039 within clade B, 0.037 within Petriky, 0.005 within clade A, and 0 within the eastern fragments of Mandena and Lokaro. This indicates that the last common ancestor of the matrilines of Mandena and Lokaro lived approximately eight times more recently than the one of the matrilines in the western area between Ambatotsirongorongo and Petriky.

The major part of the range of *M. murinus* is in western Madagascar. The populations sampled by us represent a small extension into the humid part of south-eastern Madagascar, with the littoral forest of Lokaro as the south-eastern edge of the species' range. Both the numbers of haplotypes and the sequence divergences display a trend of decreasing diversity towards this edge. A potential explanation for this trend is the recent expansion of *M. murinus* into the littoral forests of south-eastern Madagascar. Such a scenario is supported by the complementary range of *M.* cf. *rufus* within the region.

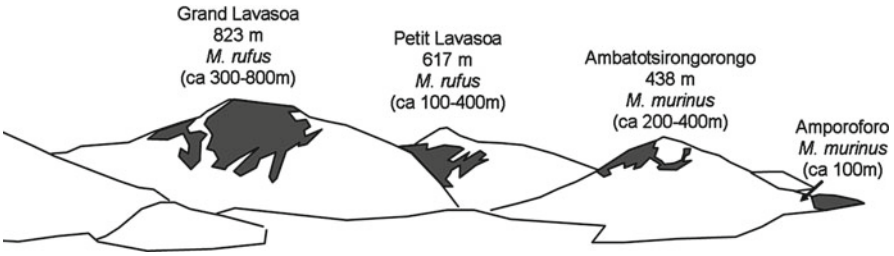


Fig. 8.2 Schematic drawing of Lavasoa–Ambatotsirongorongo viewed from the south–east. The three major peaks and their elevations are shown, along with a fourth study site (Amporoforo). Observed mouse lemur species are noted, and the approximate elevation range of each population's habitat is given in *brackets*. Forests are depicted in *gray*

Comparison of the Distributions of M. murinus and M. cf. rufus in South-Eastern Madagascar

We captured *M.* cf. *rufus* at four sites in littoral forests at Ste Luce, at three sites in the humid forests of the Anosy and Vohimena mountains, and at Petit Lavasoa (Fig. 8.1). At Grand Lavasoa, we observed the species in 2004 and 2006 but could not capture it. Of 22 sites we visited in the region, there was not one where both species occurred. The presence of *M.* cf. *rufus* within the Lavasoa mountains may well indicate that these forests were connected to the large humid forests of the Anosy mountains through a corridor in the recent past. Paleoecological data (Burney 1993) support the following scenario: a formerly large, continuously distributed humid forest that formed the preferred habitat of *M.* cf. *rufus* retreated as a response to aridification in southern Madagascar within the last 3,000 years. Remnants of humid forest and fragmented *M.* cf. *rufus* populations remain, where mountains act as climatic barriers. The disruption of the humid forest corridor between the Anosy and Lavasoa mountains opened a corridor for the intrusion of *M. murinus*, which then began to colonize the littoral forests.

The importance of mountain barriers to the distribution of both species is particularly visible in the Lavasoa–Ambatotsirongorongo mountains. Fragments of humid forest remain mainly on the southern flanks of the three major peaks, Grand Lavasoa (823 m), Petit Lavasoa (617 m), and Ambatotsirongorongo (438 m) (Fig. 8.2). In the forests of Grand Lavasoa and Petit Lavasoa, there are populations of *M.* cf. *rufus*. On easternmost and lower Ambatotsirongorongo, however, *M. murinus* occurs exclusively. The Lavasoa–Ambatotsirongorongo mountains can thus be regarded as a micromodel of the Anosy region and of the retreat and expansion of forest types and their resident mouse lemur species.

Acknowledgments We thank the commission tripartite of the Direction des Eaux et Forêts for authorization and support of this study, which was conducted under the Accord de Collaboration between the Université d'Antananarivo (Département de Biologie Animale and Département d'Anthropologie et de Biologie Evolutive) and Hamburg University. Tantely Andrianjazalahatra,

Refaly Ernest, Jörg Ganzhorn, Petra Lahann, Bakoly M. Rakotondratsima, Roger E. Ramarokoto, Nina Rüdel, Jutta Schmid, and Jörg Schüller are gratefully acknowledged for the contribution of sample material. We are indebted to QIT Madagascar Minerals for logistical support and to the Deutsche Forschungsgemeinschaft (Ga 342/9-1; Zi 568/2-2) for financial support for this study.

References

Burney DA (1993) Late Holocene environmental changes in arid southwestern Madagascar. Quat Res 40:98–106

Donque G (1972) The climatology of Madagascar. In: Battistini R, Richard-Vindard G (eds) Biogeography and ecology in Madagascar. W. Junk, The Hague, pp 87–144

Fredsted T, Pertoldi C, Olesen JM, Eberle M, Kappeler PM (2004) Microgeographic heterogeneity in spatial distribution and mtDNA variability of gray mouse lemurs (*Microcebus murinus*, Primates: Cheirogaleidae). Behav Ecol Sociobiol 56:393–493

Goudet J (2002) FSTAT, a program to estimate and test gene diversities and fixation indices (version 2.9.3.2). http://www.unil.ch/izea/softwares/fstat.html

Hapke A, Rakotondravony D, Ramanamanjato JB, Ramilijaona O, Randria G, Zischler H (2007) Mitochondrial genetic data indicate a recent range expansion of Gray Mouse Lemurs (*Microcebus murinus*) in the littoral forests of southeastern Madagascar. In: Ganzhorn JU, Goodman SM, Vincelette M (eds) Biodiversity, ecology, and conservation of littoral ecosystems in southeastern Madagascar, Tolagnaro (Fort Dauphin). Smithsonian Institution SI/MAB Series, Washington, DC, pp 273–280

Hasegawa M, Kishino H, Yano T-A (1985) Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. J Mol Evol 22:160–174

Kumar S, Tamura K, Nei M (2004) MEGA3: integrated software for molecular evolutionary genetics analysis and sequence alignment. Brief Bioinform 5:150–163

Lowry PP, Faber-Langendoen D (1991) Madagascar Minerals Project, Contract no. MMC-0093 and MMC-0109. Environmental Impact Assessment Study. Part I: Natural environment. Appendix III: Flora and vegetation study

Martin RD (1972) A preliminary field study of the lesser mouse lemur (*Microcebus murinus* J. F. Miller, 1777). Zeit Tierpsychol Suppl 9:43–89

Melnick DJ, Hoelzer GA (1992) Differences in male and female macaque dispersal lead to contrasting distributions of nuclear and mitochondrial DNA variation. Int J Primatol 13:379–393

Perwitasari-Farajallah D, Kawamoto Y, Suryobroto B (1999) Variation in blood proteins and mitochondrial DNA within and between local populations of longtail macaques, *Macaca fascicularis* on the island of Java, Indonesia. Primates 40:581–595

Radespiel U, Lutermann H, Schmelting B, Bruford MW, Zimmermann E (2003) Patterns and dynamics of sex-biased dispersal in a nocturnal primate, the grey mouse lemur, *Microcebus murinus*. Anim Behav 65:709–719

Rasoloarison RM, Goodman SM, Ganzhorn JU (2000) Taxonomic revision of Mouse Lemurs (*Microcebus*) in the western portions of Madagascar. Int J Primatol 21:963–1019

Ratsivalaka-Randriamanga S (1985) Recherches sur le climat de Tolagnaro (ex Fort Dauphin) (Extrême Sud de Madagascar). Madag Rev Géogr 46:47–67

Ratsivalaka-Randriamanga S (1987) Climat et végétation de la région de Fort-Dauphin. Recherches pour le Développement, Série Sciences de l'Homme et de la Société 3 (premier semestre):51–64

Strimmer K, von Haeseler A (1996) Quartet puzzling: a quartet maximum-likelihood method for reconstructing tree topologies. Mol Biol Evol 13:964–969

Weisrock DW, Rasoloarison RM, Fiorentino I, Ralison JM, Goodman SM, Kappeler PM, Yoder AD (2010) Delimiting species without nuclear monophyly in Madagascar's mouse lemurs. PLoS One 5:e9883

Yoder AD, Burns M-M, Genin F (2002) Molecular evidence of reproductive isolation in sympatric sibling species of mouse lemurs. Int J Primatol 23:1335–1345

Chapter 9
Habitat Use by the Red Slender Loris (*Loris tardigradus tardigradus*) in Masmullah Proposed Forest Reserve in Sri Lanka

Lilia Bernede, Simon K. Bearder, and Asoka Gunawardene

Abstract We investigated habitat preferences and, specifically, variable use of habitat by members of a population of *Loris tardigradus tardigradus* to assess their ecological plasticity, i.e., ability to respond to environmental changes. We assessed habitat structure (tree heights, connectivity, floristic composition, and liana abundance) and radio-tracked 14 adult lorises in Masmullah Proposed Forest Reserve (MPFR) in Sri Lanka. The loris population of MPFR has not adapted to exploiting the agricultural environment surrounding and fragmenting the forest, staying within the remaining narrow, isolated forest tracts. However, the animals do show some accommodation to habitat changes, making use of regenerating plantations and forest edges, possibly because of their higher arthropod abundance.

L. Bernede (✉)
Applied Road Ecology Group, Environmental Futures Centre and Griffith School of Environment, Griffith University, Nathan, QLD 4111, Australia

Nocturnal Primate Research Group, School of Social Sciences and Law, Oxford Brookes University, Oxford OX3 0BP, UK
e-mail: l.bernede@griffith.edu.au

S.K. Bearder
Nocturnal Primate Research Group, School of Social Sciences and Law, Oxford Brookes University, Oxford OX3 0BP, UK
e-mail: skbearder@brookes.ac.uk

A. Gunawardene
Department of Animal Science, Faculty of Agriculture, University of Ruhuna, Mapalana, Kamburupitiya, Sri Lanka
e-mail: asokag@ansci.ruh.ac.lk

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_9,

Resume Nous avons étudié les types d'habitat préférés par *Loris tardigradus tardigradus*, et spécifiquement les différences observées au sein d'une population de cette espèce, afin d'évaluer sa plasticité écologique, i.e. sa capacité à répondre aux changements environnementaux. Nous avons caractérisé la structure de l'habitat (hauteur des arbres, connectivité, composition floristique et abondance en lianes) et radio-pisté 14 loris adultes à Masmullah, au Sri Lanka, dans la zone incluse dans une Proposition de Classement en Réserve Forestière. La population de loris de cette possible future réserve ne s'est pas adaptée à la mise en culture et la fragmentation de l'habitat, et demeure cantonnée à d'étroites bandes de forêt. Cependant, les animaux se sont quelque peu adaptés au changement, et utilisent les plantations abandonnées et les lisières, peut-être du fait d'une plus grande abondance en arthropodes.

Introduction

When environments change, animals must seek out habitats for which they are already adapted while responding appropriately to the changes occurring around them. We investigated the ability of *Loris tardigradus tardigradus* to respond behaviorally to changes in their environments, termed ecological plasticity (Morse 1980), by examining habitat preferences of, and variation in microhabitat use by, a population of red slender lorises in south-western Sri Lanka.

Two loris species are currently recognized: the red slender loris, *L. tardigradus* (Sri Lanka) and the gray slender loris, *L. lydekkerianus* (India and Sri Lanka). Within Sri Lanka, slender lorises occur in habitats ranging from montane cloud forest to thorny scrub forest. The endangered *L. t. tardigradus* (IUCN 2008) is limited to the diminishing rainforests of south-western Sri Lanka.

We conducted a radio-tracking study in Masmullah Proposed Forest Reserve (MPFR) to describe the behavioral flexibility of the red slender loris. Our objectives were to describe preferred habitat and microhabitat characteristics and to investigate whether variations in habitat use could be detected among individuals. We posed the following questions:

1. In a small forest fragmented by agricultural fields and plantations, do slender lorises make use of all available vegetation?
2. Are there intrapopulation variations in microhabitat use and are microhabitat preferences a reflection of available resources?

Methods

MPFR (6°20′N and 80°35′E) measures approximately 420 ha, 65% of which is forest and scrubland, ~23% forest plantations (96 ha), and ~12% agricultural land (51 ha). The radio-tracking study took place in an area measuring approximately 135 ha.

To assess floristic composition, forty 10 m × 10 m quadrats were placed randomly and trees with a CBH > 10 cm counted and identified. Dominant species were inferred from their Importance Value Index (IVI; Pascal and Pelissier 1996), which estimates the overall importance of each species in the community structure. The IVI of a species is the summed percentage values for its relative frequency, relative density, and relative dominance (Curtis 1959). Percentage cover of bamboo was estimated using the Braun-Blanquet scale (Kent and Coker 1992). Five home gardens at the forest edge were also visited.

Lorises rely on substrate networks to move through the forest (see also Chap. 38), so we assessed forest connectivity by eye by selecting 130 trees at random and estimating their degree of connection to other trees and lianas within a 5-m radius. Connectivity estimates were grouped into quartiles: 0–25%; 26–50%; 51–75%; and 76–100%. Abundance of lianas and vines was also estimated by eye according to the categories: absent/rare, occasional, frequent, or abundant.

Fourteen adult lorises (eight females and six males) were radio tracked, and the following data recorded using instantaneous point sampling at 5-min intervals: habitat type, height of animal, and substrate type. Because 5-min point samples are not independent, percentages for each variable and each animal were calculated. Tree species used, connectivity, and liana abundance within a 5-m radius of a sighting were recorded *ad libitum*. A new record was made when the animal had moved at least 5 m from its previous location. Intersexual differences were investigated using the Mann–Whitney *U*-test, and measures of association were tested using Spearman's correlation coefficient. The tests were two-tailed, and significance levels set at $P < 0.05$.

Because we did not have the expertise to identify all plant species, and the slender lorises compounded this difficulty by preferring saplings to mature trees, we recorded only the eight most dominant tree species. Data collected on plant species, connectivity, and liana abundance are expressed as percentages of total observations ($n = 6{,}778$). Results are expressed as mean ± SD, unless otherwise stated.

Results

Vegetation Characteristics and Microhabitat Availability

The study site consisted of 44% natural forest, 21% scrubland, 12% agricultural plantations (mostly abandoned paddy fields), and 23% forest plantations (two actively managed and two abandoned pine forests). The loris population was estimated at 30–40 individuals (Bernede 2009). Table 9.1 lists microhabitat characteristics for each habitat type.

In vegetation surveys, 49 plant species were recorded and their IVIs calculated. Of these taxa, lorises ($N = 14$) used the eight most dominant species (Table 9.2) on average 58.6 ± 43.4% of the time. The leguminous *Humboldtia laurifolia* had the

Table 9.1 The eight most dominant tree species in MPFR based on IVI in 40 random plots across the study site

Plant species	Relative density (%)	Relative frequency (%)	Relative basal area (%)	Importance value index (IVI) [Maximum possible value = 300]
Humboldtia laurifolia	39.27	86.9	19.8	145.9
Swietenia macrophylla	5.12	49.1	10.4	77.1
Dipterocarpus zeylanicus	6.51	53.9	13.6	74.4
Artocarpus nobilis	4.08	49.6	6.2	69.1
Semecarpus walkeri	4.58	52.3	1.8	58.7
Dillenia retusa	3.65	37.9	11.7	52.5
Mangifera zeylanicus	2.50	48.9	1.1	51.3
Horsfieldia iryaghedhi	2.22	30.2	2.4	34.9

highest IVI overall (145.9), while *Ochlandra stridula* (bamboo) showed high cover in subhabitats that were not dominated by *H. laurifolia*. An introduced mahogany species, *Swietenia macrophylla*, had the second highest IVI (77.1), followed by *Dipterocarpus zeylanicus* (74.4). The most common connectivity level recorded was 0–25% (54% of 130 points), while lianas and vines were generally rare (27.3%) or occasional (21.2%). The average tree height recorded in the study area was 12.3 ± 5.5 m.

Habitat and Microhabitat Use

Lorises at MPFR never used managed plantations and agricultural fields (Table 9.1). They preferred interior forest (83.4 ± 12.5%) to edge habitats (12.3 ± 11.5%) and regenerating plantations (5.5 ± 10.6%) ($\chi^2 = 69.920$, df = 2, $P < 0.001$). There were no significant sex differences in use of different habitat types (edge: $P = 0.147$; forest: $P = 0.917$; regenerated: $P = 0.814$).The microhabitat parameters most frequently recorded for males and females are shown in Table 9.3.

Height: Lorises were chiefly found between 3 and 5 m (27.5 ± 12.4%) or between 6 and 8 m (27.3 ± 16.8%). There was no significant sex difference in use of the various height categories (<2 m: $P = 0.852$; 3–5 m: $P = 0.282$; 6–8 m: $P = 0.755$; 9–11 m: $P = 0.345$; >12 m: $P = 0.282$).

Connectivity: Lorises used areas of 0–25% connectivity significantly more frequently than areas with higher connectivity (median = 68.6%; $\chi^2 = 27.85$, df = 3, $P < 0.001$). There was no significant sex difference in preferred degree of connectivity (0–25%: $P = 0.284$; 26–50%: $P = 0.622$; 51–75%: $P = 0.222$; 76–100%: $P = 0.998$).

Lianas: Lorises mostly used areas with abundant (>5) lianas (33.5 ± 23.5%) followed by areas where lianas were frequent (4–5) (28.8 ± 23.7%), occasional (2–3) (27.2 ± 31.8%), and absent/rare (0–1) (10.5 ± 14.3%).

Table 9.2 Microhabitat characteristics of four habitat types found within the study site

Habitat type and extent	Agricultural land (~20 ha)	Forest plantation (~50 ha)	Regenerated plantations (~1 ha)	Home gardens	Forest (~64 ha)
Slender loris presence	X	X	✓	X	✓
Connectivity (%)	None	None	0–25	26–50	0–25
Lianas and vines (%)	None	None	None	None	25–50
Plant height (m)	N/A	15–20 m	Trees: 15–20 m Shrubs: 1.5–2 m	Mean = 17.2 ± 2.9	Mean = 12.3 ± 5.5
Most common plant species	*Lantana* spp. *O. stridula*	*Pinus* spp.	*Pinus* spp. *Hedyotis fruticosa; Clerodendrum infortunatum; Alstonia macrophylla*	*A. scholaris*; *Mangifera indica*; *Artocarpus heterophyllus; Areca catechu; Cocos nucifera*	See Table 9.1

Table 9.3 Table showing the most frequently recorded microhabitat category of connectivity and liana abundance within a 5-m radius, for 14 adult lorises [males (M) $n=6$, females (F) $n=8$] and the percentage use of most dominant plant species in the forested habitat ($n=802$)

Microhabitat parameters	Microhabitat category represented by highest percentage of use
Connectivity (%)	M: 0–25
	F: 0–25
Abundance of lianas and vines	M: abundant
	F: frequent
Substrate type	M: branches
	F: branches
Plant species	Percentage of identified species ($n=802$)
O. stridula	M: 15.9
	F: 30.8
H. laurifolia	M: 21.9
	F: 37.3
D. retusa	M: 32.9
	F: 14.4
M. zeylanicus	M: 6.1
	F: 4.8
A. nobilis	M: 11.0
	F: 3.3
S. walkeri	M: 8.5
	F: 6.4
D. zeylanicus	M: 2.5
	F: 1.3
S. macrophylla	M: 1.3
	F: 1.8

Substrate type: Lorises used branches more frequently than other support types (38.5 ± 13.1%), followed by lianas (19.4 ± 16.1%). Very small-sized supports were used rarely [terminal branches (5.7 ± 9.7%) and vines (3.4 ± 4.1%)] and lorises seldom descended to the ground (2.8 ± 6.4%). Intersexual differences for frequencies of branch use ($U=8.0$, $P=0.06$, $N=8, 6$) and liana use ($U=8.0$, $P=0.06$, $N=8, 6$) approached significance, with males using lianas more frequently than females (males: 29 ± 18% and females: 11.2 ± 8.9%) and branches less frequently than females (males: 31.3 ± 11.9% and females: 44.7 ± 11.4%).

Plant species: Table 9.3 shows the mean percentage use of the eight most dominant plant species. Lorises ($N=14$) used *Humboldtia laurifolia* more frequently than other dominant plant species (29.6 ± 21.4%), followed by *O. stridula* (23.4 ± 22.3%). *Swietenia macrophylla* was the least used dominant species (1.6 ± 5.3%). The frequency of use of *H. laurifolia* and *O. stridula* by females was almost double that by males (Table 9.3), but the difference was not statically significant (*H. laurifolia*: $U=172.0$, $N=8, 6$; *O. stridula*: U: 179.5, $N=8, 6$).

Discussion

Vegetation Characteristics and Habitat Use

The loris population in MPFR has not expanded its ecology to include exploitation of the agricultural environment surrounding and fragmenting the forest and is restricted to narrow, isolated forest tracts. However, the lorises have accommodated habitat modifications by making use of regenerating plantations and edges, which have a high abundance and diversity of arthropods (Richter et al. 2006). Interior habitats were preferred, possibly on account of microhabitat characteristics. Home gardens which had relatively high connectivity and tree species found at forest edges and used by lorises (e.g., *Mangifera zeylanica*) were never visited. Nekaris (Nekaris and Jayewardene 2004) noted that *L. t. tardigradus* does not fare well in areas of high anthropogenic disturbance, unlike the northern *L. l. lydekkerianus*, which is found regularly along roadsides and in home gardens (see also Chap. 38).

Microhabitat Preferences and Intrapopulation Variation

Height: Height use by MPFR lorises corresponded well with the average height of some of the dominant plant species, *H. laurifolia* (4.9 m ± 1.0), *Dillenia retusa* (4.0 m ± 1.2), and *O. stridula* (<3 m) but is lower than the average tree height recorded in MPFR. Females tended to use smaller tree species and shrubs more frequently than males, particularly for foraging activities.

Connectivity: Lorises in MPFR used areas and trees with the most common level of overall connectivity (0–25%) but preferred localities with a higher than average abundance of lianas. This preference may be because lianas provide a climbing network in areas where canopy continuity is low. Lianas were used predominantly for traveling (Bernede 2009).

Plant species: The preference lorises showed for *H. laurifolia* may have been influenced by the mutualistic relationship between the plant and an ant species that inhabits its hollow internodes (Krombein et al. 1999; Nekaris et al. 2005). Bamboo, too, is likely to provide a good environment for insectivory: a study of arthropod abundance in a Peruvian lowland rainforest revealed that arthropod density was higher in bamboo than in other vegetation types (Pearson and Derr 1986). Thus, the loris preference for these two plant species may reflect not only their high abundance across MPFR but also their attractiveness to arthropods.

Dillenia retusa, like *H. laurifolia*, is a small tree found typically in disturbed sites and scrubland of the wet lowlands but had a lower IVI value than *H. laurifolia* (52.5 as opposed to 145.9). It was nevertheless used more frequently than *S. macrophylla*, a dominant species with an IVI value of 77.1. Arthropod abundance was not measured on *D. retusa*, but the large number of fruits produced by the trees is likely to attract many insects.

Intrapopulation variation: The lack of significance in intrapopulation variation found in this study may have been the result of pooling data from individuals that shared home ranges with data from "solitary" animals (Bernede 2009). Further investigation of differences between members of a group, particular information on group size, is necessary for a fuller understanding of the role of microhabitat preference and resource partitioning within a population, and how these may be affected by ranging patterns.

Conclusion

Red slender lorises in MPFR exhibited limited ecological plasticity at both microhabitat and habitat levels, mostly in proportion to the availability of resources. They showed a preference for areas with high liana abundance and for certain tree species and have not adapted to anthropogenic habitats like home gardens or managed agricultural lands, although they do make use of regenerating forest plantations. In a country where little natural forest remains, the restoration of abandoned forest plantations and the creation of corridors between remaining forest patches would increase the extent of habitat available to red slender lorises and the viability of currently isolated populations.

Acknowledgments We thank the Departments of Forestry and Wildlife Conservation for providing research permits and A.S. Beresford and K. Davey for field assistance. We are grateful to Oxford Brookes University, P.S.G.B., Cleveland Metroparks Zoo, the L.S.B. Leakey Foundation, and National Geographic for additional financial assistance.

References

Bernede L (2009) A study of the social and behavioural ecology of the red slender loris (*Loris tardigradus tardigradus*) in Masmullah Proposed Forest Reserve, Sri Lanka. Unpublished PhD Thesis, Oxford Brookes University, Oxford

Curtis JT (1959) The vegetation of Wisconsin: an ordination of plant communities. University of Wisconsin Press, Madison, WI

IUCN Red List (2008) Species information on *Loris tardigradus tardigradus*. Accessed last on 29 Sept 2011. Available at http://www.iucnredlist.org/apps/redlist/details/12375/0

Kent M, Coker P (1992) Vegetation description and analysis. Belhaven Press, London

Krombein KV, Norden BB, Rickson MM, Rickson FR (1999) Biodiversity of the domatia occupants (ants, wasps, bees and others) of the Sri Lankan myrmecophyte *Humboldtia laurifolia* (Fabaceae). Smithsonian Contributions to Zoology 603:1–33

Morse DH (1980) Behavioral mechanisms in ecology. Harvard University Press, Cambridge, MA

Nekaris KAI, Jayewardene J (2004) Distribution of slender lorises in four ecological zones in Sri Lanka. J Zool 262:1–12

Nekaris KAI, Liyanage WKDD, Gamage SN (2005) Influence of forest structure and composition on population density of the red slender loris *Loris tardigradus tardigradus* in Masmullah Proposed Forest Reserve, Sri Lanka. Mammalia 69:201–210

Pascal J-P, Pelissier R (1996) Structure and floristic composition of a tropical evergreen forest in South-West India. J Trop Ecol 12:191–214

Pearson DL, Derr JA (1986) Seasonal patterns of lowland forest floor arthropod abundance in southeastern Peru. Biotropica 18:244–256

Richter A, Klein AM, Tscharntke T, Tylianakis JM (2006) Abandonment of coffee agroforests increases insect abundance and diversity. Agroforest Syst 69:175–182

Chapter 10
Forest Fragmentation Imperils Red Slender Lorises (*Loris tardigradus tardigradus*) in South-Western Sri Lanka

K. Anne-Isola Nekaris, Sarah M. Jaffe, and Giuseppe Donati

Abstract The red slender loris (*Loris tardigradus tardigradus*) is endemic to Sri Lanka's southern rainforests, where less than 2% of their habitat remains in small, fragmented patches. Because of continued encroachment on these small areas, the species is considered Endangered. We present data on red slender loris abundance in nine of the last remaining forest patches in Sri Lanka's Wet Zone and examine the relationship between habitat characteristics and abundance. Slender lorises were present at 7 out of 9 patches, and 44 animals were encountered. Density estimates ranged from 3.4 to 28 lorises/km^2 with linear encounter rates of 0.1–1.1 lorises/km. Patch size heavily influenced encounter rate, with the largest patches containing more lorises. Removing the effect of patch size, we explored whether support size, undergrowth continuity, number of lianes/vines, and canopy continuity influenced loris density. We found slight evidence that increased numbers of lianes and vines were associated with decreased numbers of lorises. Although lorises rely on continuous substrates for movement, increased numbers of lianes and vines are also associated with the smallest and most disturbed habitats. In order to persist, red slender lorises require continuous forest. Unless forest encroachment can be halted and reforestation programmes started, their future in all but the largest of Sri Lanka's remaining forest patches is bleak.

Resume Le loris rouge (*Loris tardigradus tardigradus*) est endémique de la forêt pluviale du sud de Sri Lanka, où moins de 2% de son habitat subsiste sous forme de petits fragments isolés. Parce que ces fragments sont détruits continument, l'espèce est considérée en danger d'extinction. Nous présentons des estimations de l'abondance du loris rouge obtenues pour neuf des fragments de forêt subsistants dans la partie humide de Sri Lanka, et examinons les caractéristiques de ces habitats.

K.A.-I. Nekaris (✉) • S.M. Jaffe • G. Donati
Nocturnal Primate Research Group, School of Social Sciences and Law,
Oxford Brookes University, Oxford OX3 0BP, UK
e-mail: anekaris@brookes.ac.uk; sarahmjaffe@gmail.com; gdonati@brookes.ac.uk

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_10,

Des loris ont été trouvés dans 7 fragments sur 9, et 44 animaux ont été rencontrés. La densité estimée était de 3.4 à 28 loris/km2, avec un taux de rencontre linéaire de 0.1 à 1.1 loris/km. La taille des fragments avait une très forte influence sur le taux de rencontre, avec davantage de loris rencontrés dans les plus grands fragments. Nous avons exploré les effets possibles de la taille des supports, de la continuité du sous-bois et de la canopée, et la présence de lianes, indépendamment de la taille des fragments. La densité de loris tendait à diminuer légèrement quand le nombre de lianes augmentait. Bien que les loris aient besoin de supports continus, la présence de nombreuses lianes est souvent observée dans les plus petits et les plus dégradés des fragments. Les loris ont besoin, pour subsister, de forêt continue. A moins que la destruction de la forêt ne cesse, et qu'un programme de reforestation soit initié, leur avenir dans les forêts de Sri Lanka est compromis, à l'exception des plus grands fragments.

Introduction

Slender lorises (*Loris* spp.) are nocturnal primates known for their specialized, non-saltatory locomotion (Sellers 1996). Although originally thought to be so slow that their habitat requirements were minimal (Petter and Hladik 1970), we now know that slender lorises make regular use of home ranges comparable in size to other similarly sized nocturnal primates (Nekaris 2003). It has been suggested that, contrary to animals that can leap over large gaps, areas inhabited by lorises should contain continuous canopy (Kar-Gupta 1995; Singh et al. 1999; see also Chap. 38) so that lorises need not travel on open ground, where they are vulnerable to predation (Nekaris et al. 2007).

Red slender lorises (*L. tardigradus tardigradus*) are endemic to southern Sri Lanka, a region characterized by dramatic forest loss and fragmentation (Mill 1995). Habitat loss is identified as the greatest threat to red slender lorises, listed as Endangered by the IUCN (2008). Nekaris and Jayewardene (2004) found lorises to be rare at several sites within their range and to be absent from the smallest forests studied (Douglas et al. 2007). Few data are available, however, that quantify the relationship between microhabitat and loris abundance, findings crucial for determining conservation action plans (SAMD 2008).

We present data on slender loris abundance in nine of the last remaining forest patches in Sri Lanka's Wet Zone and examine the relationship between habitat characteristics and abundance. In particular, we explore whether the following features influence loris density: support size, undergrowth continuity, and canopy continuity.

Methods

Data were collected on 72 days from June to August 2004 at nine sites in Sri Lanka's Southern Province (Fig. 10.1, Table 10.1). With the exception of one site protected by a local land owner (Bangamukande), all sites are protected by the

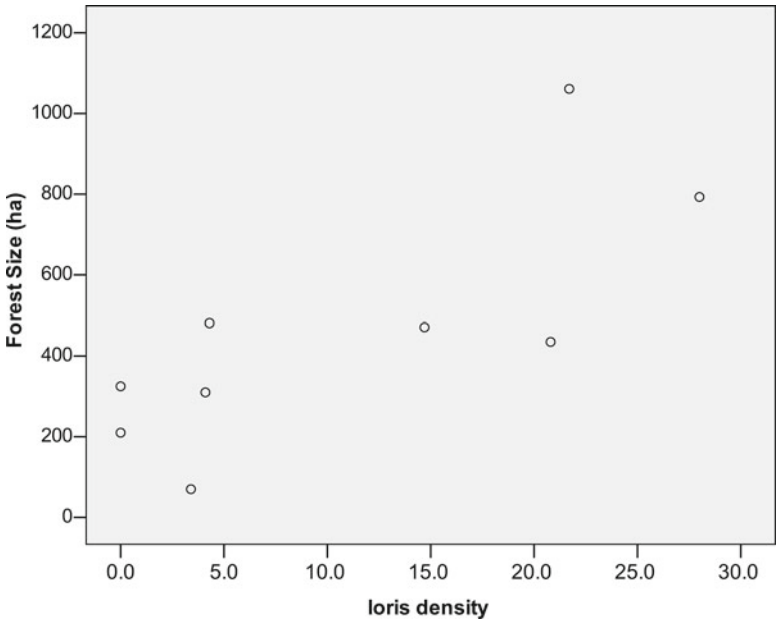


Fig. 10.1 Plot of the relationship between forest fragment size and red slender loris density

Table 10.1 Sizes of forest fragments at the time of the study, a representative geographic coordinate for each site, distance covered on foot, and density of animals at each site; sites listed in descending order of abundance

Study site (size in ha)	Representative geographic coordinates	Days	Distance walked (km)	Animals per km	Animals per km^2
Masmullah (793)	6°02′59.80″N 80°35′41.72″E	16	13.90	1.1	28.0
Kottawa (435)	6°4′59″N 80°20′8 ″E	8	14.70	0.7	20.8
Kakanadura (471)	5°59′13.89″N 80°35′42.23″E	7	13.20	0.5	14.7
Oliyagankele (481)	6°05′11.52″N 80°31′33.22″E	9	13.05	0.2	4.3
Wattahena (210)	6°0′0″N 80°27′0″E	5	6.75	0.1	4.1
Bangamukande (28)	6°21′00.97″N 80°13′16.25″E	14	8.29	0.1	3.4
Polgahaivalakande (325)	6°17′0″N 80°17′0″E	5	7.80	0	0
Welihena (310)	6°07′15.32″N 80°30′35.58″E	3	6.00	0	0
Total:		72	92.64	0.5 ± 0.4	10.8 ± SD 10.6

Forest Department of Sri Lanka. Despite this, all showed signs of anthropogenic disturbance (including logging and agriculture) and closely bordered on villages and/or roads. To estimate loris abundance, we selected line transects at random at each site and walked them either from sunset to midnight or midnight to sunrise (Sutherland 2002). Two to three researchers walked at a pace of 500 m/h, using a halogen head lamp with a red filter to scan all levels of the vegetation (Nekaris et al. 2008). Line transect lengths were derived using a laser rangefinder and confirmed with GPS reference points. Upon spotting an animal, its perpendicular distance to the line was recorded using a measuring tape, and the tree on which it was located was flagged. Only confirmed visual sightings of slender lorises were used to estimate abundances, but we also recorded the loris' distinctive loud whistle whenever it was heard. Strip width was determined by eliminating the furthest 10% of observations on either side of the line. Density was estimated using the following formula: $D = n/2wl$, where n is the number of animals seen, w is the strip width, and l is the transect length (Sutherland 2002). In order to compare our data with other loris surveys (e.g., Singh et al. 1999), a linear encounter rate was estimated.

The point-quarter center method for vegetation sampling was adapted to record several characteristics of microhabitat (Southwood and Henderson 2000). Random plots were placed 15 m from areas where we spotted lorises following a randomly selected compass bearing; on transects where no lorises were encountered, plots were placed at a locality along the transect chosen with a random number table. The following variables were collected: canopy continuity and undergrowth continuity (measured by the ground cover of saplings and plants large enough to provide passage for a loris) between the point center and the nearest tree using the Braun-Blanquet scale; substrate size and angle at 3.5 m, the preferred height of red slender lorises; and number of vines connecting the closest tree to the point center to its nearest neighbor (Lacher and Cleber 2001; Nekaris et al. 2005). Normality of the data was confirmed using Kolmogorov–Smirnov tests, and parametric tests were used for the analyses. To test whether microhabitat variables have an effect on abundance independent of the effect of fragment size, we ran ANCOVA models between the variables using fragment size as a covariate, after transforming the original independent variables from numeric into categorical variables (Zar 1999).

Results

Nearly 100 km were walked during the survey. Slender lorises were present at seven out of nine patches (Table 10.1), and 44 animals were encountered in total. Density estimates ranged from 3.4 to 28 lorises/km^2 with linear encounter rates of 0.1–1.1 lorises/km. At all seven sites, presence was confirmed with clear visual sightings. The characteristic loud whistle of *Loris* was heard at all seven sites. Although lorises may still prove to be present at Welihena and Polgahaivalakande, absence of both sightings and whistles indicates that, if they are present, they occur at very low densities. Lorises were spotted exclusively within forest reserves; they were never seen along village roads or in gardens.

Table 10.2 Microhabitat features compared across sites represented by either the average and standard deviation, or the dominant habitat category

Study site	Tree height ***F	% Tree cover***χ	Canopy continuity***χ	No. vines ***F	Branch size***χ	Sub-strate angle***χ
Masmullah ($n=123$)	7.1 ± 5.7	0–25%	0–25%	0.8 ± 1.2	>30 cm	Vertical
Dandeniya ($n=75$)	4.7 ± 2.8	0–25%	26–50%	2.4 ± 1.6	1–5 cm	Oblique
Kottawa ($n=78$)	5.1 ± 3.4	26–50%	0–25%	0.9 ± 1.2	>30 cm	Vertical
Kakanadura ($n=93$)	6.8 ± 5.0	0–25%	2–50%	1.2 ± 1.6	>30 cm	Vertical
Oliyagankele ($n=126$)	6.3 ± 4.3	0–25%	0–25%	1.5 ± 1.4	>30 cm	Vertical
Wattahena ($n=80$)	4.9 ± 2.7	26–50%	26–50%	0.9 ± 1.3	1–5 cm	Vertical
Bangamukande ($n=50$)	12.0 ± 0.4	0–25%	0–25%	0.7 ± 1.4	>30 cm	Vertical
Polgahaivalakande ($n=80$)	5.6 ± 3.9	26–50%	0–25%	1.9 ± 1.8	1–5 cm	Vertical
Welihena ($n=80$)	5.4 ± 3.0	0–25%	0–25%	1.4 ± 1.5	1–5 cm	Vertical

Both analysis of variance (F) and chi-squared cross tabulation tests (χ) revealed that sites differed significantly in microhabitat components ($p \leq 0.001$)

Although a low percentage of canopy continuity and ground covered by saplings characterized all sites, they differed significantly from one another for all microhabitat variables measured (Table 10.2). A single factor, forest patch size, correlated strongly with loris abundance (Pearson's $r=0.778$, $p \leq 0.01$) (Fig. 10.2). Given this correlation, we removed the effect of fragment size to explore the effects of microhabitat variables on loris abundance. The only significant effect observed was a negative relationship between number of vines and lianas and loris abundance (ANCOVA: $F=18.65$, df = 2, $n=9$, $p \leq 0.005$). Indeed, the total model that accounted for the effect of the number of vines, taking fragment size into account, explained 93% of the variance in loris abundance. The only other variable that approached significance was branch size (ANCOVA: $F=4.96$, df = 1, $n=9$, $p=0.067$).

Discussion

Most previous studies of slender lorises have estimated their abundance linearly. The linear results obtained in this study ranged from 0.1 to 1.0 animals/km. These figures are comparable to the lower end of estimates for slender lorises in previous studies in India and Sri Lanka (Singh et al. 1999, 2000; Nekaris and Jayewardene 2004; Kumara et al. 2006; Chap. 38). They are also comparable to the generally low abundance estimates of Southeast Asian slow lorises (Nekaris et al. 2008). At two sites (Wattahena and Bangamukande), only one animal was seen in 19 days of survey. Indeed, at Bangamukande, the smallest site in the sample, encounter rates may even be lower, as only two others were ever seen during three other field seasons,

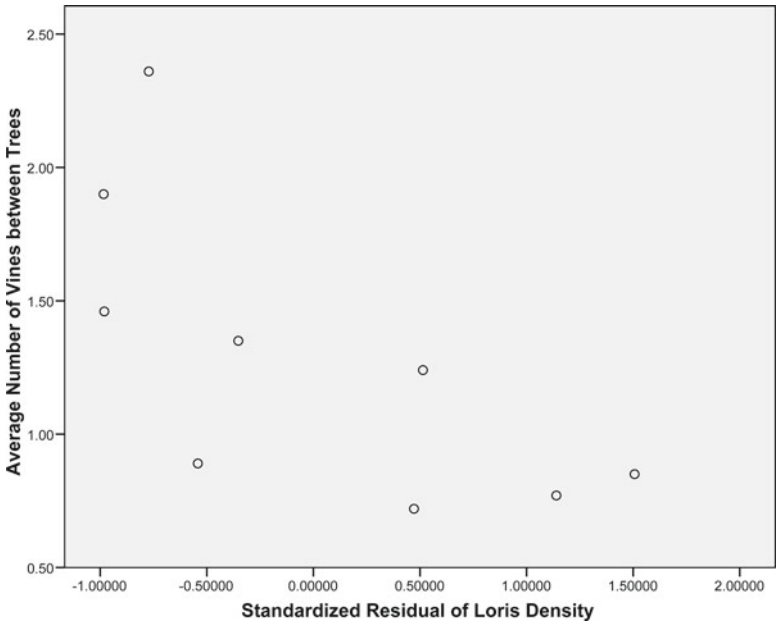


Fig. 10.2 Even when the effect of forest size is taken into account, a significant negative relationship is still found between abundance (residual displayed here for comparative purposes) of red slender lorises and number of vines. Higher numbers of vines are indicative of increased forest disturbance

which included extensive nocturnal surveys (Bernede 2003). These results lend support to the latest IUCN (2008) Red List assessment of *Loris tardigradus tardigradus* as Endangered.

Contrary to our expectations, most sites, whether lorises were present or not, had a combination of low canopy and undergrowth cover, and predominantly vertical substrates that are less suitable for lorises (Nekaris and Jayewardene 2004). These features may explain why loris abundances were low in comparison with other studies. A feature expected to be positively associated with loris presence, the number of vines and lianas connecting trees, was, in fact, negatively correlated. Increased vines and lianas are also a sign of severe anthropogenic disturbance, usually caused by logging and unrestricted access to the forest (Bhuyan et al. 2003).

Canopy continuity has been proposed as an important factor in determining arboreal mammal abundance (Malcolm 2000; Lacher and Cleber 2001) and identified as crucial for slender lorises (Singh et al. 1999) but was not significantly associated with loris abundance in this study. Arboreal continuity in general is often related to the tangled vegetation characteristic of disturbed areas and tree fall zones (Molino and Sabatier 2001; Nekaris et al. 2005). Many species of small arboreal mammals commonly occur at higher abundance in disturbed areas (Lambert et al. 2006), and disturbed areas should not be ruled out as a conservation priority (Wells et al. 2007). A method for comparing connectivity at all forest levels should be devised to assess further the suitability of these habitats for red slender lorises.

Although the impact of disturbance may appear positive in the short term (Lovejoy et al. 1986), small arboreal animals in particular may be extremely vulnerable to rapid decline following a reduction in resource availability (Wells et al. 2007). Nekaris and Jayewardene (2004) surveyed Masmullah and Oliyagankele in 2001; for both sites, estimates were lower in 2004. In a long-term study at Masmullah, Bernede (personal communication) also commented on a marked decrease in encounter rate. Indeed, Forest Department records show a decrease in the size of this forest from 793 ha in 2001 to 296 ha in 2005. The main cause of this seems to be human encroachment, including use of forested land for rice paddies, cattle grazing, and logging for firewood (Ashton et al. 2001). For example, one of the major areas in Masmullah where Nekaris et al. (2005) conducted their study in 2002 had been burnt down in 2005. These observations support our major finding that forest fragment size directly affects the abundance of slender lorises.

Conclusion

Slender lorises are threatened by multiple factors not limited to deforestation, compounding the need for conservation intervention. Our study shows that habitat loss and decreasing patch sizes over time have contributed to their ongoing population decline. An unremitting trend due to agricultural and logging demands will probably lead to short-term local extinctions of red slender lorises in Sri Lanka. Habitat protection and expansion of the protected areas network are essential for the survival of the remaining wild populations of red slender lorises.

Acknowledgments We thank Judith Masters and Carol Scheepers for organizing the International Congress on Prosimians and for inviting us to participate in this volume. We thank the Department of Forestry and the Department of Wildlife Conservation for research permits to carry out this study. We are grateful to the following individuals who assisted in the project: S. Wimalasuriya and G. de Silva Wijeyeratne for logistical aid and M. Abare, S. Gamage, E. Leavitt, Madumadarawa, Nallaka, and J. Stokes for assistance in the field. Funds for the project were provided by People's Trust for Endangered Species, Columbus Zoological Park and Aquarium, Primate Action Fund of Conservation International, and Primate Conservation Inc.

References

Ashton PMS, Gunatilleke CVS, Singhakumara BMP, Gunatilleke IAUN (2001) Restoration pathways for rain forest in southwest Sri Lanka: a review of concepts and models. For Ecol Manage 154:409–430

Bernede L (2003) Biodiversity assessment of a regenerating rainforest patch at Bangamukande Estate, Pitigala, Galle District, Sri Lanka. Unpublished MSc dissertation, Oxford Brookes University, Oxford

Bhuyan P, Khan ML, Tripathi RS (2003) Tree diversity and population structure in undisturbed and human-impacted forest stands of tropical wet evergreen forest in Arunachal Pradesh, Eastern Himalayas, India. Biodivers Conserv 12:1753–1773

Douglas PH, Moore RS, Wimalasuriya S, Gunawardene A, Nekaris KAI (2007) Microhabitat variables influencing abundance and distribution of diurnal primates (*T. vetulus vetulus* and *Macaca sinica aurifrons*) in a fragmented rainforest network in southern Sri Lanka. Eur Fed Primatol Conf Proc. Charles University, Prgaue, p 17

IUCN Red List (2008) Species information on *Loris tardigradus tardigradus*. Accessed last on 29 Sept 2011. Available at http://www.iucnredlist.org/apps/redlist/details/12375/0

Kar-Gupta K (1995) Slender loris, *Loris tardigradus*, distribution and habitat use in Kalakad-Mundanthurai Tiger Reserve, India. Folia Primatol 69(Suppl 1):401–402

Kumara HN, Singh M, Kumar S (2006) Distribution, habitat correlates, and conservation of loris lydekkerianus in Karnataka, India. Int J Primatol, 27(4):941–969

Lacher TE, Cleber JRA (2001) Terrestrial small mammal richness and habitat associations in an Amazon forest-cerrado contact zone. Biotropica 33:171–181

Lambert TD, Malcolm JR, Zimmerman BL (2006) Amazonian small mammal abundances in relation to habitat structure and resource abundance. J Mammal 87:766–776

Lovejoy TE, Bierregaard RO Jr, Rylands AB, Malcolm JR, Quintela CE, Harper LH, Brown KS Jr, Powell AH, Powell GVN, Schubart HOR, Hays MB (1986) Edge and other effects of isolation on Amazon forest fragments. In: Soulè ME (ed) Conservation biology. The science of scarcity and diversity. Sinauer Associates, Sunderland, MA, pp 257–285

Malcolm JR (2000) Influence of timber extraction routes on central African small-mammal communities, forest structure and tree diversity. Conserv Biol 14:1623–1638

Mill RR (1995) Regional overview: Indian subcontinent. In: Davis SD, Haywood VH, Hamilton AC (eds) Centres of plant diversity: a guide to strategy for their conservation, vol 2: Asia, Australia and the Pacific. World Wildlife Fund for Nature and the IUCN Press, Cambridge, pp 62–135

Molino JF, Sabatier D (2001) Tree diversity in tropical rain forests: a validation of the intermediate disturbance hypothesis. Science 294:1702–1704

Nekaris KAI (2003) Spacing system of the Mysore slender loris (*Loris lydekkerianus lydekkerianus*). Am J Phys Anthropol 121:86–96

Nekaris KAI, Jayewardene J (2004) Distribution of slender lorises in four ecological zones in Sri Lanka. J Zool 262:1–12

Nekaris KAI, Liyanage WKDD, Gamage S (2005) Relationship between forest structure and floristic composition and population density of the southwestern Ceylon slender loris (*Loris tardigradus tardigradus*) in Masmullah Forest, Sri Lanka. Mammalia 69(2):1–10

Nekaris KAI, Pimley ER, Ablard K (2007) Anti-predator behaviour of lorises and pottos. In: Gursky SG, Nekaris KAI (eds) Primates and their predators. Springer Media, New York, pp 220–238

Nekaris KAI, Blackham G, Nijman V (2008) Conservation implications of low encounter rates of five nocturnal primate species (*Nycticebus* spp.) in Asia. Biodivers Conserv 17:733–747. doi:10.1007/s10531-007-9308-x

Petter J-J, Hladik CM (1970) Observations sur le domaine vital et la densité de population de *Loris tardigradus* dans les forêts de Ceylan. Mammalia 34:394–409

SAMD (Southeast Asian Mammal Databank) (2008) Accessed on 29 Sept 2011. Available at http://www.ieaitaly.org/samd/

Sellers W (1996) A biomechanical investigation into the absence of leaping in the locomotor repertoire of the slender loris (*Loris tardigradus*). Folia Primatol 67:1–14

Singh M, Lindburg DG, Udhayan A, Kumar MA, Kumara HN (1999) Status survey of the slender loris in Dindigul, Tamil Nadu, India. Oryx 33:31–37

Singh M, Kumar MA, Kumara HN, Mohnot SM (2000) Distribution and conservation of slender lorises in Southern Andhra Pradesh, South India. Int J Primatol 21:721–730

Southwood TRE, Henderson PA (2000) Ecological methods, 3rd edn. Blackwell, Oxford

Sutherland WJ (2002) Mammals. In: Sutherland WJ (ed) Ecological census techniques: a handbook. Cambridge University Press, Cambridge, pp 260–278

Wells K, Kalko EKV, Lakim MB, Pfeiffer M (2007) Effects of rain forest logging on species richness and assemblage composition of small mammals in Southeast Asia. J Biogeogr 34:1087–1099

Zar JH (1999) Biostatistical analysis, 4th edn. Prentice Hall, New Jersey

Chapter 11
Head Posture and Visual Orientation in *Loris tardigradus* During Locomotion on Oblique Supports

Nancy J. Stevens and Christopher P. Heesy

Abstract Primates moving through the trees must cope with a three-dimensional network of branches that differ in angular orientation. On oblique supports, an animal must not only avoid toppling or sliding off of a branch, it may also need to adjust its visual field orientation along the path of movement. Previous studies have found that primate quadrupeds walking on top of horizontal supports direct the orbital plane more inferiorly, whereas suspensory primates moving beneath branches direct the orbital plane more superiorly. If primates adjust the visual path to reflect substrate position, they should incline the orbital plane more on inclines than on declines. Alternatively, eye mobility within the orbits may permit collection of sufficient visual information without reorienting angular posture of the head. Lorisids are adept arboreal quadrupeds that routinely negotiate inclines and declines. We collected 150 strides of kinematic data on head postures for two adult slender lorises (*Loris tardigradus*) during locomotion on horizontal and oblique supports. In general, lorises adjusted head posture as predicted, directing orbits more superiorly on inclines and more inferiorly on declines. However, we observed higher angles on declines than predicted by substrate angle alone, suggesting that other locomotor and vestibular issues also influence head orientation.

Resume Lors des déplacements dans les arbres, les primates doivent se repérer au sein d'un réseau de branches dont les orientations diffèrent. Sur un support oblique, les animaux ne doivent pas seulement éviter de basculer ou de glisser, ils doivent

N.J. Stevens (✉)
Department of Biomedical Sciences, Center for Ecology and Evolutionary Studies and Heritage College of Osteopathic Medicine, Ohio University,
228 Irvine Hall, Athens, OH 45701, USA
e-mail: stevens@ohio.edu

C.P. Heesy
Department of Anatomy, Arizona College of Osteopathic Medicine, Midwestern University,
19555 N, 59th Avenue, Glendale, AZ 85308, USA
e-mail: cheesy@midwestern.edu

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_11,

aussi ajuster leur champ de vision à leur trajectoire. Des études antérieures ont montré que les primates quadrupèdes se déplaçant sur un support horizontal dirigent leur plan orbitaire vers le bas alors que les primates suspenseurs dont les déplacent se font sous les branches le dirigent vers le haut. Si les primates ajustaient l'orientation visuelle au support, ils devraient plus incliner leur plan orbitaire vers le haut pour des supports montants que descendants. Alternativement, la mobilité des yeux dans les orbites devrait permettre d'acquérir des informations suffisantes pour ne pas réorienter la position de la tête. Les lorisidés sont des quadrupèdes arboricoles qui évoluent fréquemment sur des supports montants et descendants. 150 enregistrements cinématiques se focalisant sur la position de la tête ont été collectés sur deux individus adultes de loris grêles (*Loris tardigradus*) lors de leur locomotion en supports obliques et horizontaux. En général, les loris ajustent la position de leur tête comme attendu, dirigeant les orbites vers le haut en montées et vers le bas en descentes. Cependant, l'angle de la tête en descente en bien plus fort que celui du support, suggérant que d'autres variables locomotrices et vestibulaires influencent la position de la tête.

Introduction

Most primates live and move about in three-dimensional, complex, arboreal habitats and traverse branches that vary unpredictably in their angular orientations (Grand 1972, 1984). Balancing and moving about on oblique supports requires postural and gait accommodations (Rollinson and Martin 1981; Stevens 2003, 2006; Nyakatura et al. 2008). Although head posture during locomotion may relate functionally to balance and visual orientation, the topic has received little experimental attention in arboreal nonhuman primates (e.g., Dabelow 1929; reviewed in Ross 1995). Stability of the head during locomotion is required to minimize disturbances to the visual and vestibular systems, both of which contribute to planning and execution of the travel path during the locomotor cycle (Spoor and Zonneveld 1998; Goldberg 2000; Goldberg and Hudspeth 2000; Patla et al. 2002; Hollands et al. 2004; Vallis and Patla 2004; Bagesteiro et al. 2006).

Visually directed animals may maximize the amount of the visual field perceived both above and below the horizontal in order to extract information on heading and locomotor velocity, as well as to perceive "time to intercept" for objects and obstacles within the travel path (Lee 1980; Gibson 1986; Schubert et al. 2003). This suggests that animals require stability of gaze direction, and to some degree, the head to align the visual field with the travel path. Studies on humans demonstrate that translations of the head due to locomotor velocity are minimized by compensatory head pitch (e.g., Hirasaki et al. 1999; Kao and Ringenbach 2004). Hildebrand (1959, 1961) noted cheetahs (*Acinonyx jubatus*) maintaining stable head and orbit posture during high speed running on a flat substrate. Dunbar et al. (2004) observed greater stabilization of head posture during galloping than walking in Old World monkeys negotiating horizontal terrestrial substrates. Arboreal primates face still more challenges related to balance and movement in a more structurally complex habitat, and

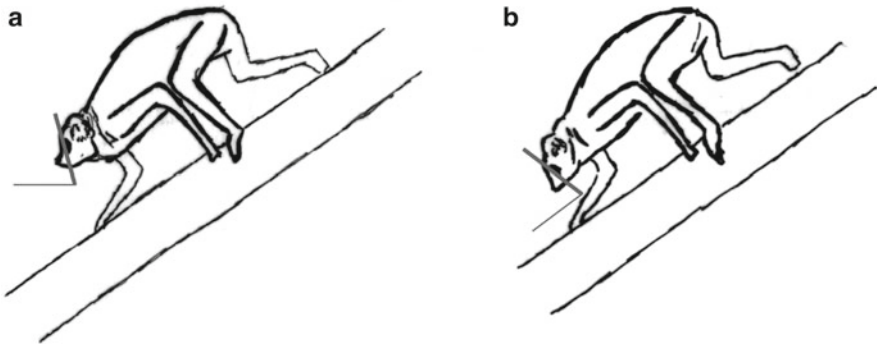


Fig. 11.1 Angles calculated in this study (**a**) orbit–ground angle, the angle between the orbital plane in lateral view and the *x*-axis and (**b**) orbit–substrate angle, the angle between the substrate and the orbital plane in lateral view

head posture may be influenced by the demands of both the visual and vestibular systems. Indeed, when walking on top of horizontal supports, arboreal primate quadrupeds direct the orbital plane more inferiorly, whereas suspensory primates moving beneath branches direct the orbital plane more superiorly (Strait and Ross 1999). Little is known about how head posture responds during arboreal quadrupedalism on the vast array of obliquely oriented supports that prosimian primates regularly utilize. We hypothesize that primates alter head posture when walking atop supports of differing angular orientations. Alternatively, the mobility of the eyes within the orbits may be sufficient to permit the collection of visual information without reorienting the angular posture of the head.

If arboreal primates orient gaze (and orbit) direction along the locomotor substrate like terrestrial taxa, one would predict that head posture varies according to substrate inclination, with absolute orbit inclinations measuring 30° higher on 30° inclines, 30° lower on 30° declines, and so forth. We expect the orbit–substrate angle to remain constant, or minimally, to exhibit a range of values that keep the substrate within the working visual field (Fig. 11.1). In this study, we quantify orbit and head orientation during locomotion on angular substrates in slender lorises (*Loris tardigradus*), adept arboreal, quadrupedal prosimians that regularly traverse variably oriented substrates in the wild (Nekaris and Stevens 2007).

Methods

Subjects

We followed the principles of ethical treatment of nonhuman primates, using noninvasive kinematic data collection protocols approved by the Institutional Animal Care and Use Committees (IACUC) at Stony Brook University, Duke University,

Table 11.1 Orbit orientations at forelimb lift-off on declined, horizontal, and inclined supports

		Orbit–ground angle		Orbit–substrate angle	
Substrate	*N*	Mean	SD	Mean	SD
60° decline	30	14.33	7.14	74.33	7.14
30° decline	30	32.78	9.12	62.78	9.12
Horizontal	30	59.47	7.92	59.47	7.92
30° incline	30	82.01	7.90	52.01	7.90
60° incline	30	113.94	7.07	53.94	7.07

See Fig. 11.1 for orbit–ground angle and orbit–substrate angle calculation

and Ohio University. Study subjects included two adult *Loris tardigradus* individuals housed at the Duke University Lemur Center (DLC). Laboratory animals had regular access to naturalistic supports in their large enclosures, enabling them to move in a way reflective of their wild counterparts. Animals moved upon simulated branches constructed from 2.44 m sections of polyvinyl chloride (PVC) pipes, 2.5 cm in diameter, coated with a nonslip surface and oriented horizontally and at 30° and 60° angles from the horizontal. Animals had access to these substrates in their naturalistic enclosures prior to data collection, minimizing the impact of the experimental setting on their performance. Stevens (2003) provides a more comprehensive description of the experimental setup. Using standard 2D kinematic techniques, we positioned cameras to capture lateral views of the study subjects, placing Panasonic AG-195 VHS video cameras 4 m from the path of movement of the subjects, a sufficient distance to reduce parallax (Spencer and Spencer 1995). We optimized frame rates to catch rapid movements by splitting interlaced video fields to achieve 60 Hz, setting shutter speeds at 1/1,000 s to reduce motion blur.

Using Peak Motus (version 9.1) to import video clips, we collected 15 symmetrical strides per individual per substrate, selecting strides with no visible changes in speed, the total number of individual ($n=2$) and support ($n=5$) combinations yielding 150 strides (Table 11.1). The orbital plane refers to the plane made by connecting three anatomical points along the orbit: orbitale superioris, orbitale inferioris, and orbitale anterioris (Cartmill 1970). Lorises have more convergent (similarly facing) but less frontated (vertically oriented) orbits than most primates (Cartmill 1970, 1972; Ross 1995), and the orbital inclination can be approximated in lateral view by a line connecting the upper and lower borders of the orbit. The orbital plane is virtually perpendicular to the sagittal plane in lorises (Cartmill 1970, 1972; Ross 1995). We digitized the orbit at forelimb and hind limb touch down (the first frame in which the limb contacted the support), midstance, and lift-off (the last frame in which the limb contacts the support) to measure head orientation relative to the substrate and gravity vector. We measured orbital angular data relative to the ground (orbit–ground angle, Fig. 11.1a) and adjusted to the support (orbit–substrate angle, Fig. 11.1b) by adding or subtracting 30° or 60°. In addition, we calculated speed using markers placed at 5 cm intervals along the support.

As kinematic data cannot be expected to follow a normal distribution, we employed the Kolmogorov–Smirnov test to assess normality of the data. We rank

transformed nonnormally distributed data and then used an ANCOVA to take into account kinematic differences related to velocity (Conover and Iman 1981; Sokal and Rohlf 1981).

Results

Lorises showed regular head posture patterns during locomotion. For any given support orientation, we found fairly consistent mean orbital inclinations throughout the stride cycle. Despite variation in head angle in different subjects and in individual strides, each individual typically carried its head at a constant angular orientation from forelimb touchdown through hind limb toe off (Fig. 11.2).

Consistent differences in head posture emerged among supports of different angular orientations, with significantly lower orbit–ground angles observed on declined supports and significantly higher angles observed on inclined supports (Fig. 11.3a). This indicates that, as predicted, lorises exhibited more superiorly directed orbits on inclines and more inferiorly directed orbits on declines ($p < 0.001$ for all comparisons).

Head posture was not completely explained by support orientation alone. We had predicted similar orbit–substrate angles on all support types. Although head postures generally tracked substrate angle on horizontal and inclined supports, we observed departures from the predicted pattern on 30° and 60° declines. Figure 11.3b demonstrates orbit–substrate angles at forelimb lift-off. On steep declines, orbits were significantly more superiorly directed than would be predicted if the visual tracking of the substrate constituted the sole determinant of head posture ($p < 0.001$).

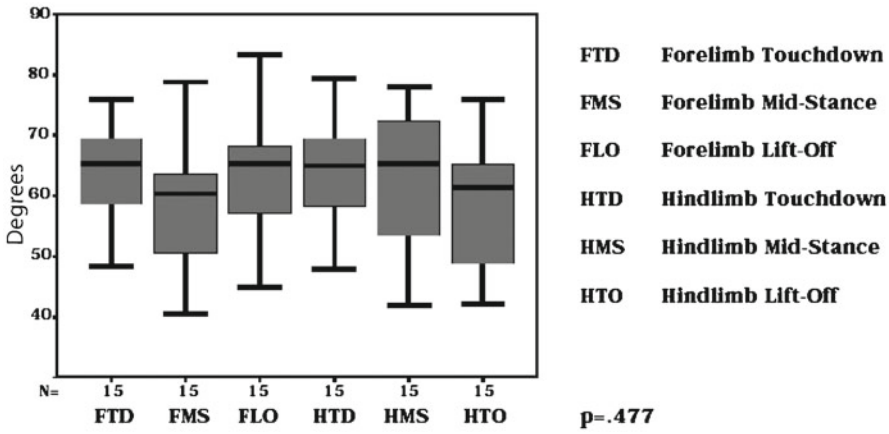


Fig. 11.2 Orbit–ground angles for female loris on horizontal branches. Angles were not significantly different at forelimb and hind limb touchdown, midsupport, and lift-off events, indicating head posture stability throughout the stride cycle. Male loris exhibited similar pattern

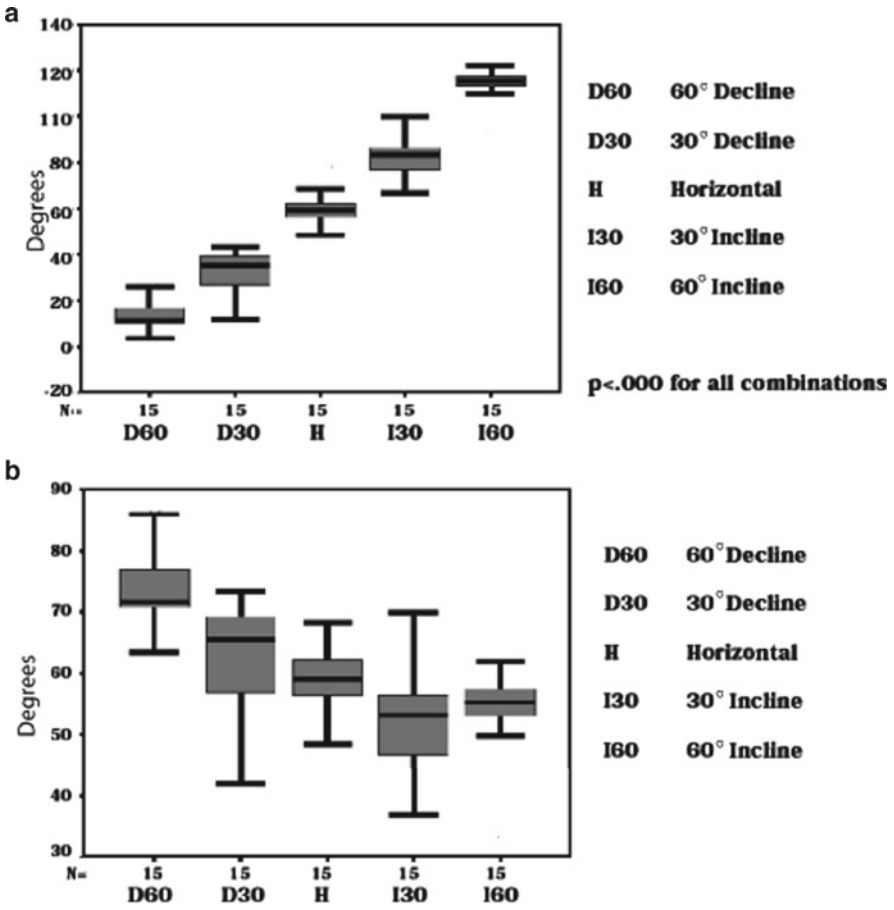


Fig. 11.3 Head posture for female loris at forelimb lift-off as a function of support orientation. (**a**) Orbit–ground angles were significantly different among all support types ($p < 0.001$ for all contrasts). (**b**) Orbit–substrate angle was higher than expected on declines, significantly so on 60° declines. The male loris exhibited a similar pattern

Discussion and Conclusions

The data presented here for *Loris tardigradus* suggest that head stability is important during arboreal locomotion, as mean head posture remains relatively constant throughout a stride cycle. These results are generally similar to those collected for terrestrial primates (Hirasaki et al. 1999). The alignment of the visual field also appears to play an influential role in head posture during travel, as lorises make clear accommodations on oblique supports, directing their orbits significantly more superiorly on inclines and more inferiorly on declines. These data expand upon

previous studies of terrestrial primates traversing horizontal substrates (Strait and Ross 1999), and both studies indicate that primates generally align their visual fields with the locomotor substrate. However, the relatively higher orbit–substrate angles observed on steep declines indicate that substrate orientation alone is not sufficient to predict head posture. On steep declines lorises exhibit less declined head postures than expected, possibly reflecting a tendency to look further ahead to compensate for potentially greater acceleration during forward locomotion due to gravity.

Balance during arboreal locomotion requires vestibular system stability and proprioception. The maintenance of head stability within a stride cycle reported here, along with the alteration of head posture on steep declines, may together reflect ways of accommodating and reducing perturbations to the vestibular system. The combined imperatives of balance and stability in the arboreal setting are particularly compelling given the discovery of high velocity locomotion in wild slender lorises negotiating supports of differing angular orientations (Nekaris and Stevens 2007). Future studies are needed to address the relative contributions of visual orientation and vestibular integrity during prosimian arboreal locomotion on oblique substrates.

Acknowledgments We thank J. Masters for assembling this volume, and acknowledge P.M. O'Connor, M. Hall, S.G. Larson, B. Demes, J.G. Fleagle, C. Ross, and W.L. Jungers for helpful comments on the study. Many individuals assisted during data collection at the Duke Lemur Center including D. Haring, L. Jolley, M. Lauer, W. Hess, D. Brewer, B. Grossi, and C. Stahala, and we also acknowledge the IACUC committees at Stony Brook, Ohio, and Duke Universities. Helpful suggestions from R.H. Crompton, J. Masters, and one anonymous reviewer improved the manuscript. Research was supported by the Sigma Xi, LSB Leakey, and National Science Foundations.

References

Bagesteiro L, Sarlegna F, Sainburg R (2006) Differential influence of vision and proprioception on control of movement distance. Exp Brain Res 171:358–370

Cartmill M (1970) The orbits of arboreal mammals: a reassessment of the arboreal theory of primate evolution. PhD dissertation, University of Chicago

Cartmill M (1972) Arboreal adaptations and the origin of the order primates. In: Tuttle R (ed) The functional and evolutionary biology of primates. Aldine, Chicago, pp 97–122

Conover WJ, Iman RI (1981) Rank transformations as a bridge between parametric and nonparametric statistics. Am Stat 35:124–133

Dabelow A (1929) Uber Korrelationen in der phylogenetischen Entwicklung der Schadelform I. Die Beziehungen zwischen Rumpf und Schadelform. Gegenbaurs Morphol Jahrb 63:1–49

Dunbar DC, Badam GL, Hallgrimsson B, Vielledent S (2004) Stabilization and mobility of the head and trunk in wild monkeys during terrestrial and flat-surface walks and gallops. J Exp Biol 207:1027–1042

Gibson JJ (1986) The ecological approach to visual perception. Lawrence Eribaum, New Jersey

Goldberg ME (2000) The control of gaze. In: Kandel ER, Schwartz JH, Jessell TM (eds) Principles of neural science, 4th edn. McGraw-Hill, New York, pp 782–800

Goldberg ME, Hudspeth AJ (2000) The vestibular system. In: Kandel ER, Schwartz JH, Jessell TM (eds) Principles of neural science, 4th edn. McGraw-Hill, New York, pp 801–815

Grand TI (1972) A mechanical interpretation of terminal branch feeding. J Mammal 53:198–201

Grand TI (1984) Motion economy within the canopy: four strategies for mobility. In: Rodman PS, Cant JGH (eds) Adaptations for foraging in nonhuman primates. Columbia University Press, New York, pp 54–72

Hildebrand M (1959) Motions of the running cheetah and horse. J Mammal 40:481–495

Hildebrand M (1961) Further studies of the locomotion of the cheetah. J Mammal 42:84–91

Hirasaki E, Moore ST, Raphan T, Cohen B (1999) Effects of walking velocity on vertical head and body movements during locomotion. Exp Brain Res 127:117–130

Hollands M, Ziavra N, Bronstein A (2004) A new paradigm to investigate the roles of head and eye movements in the coordination of whole-body movements. Exp Brain Res 154:261–266

Kao JC, Ringenbach SDR (2004) Variability in head movement during gait transitions. Percept Mot Ski 99:1217–1229

Lee DN (1980) The optic flow field: the foundation of vision. Philos Trans R Soc Lond B Biol Sci 290:169–179

Nekaris KAI, Stevens NJ (2007) Not all lorises are slow: rapid arboreal locomotion in *Loris tardigradus* of Sri Lanka. Am J Primatol 69:112–120

Nyakatura JA, Fischer MS, Schmidt M (2008) Gait parameter adjustments of cotton-top tamarins (*Saguinus oedipus*, Callitrichidae) to locomotion on inclined arboreal substrates. Am J Phys Anthropol 135:13–26

Patla AE, Niechwiej E, Racco V, Goodale MA (2002) Understanding the contribution of binocular vision to the control of adaptive locomotion. Exp Brain Res 142:551–561

Rollinson J, Martin RD (1981) Comparative aspects of primate locomotion with special reference to arboreal cercopithecines. Symp Zool Soc Lond 48:377–427

Ross CF (1995) Allometric and functional influences on primate orbit orientation and the origins of the Anthropoidea. J Hum Evol 29:201–227

Schubert M, Bohner C, Berger W, Sprundel MV, Duysens JEJ (2003) The role of vision in maintaining heading direction: effects of changing gaze and optic flow on human gait. Exp Brain Res 150:163–173

Sokal R, Rohlf F (1981) Biometry, 3rd edn. W. H. Freeman, San Francisco

Spencer MA, Spencer GS (1995) Technical note: video-based three dimensional morphometrics. Am J Phys Anthropol 96:443–453

Spoor F, Zonneveld F (1998) Comparative review of the human bony labyrinth. Yearb Phys Anthropol 41:211–251

Stevens NJ (2003) The influence of substrate size, orientation and compliance upon prosimian arboreal quadrupedalism. PhD dissertation, State University of New York at Stony Brook

Stevens NJ (2006) Stability, limb coordination and substrate type: the ecorelevance of gait sequence pattern in primates. J Exp Zool 305A:953–963

Strait DS, Ross CF (1999) Kinematic data on primate head and neck posture: Implications for the evolution of basicranial flexion and an evaluation of registration planes used in paleoanthropology. Am J Phys Anthropol 108:205–222

Vallis L, Patla A (2004) Expected and unexpected head yaw movements result in different modifications of gait and whole body coordination strategies. Exp Brain Res 157:94–110

Chapter 12
Predation on Two Lemur Species in Sahamalaza Peninsula, North-Western Madagascar

Guy Hermas Randriatahina and N. Sylviane M. Volampeno

Abstract During our studies of blue-eyed black lemurs from September 2006 to March 2008 in Sahamalaza Peninsula National Park, Madagascar, we encountered predation on lemurs both by a fossa and by raptors. An infant blue-eyed black lemur fell victim to a fossa at the age of 2 weeks. A harrier hawk attacked an adult female blue-eyed black lemur, and a Madagascar buzzard killed an adult female Sahamalaza sportive lemur. We describe the antipredator behavior of blue-eyed black lemurs.

Resume Au cours de notre étude sur les lémuriens aux yeux turquoise de septembre 2006 au mars 2008 dans le Park National de la Presqu'ile Sahamalaza, nous avons rencontré des incidents de prédation sur les lémuriens incluant un fossa et des rapaces. Un enfant du lémurien aux yeux turquoise à l'âge de deux semaines a été victime à un fossa. Un faucon busard a attaqué une femelle adulte du lémurien aux yeux turquoise et un Madagascar busard a tué un adulte femelle d'un lepilemur de Sahamalaza. Nous décrivons le comportement anti-prédateur des lemuriens aux yeux turquoise.

G.H. Randriatahina (✉)
Département de Paléontologie et d'Anthropologie Biologique,
Université d'Antananarivo, Antananarivo, Madagascar

Association Européene pour l 'Etude et la Conservation des Lemuriens (AEECL),
Lot IVH 169N Ambohimanandray, Ambohimanarina, Antananarivo 101, Madagascar
e-mail: guyhrand@hotmail.com

N.S.M. Volampeno
School of Biological and Conservation Sciences, University of KwaZulu-Natal,
3209 Scottsville, South Africa

Community Centred Conservation, Lot IVH 169 N Ambohimanandray,
Ambohimanarina, Antananarivo 101, Madagascar
e-mail: sylvianevolampeno@gmail.com; sylviane@c-3.org.uk

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_12,

Introduction

Predation risk plays an important role in individual survival in wild primate populations (Cheney et al. 1988; Boesch 1991; Cowlishaw 1997; Chap. 25) and is an important factor shaping lemur social behavior (Goodman et al. 1993). Raptors, carnivores, and the Malagasy boa are the main lemur predators (Goodman et al. 1993; Rasoloarison et al. 1995; Wright and Martin 1995; Wright 1998; Rakotondravony et al. 1998). In this chapter, we report three incidences of predation of lemurs in Sahamalaza National Park that we witnessed over a 2-year study period.

Study Site

Our study was conducted in Ankarafa forest on the western side of the Sahamalaza Peninsula, where the vegetation comprises degraded semideciduous forest and sub-humid forest. Ankarafa consists of isolated forest fragments, some of which are connected to each other by corridors.

The Sahamalaza Peninsula forests are one of the principal refuges of blue-eyed black lemurs, *Eulemur flavifrons* (Mittermeier et al. 2006) and constitute the unique habitat of the Sahamalaza sportive lemurs, *Lepilemur sahamalazensis* (Andriaholirina et al. 2006). The coastal marine area of the peninsula also has a very rich ecosystem and was approved as a Marine Biosphere Reserve in 2001 (WCS/DEC Report 2001). The Sahamalaza Peninsula was inaugurated as a Coastal and Marine National Park in July 2007.

Method

As part of an ongoing study on the behavioral ecology of blue-eyed black lemurs, we examined the development of blue-eyed black lemur infants for the first 28 weeks of their lives over two successive birth seasons (September 2006 until March 2008). Five groups (four collared and one uncollared) were followed, and this gave us the opportunity to witness the predator–prey interactions reported here.

Observations

On 18 September 2006, we followed a collared group during a nocturnal survey. The group consisted of two lactating females, four adult males, and one juvenile male.

Fig. 12.1 Wounds observed on an infant blue-eyed black lemur *Eulemur flavifrons* after a fossa's attack

We heard a fossa (*Cryptoprocta ferox*) climbing a ramy tree (*Canarium madagascariensis*) over 15 m in height, 5 m away from the group. The group panicked and gave an alarm call. The lemur group was chased by the fossa, and a 2-week-old infant was subsequently attacked. After a few minutes, we heard something fall from the tree and the group calmed down. A search of the forest floor in the same vicinity the following morning revealed a dead blue-eyed black lemur infant with wounds on its mouth, ears, and neck (Fig. 12.1).

In June 2007, a Madagascar harrier hawk (*Polyboroïdes radiatus*) attacked an adult female blue-eyed black lemur in the late afternoon. The female belonged to a group that ranged close to the research camp, where we heard the group's alarm calls. The group was highly agitated, and the call was surprisingly loud. A moment later the harrier hawk flew from a tree (height approximately 15 m) and out of sight. At the same time we heard something fall down. An adult female was found on the ground, seemingly paralyzed from the attack. She emitted a call for help and few minutes later she died. There was a wound on her neck.

On 24 August 2007 we encountered a Madagascar buzzard (*Buteo brachypterus*) eating an adult female Sahamalaza sportive lemur on the ground. We approached, and the raptor flew off, giving us the opportunity to examine the remains. It is possible that the attack occurred several days before our visit, as half of the body had already been eaten (Fig. 12.2).

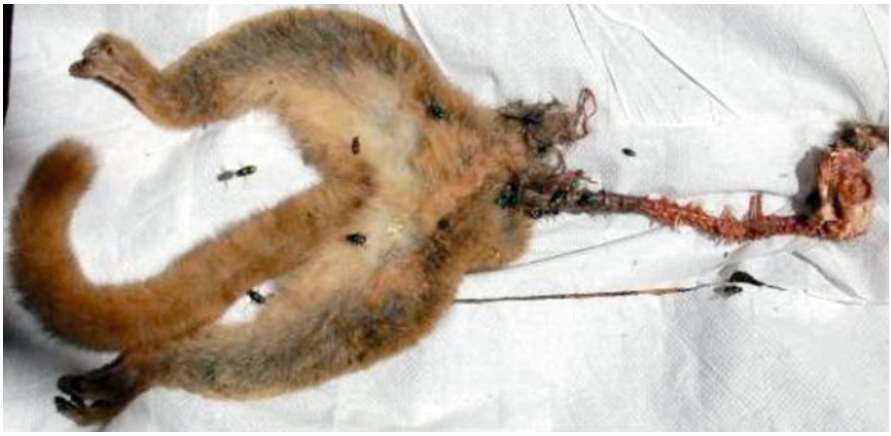


Fig. 12.2 Carcass of a female Sahamalaza sportive lemur *Lepilemur sahamalazensis* after an attack by a Madagascar harrier hawk *Polyboroïdes radiatus*

Discussion

It has been reported that predation rates on lemurs are higher than on anthropoid species (Cheney and Wrangham 1987; Janson and van Schaik 1993) and hence are likely to have evolved antipredator strategies (Dunbar 1988; Isbell 1994; Bshary and Noë 1997).

In the case of the fossa attack on the 2-week-old infant, the predator could not catch the infant and moved away after the attack because the group defended itself. Thus, the group was involved in antipredator defense behavior. Fossas have been reported to attack adult, juvenile, and infant lemurs, as seen in *Propithecus diadema edwardsi* at Ranomafana (Wright et al. 1997). In Betampona Reserve, 5 of the 13 adult black lemurs released were killed by fossas (Britt et al. 1999). During our study three infants disappeared at 13, 14, and 28 weeks, respectively, although we do not know whether this disappearance was due to illness, starvation, or predator attack. On the afternoon of 11 September 2007, the group we were following gave a loud alarm call, and we saw a fossa climbing a nearby mango tree. The fossa noticed us and moved away. As fossas are active both day and night, they attack lemurs during both periods (Wright 1998).

The attack on the female blue-eyed black lemur by the Madagascar harrier hawk may have occurred during the group's sleeping time when the animals were in their least alert state. Despite this, the group emitted a loud call, probably when roused by the attack on a group member. The raptor injured the female lemur but seemed unable to complete the kill, possibly because the female was too large. The loud vocal response given by the troop indicates antipredator behavior.

The body of the Sahamalaza sportive lemur possibly killed by the Madagascar buzzard was found near an area denuded by slash and burn in preparation for

agriculture. Marsh et al. (1987) and Johns and Skorupa (1987) reported that primate numbers in logged forests decline dramatically due to raptor predation. The tree hole of the lepilemur might have been destroyed by the slash and burn activity, leaving it vulnerable to predation. Raptors are often the principle predators of primates (Cowlishaw and Dunbar 2000). In Kibale forest, crowned hawk eagles were responsible for 84 % of predation on monkeys (Struhsaker and Leakey 1990), and Karpanty and Goodman (1999) found that harrier hawks preyed on lemurs in gallery forests near the spiny forest in south-eastern Madagascar. Moreover, owls attacked small nocturnal lemurs in dry forest (Goodman et al. 1993).

Conclusion

All of the predation incidents we witnessed on lemurs in Ankarafa forest took place during the dry season, when leaf cover was sparse. As birds are visual predators, our observations suggest that the annual loss of vegetation cover increases predation risk for lemurs. Blue-eyed black lemurs have evolved antipredator behaviors towards both aerial and terrestrial predators. Studies of predation pressure are necessary to determine its impact on the evolution of the social behavior in both blue-eyed black lemurs and Sahamalaza sportive lemurs.

Acknowledgments This research was supported by grants from Conservation International (CI), Association Européene pour l 'Etude et la Conservation des Lemuriens (AEECL), and the Third World Organization for Women in Sciences (TWOWS). We wish to thank the School of Biological and Conservation Sciences, University of KwaZulu-Natal, South Africa, the Department of Paleontology and Biological Anthropology, University of Antananarivo, IdeaWild, and Wildlife Conservation Society. We would also thank the ANGAP for giving us permission to conduct our research in Sahamalaza National Park. Special thanks are due to Judith Masters, Mike Perrin, Colleen Downs, Gisele Randria, Jean-Jacques Roeder, Kate Meares, and our local assistants.

References

Andriaholirina N, Fausser JL, Ross C, Zinner D, Thalmann U, Rabarivola C, Ravoarimanana I, Ganzhorn JU, Meier B, Hilgartner R, Walter L, Zaramody A, Langer C, Hahn T, Zimmermann E, Radespiel U, Craul M, Tomjuk J, Tattersall I, Rumpler Y (2006) Molecular phylogeny and taxonomic revision of the Sportive lemurs (*Lepilemur*, Primates). BMC Evol Biol 6:17

Britt A, Axel A, Young R (1999) Brief surveys of two classified forests in Toamasina Province, eastern Madagascar. Lemur News 4:25–27

Boesch C (1991) The effects of leopard predation on grouping patterns in forest chimpanzees. Behaviour 117:220–242

Bshary R, Noë R (1997) The formation of red colobus-diana monkey associations under predation pressure from chimpanzees. Proc R Soc Lond B Biol Sci 264:253–259

Cheney DL, Wrangham RW (1987) Predation. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 227–239

Cheney DL, Seyfarth RM, Andelman SJ, Lee PC (1988) Reproductive success in vervet monkeys. In: Clutton-Brock TH (ed) Reproductive success. University of Chicago Press, Chicago, pp 384–402

Cowlishaw G (1997) Trade-offs between foraging and predation risk determine habitat use on a desert baboon population. Anim Behav 53:667–686

Cowlishaw G, Dunbar R (2000) Primate conservation biology. University of Chicago Press, Chicago

Dunbar R (1988) Primate social systems. Chapman and Hall, London

Goodman SM, O'Connor S, Langrand O (1993) A review of predation on lemurs: implications for the evolution of social behaviour in small, nocturnal primates. In: Kappeler PM, Ganzhorn JU (eds) Lemur social systems and their ecological basis. Plenum, New York, pp 223–240

Isbell LA (1994) Predation on primates: ecological patterns and evolutionary consequences. Evol Anthropol 3:61–71

Janson CH, Van Schaik C (1993) Ecological risk aversion in juvenile primates: slow and steady wins the race. In: Pereira ME, Fairbanks LA (eds) Juvenile primates: life history, development and behavior. Oxford University Press, Oxford, pp 57–74

Johns AD, Skorupa JP (1987) Responses of rain-forest primates to habitat disturbance: a review. Int J Primatol 8:157–191

Karpanty SM, Goodman SM (1999) Diet of the Madagascar harrier-hawk, *Polyboroides radiatus*, in southeastern Madagascar. J Raptor Res 4:313–316

Marsh CW, Johns AD, Ayres M (1987) The effect of habitat disturbance. In: Gartlan JS, Marsh CW, Mittermeier RA (eds) Conservation of primates in tropical rain forest. Alan Liss, New York, pp 83–107

Mittermeier RA, Konstant WR, Hawkins F, Louis EE, Langrand O, Ratsimbazafy J, Raosoloarison R, Ganzhorn JU, Rajaobelina S, Tattersall I, Meyers DM (2006) Lemurs of Madagascar, 2nd edn. Conservation International, Washington, DC

Rakotondravony D, Goodman SM, Soarimalala V (1998) Predation on *Hapalemur griseus griseus* by *Boa manditra* (Boidae) in the littoral forest of eastern Madagascar. Folia Primatol 69:405–408

Rasoloarison R, Rasolonandrasana BPN, Ganzhorn JU, Goodman SM (1995) Predation on vertebrates in the Kirindy forest, western Madagascar. Ecotropica 1:59–65

Struhsaker T, Leakey M (1990) Prey selectivity by crowned hawk-eagles on monkeys in the Kibale Forest, Uganda. Behav Ecol Sociobiol 26:435–443

Wildlife Conservation Society, Madagascar (2001) Proposition d'une Réserve de Biosphère Marine à Madagascar. Formulaires de proposition pour le site de Sahamalaza Iles Radama. Unpublished report, Antananarivo, Madagascar

Wright PC (1998) Impact of predation risk on the behaviour of *Propithecus diadema edwardsi* in the rain forest of Madagascar. Behaviour 135:483–512

Wright PC, Heckscher SK, Dunham AE (1997) Predation on Milne-Edward's sifaka *(Propithecus diadema edwardsi*) by the fossa (*Cryptoprocta ferox*) in the rain forest of southeastern Madagascar. Folia Primatol 97:34–43

Wright PC, Martin LB (1995) Predation, pollination and torpor in two nocturnal primates: *Cheirogaleus major* and *Microcebus rufus* in the rain forest of Madagascar. In: Alterman L, Izard MK, Doyle GA (eds) Creatures of the dark. The nocturnal prosimians. Plenum, New York, pp 45–60

Part III
Behavioral Ecology

Chapter 13
Preliminary Results on the Behavioral Ecology of the Hairy-Eared Dwarf Lemur (*Allocebus trichotis*) in Andasibe, Eastern Madagascar

Karla Biebouw

Abstract I describe the results of a 4-month study in Analamazaotra Special Reserve and Forest Station, eastern central Madagascar, in which I made observations of the behavioral ecology of the elusive hairy-eared dwarf lemur, *Allocebus trichotis.* Animals were followed on 12 occasions in 8 different localities between 869 and 934 m altitude. I observed the microhabitats, supports and heights at which the animals were seen, built an ethogram including the species' behaviors and postures, and recorded all items that the animals included in their diets during this period. The Analamazaotra Special Reserve and Forest Station constitute good areas in which to study this cryptic, rare cheirogaleid.

Resume Je décris les résultats d'une étude de quatre mois menée dans la Réserve Spéciale et la Station Forestière d'Analamazaotra, centre-Est de Madagascar, pendant laquelle j'ai observé l'écologie et le comportement du rare cheirogale à oreilles velues, *Allocebus trichotis*. J'ai suivi des individus à douze reprises dans huit localités différentes entre 869 et 934 mètres d'altitude. J'ai noté le microhabitat, les supports et la hauteur à laquelle l'espèce a été vue, construit un éthogramme contenant les comportements et postures observés, et enregistré tous les types de nourriture ingérés pendant cette période. La Réserve Spéciale et la Station Forestière d'Analamazaotra constituent une région prometteuse pour l'étude de ce rare cheirogale énigmatique.

K. Biebouw (✉)
Nocturnal Primate Research Group, School of Social Sciences and Law,
Oxford Brookes University, Oxford OX3 0BP, UK
e-mail: kbiebouw@yahoo.com

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_13,

Introduction

The hairy-eared dwarf lemur, *Allocebus trichotis*, is a small nocturnal cheirogaleid classified as Data Deficient by the IUCN (2008). Prior to its recent rediscovery (Meier and Albignac 1989), the species was known only from five museum specimens and believed to be extinct. Individuals weigh around 70 g have a head–body length of ±13 cm and a tail of ±15 cm (Meier and Albignac 1991; Rakotoarison et al. 1997). Sightings of the species were reported in eastern tropical rainforests between Maromiza forest and Marojejy National Park (Table 13.1). The goal of my study was to locate *A. trichotis* in the Analamazaotra Special Reserve and Forest Station and record as much of the behavioral ecology of the species as possible over a 4-month period. In particular, I aimed to determine the exact location of the species in the Special Reserve and Forest Station; identify the types of microhabitats, supports and heights at which the animals were seen; build an ethogram including the species' behaviors and postures and describe the animals' diet.

Methods

I conducted the study in the Andasibe area of central eastern Madagascar (18°55′S, 48°25′E), including the Analamazaotra Special Reserve (810 ha) and Forest Station (250 ha) (Fig. 13.1), which comprises disturbed, mid-altitude, primary eastern rainforest (850–950 m) (Dolch 2003). Observations were carried out during the rainy season, from late January to mid-May, when most nocturnal lemurs are active, and included a total of 239 h of nocturnal walks (147 h in the Special Reserve and 44 h in the Forest Station) following existing trails. I generally started the walks, which lasted 3–4 h on average, around sunset. I walked at a slow pace (approximately

Table 13.1 Sightings of *A. trichotis* reported in the literature and obtained from personal communications

References	Area
Meier and Albignac (1991)	Mananara region
Rakotoarison et al. (1997)	Vohidrazana forest (near Andasibe)
	Zahamena Integral Nature Reserve
	Cap Masoala
	Anjanaharibe-Sud Special Reserve
Schuetz and Goodman (1998)	Anjanaharibe-Sud Special Reserve
Andriamasimanana et al. (2001)	Zahamena National Park
Garbutt (2001)	Analamazaotra Special Reserve
Goodman and Raselimanana (2002)	Marojejy Nature Reserve
Marquart personal communication (2006)	Maromiza forest near Andasibe
Garbutt personal communication (2006)	Mantadia National Park

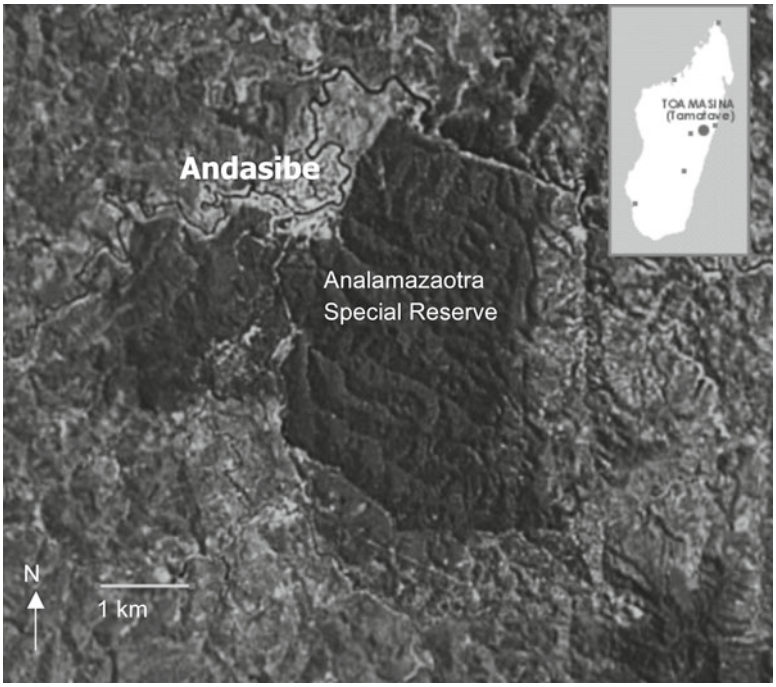


Fig. 13.1 Map of the Andasibe and Analamazaotra Special Reserve and Forest Station

1 km/h) with my assistant and two local guides, scanning the surrounding forest at all levels using Petzl Myolite halogen headlamps and Maglite 2D-cell flashlights to detect eyeshine. Once an animal was detected, it was identified using Minolta Activa 12 × 50 WP FP binoculars. On locating *A. trichotis*, I recorded its position using a handheld Garmin e-trex Vista GPS unit and followed and observed the individual for as long as possible. The hairy-eared dwarf lemur can be distinguished from the sympatric mouse and dwarf lemurs by its size, color, posture and movement pattern: it is smaller than *Cheirogaleus* spp. and larger than *Microcebus* spp.; it has a gray back as opposed to the rufous-brown of the mouse lemurs, and a dark tail generally held curled up, whereas the tail is usually straight in *Cheirogaleus* and it moves in a sporadic fashion with frequent starts and stops, similar to *Microcebus*. *Allocebus* is most easily confused with juvenile dwarf lemurs. A good view of the head and ear tufts is essential for unambiguous determination. *Ad libitum* observations also included video recordings using a Sony DCR-HC22E Handycam video camera with NightShot. I recorded all occurrences of feeding or foraging behavior, and noted the different types of microhabitats (tree trunk, tree crown, tangle or liana), supports (liana, trunk or branch size and orientation) and heights at which the animals were sighted.

Results

Sightings

Allocebus trichotis was followed on 12 occasions, 8 times in the Special Reserve and 4 times in the Forest Station, in 8 different locations at altitudes between 869 and 934 m (Table 13.2). The GPS unit was not always able to contact satellites in the forest, and the location had to be recorded in an area with lower canopy cover (i.e., near a trail or clearing). If a clear area was within 5 m of the animal's location, I took a GPS waypoint there. If not, the GPS location could not be recorded and the local name of the sight locality was noted instead. Animals were first sighted between 18:50 and 21:30 and followed for a total of 20 h and 20 min (i.e., 8.5% of the total effort time). Follow times varied from as little as 4 min to 6 h (median = 52 min 30 s). It is important to note that follow time was different from the actual observation time, as animals were regularly out of sight. Very often the animal could still be located by its eye-shine, but its behavior could not be observed in detail. Follows generally ended with the focal individual being lost, either because it moved away or was too high in the canopy, and relocation efforts were abandoned if the animal could not be found again within 1 h. Individuals were usually solitary,

Table 13.2 List of hairy-eared dwarf lemur sightings in the Analamazaotra Special Reserve (RS) and Forest Station (SF) during the study

Date	Site	First sighting	Length of observation	Number of individuals	GPS location	Altitude (m)
20 Feb 2006	RS	20:45	02:45	1	S 18°56′29.2″ E 48°25′04.3″	934
06 Mar 2006	RS	21:30	06:00	1	S 18°56′39.4″ E 48°25′11.0″	929
07 Mar 2006	RS	18:50	01:02	3	S 18°56′36.8″ E 48°25′10.2″	900
07 Mar 2006	RS	20:16	00:29	1	S 18°56′42.7″ E 48°25′10.7″	928
31 Mar 2006	RS	20:15	05:07	1	S 18°56′28.2″ E 48°25′05.8″	934
05 April 2006	RS	19:02	00:38	1	S 18°56′28.2″ E 48°25′05.8″	934
07 April 2006	RS	19:32	02:04	1	S 18°56′28.2″ E 48°25′05.8″	934
13 April 2006	SF	20:44	01:11	1	Not recorded	Not recorded
24 April 2006	SF	21:11	00:04	1	Not recorded	Not recorded
27 April 2006	SF	19:52	00:11	1	Not recorded	Not recorded
27 April 2006	RS	21:14	00:06	1	S 18°56′38.3″ E 48°25′03.6″	869
04 May 2006	SF	20:17	00:43	1	Not recorded	Not recorded

but on one occasion I observed three animals, probably two adults and a juvenile, playing and grooming each other in a tangle of branches about 10 m up in a tree.

Allocebus trichotis was active throughout the study period (February–May). Further sightings of *A. trichotis* were reported by local guides on 24 June 2006 and 29 July 2006, indicating that the species might not hibernate contrary to the conclusions of Petter et al. (1977) and Rakotoarison et al. (1997).

Microhabitats, Supports and Tree Heights Used

Individuals were observed in tangles of vegetation, on lianas, in tree crowns including the small terminal branches and on tree trunks and forks. They used small and medium lianas, medium and large tree trunks, small terminal branches of trees or tangles of vegetation and medium tree branches and tree forks. Tree genera used by the species included *Symphonia*, *Blotia* and *Terminalia* and a palm tree. Animals were seen at heights between 0.5 and 17 m. The median height at first sight was 4 m ($n = 10$).

Ethogram

Resting postures: A hairy-eared dwarf lemur was considered to be resting if it was stationary, either asleep or awake, but with limited head movement. Different postures observed include:

- "Horizontal": The animal was resting flat against a medium branch or with hands and feet holding one or several small branches and arms and legs close to the body. The tail was generally curled.
- "Vertical head down": The animal's body was flat against a medium trunk; legs and/or arms were wrapped around the trunk, or hands were on the trunk on each side of the body close to the chest. The tail was generally curled.
- "Vertical head up": Similar to above but with arms wrapped around or on the trunk and feet on the trunk. The tail was generally curled.
- "Tail-wrap": The animal was curled up on itself with the tail wrapped around its body and resting over its hands and feet.

Monitoring behaviors: An animal was considered to be monitoring its environment if it was stationary and looking around frequently. An individual could do this in the "horizontal", "vertical head down" and "vertical head up" postures described above, or it could "wrap". The latter involves the animal curling its body around a horizontal or vertical branch or trunk, generally head down, to check the habitat bellow it. Individuals were also observed to twist their heads from side to side ("head twist") which I associated with listening.

Types of locomotion: Locomotion was generally quadrupedal along horizontal or vertical supports. On vertical supports, the animal generally moved head first either up or down, although on one occasion, an animal moved down backwards for a short distance before turning around quickly to continue descending head first. Movement patterns were often sporadic, with short bouts of locomotion interrupted by pauses to monitor the habitat. Horizontal jumps of up to 2 m were observed, as well as short horizontal and vertical jumps between branches. In preparation for a long jump, the animal crouched with the tail straight and pushed off with arms and legs. During the jump, arms were held straight at the side of the body and legs and tail were extended behind. Animals were also observed to jump from trunk to trunk at lower levels of the forest. Landing could not be observed in detail.

Other behaviors: Hairy-eared dwarf lemurs groomed themselves by either scratching with the foot or using the mouth: they have large grooming claws on the second pedal digit, and I assumed they used their mandibular tooth combs, as I observed up-and-down head movements. Observed social behaviors included allogrooming, where two individuals groomed each other or one individual groomed another, and play or chase, during which animals moved around quickly chasing each other and wrestling. I also heard vocalizations, but the role of these remains to be determined.

Foraging Behavior and Diet

A hairy-eared dwarf lemur was considered to be foraging when it moved around a small area (i.e., in the same tree or in the canopy of several adjacent trees) and made frequent stops to monitor its surroundings. When trying to catch flying insects, it extended its body towards the prey and/or extended one or both hands to grab it. This movement was sometimes extremely fast and took less than 1 s. Animals also jumped towards insects while holding on to the supports with their feet, ending in a vertical hanging position. An individual was observed using its very long and flexible tongue to lick at the bark of small terminal branches, possibly to collect water or tree/insect exudates. In two instances, animals were observed collecting food items directly by mouth and were seen chewing, but the nature of the food could not be determined.

Between February and May almost 70% of the observed food consumption involved flying insects (Fig. 13.2). Other food sources probably included gum or insect exudates as well as leaves and fruits, as animals were seen licking branches. The speed of the insect catching movement did not guarantee success, as I observed five cases in which individuals failed to catch their prey. This still yielded an 80% success rate, however.

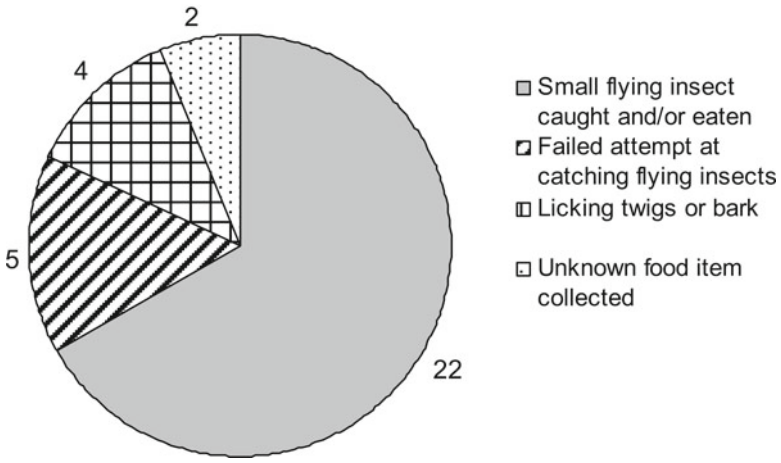


Fig. 13.2 Diet of *Allocebus trichotis* based on all occurrences of feeding behavior (number of observations are presented around the pie chart)

Discussion

The main objective of this study was to confirm the presence of the hairy-eared dwarf lemur in the Analamazaotra Special Reserve and/or Forest Station of Andasibe, in central eastern Madagascar. I observed the species to be present in both protected areas, and "bas fond" and "be fotaka" in the Special Reserve and "mad-arbre" in the Forest Station were particularly good sites to see hairy-eared dwarf lemurs. However, observations require patience, as follows constituted less than 10% of total time spent. Searches should start near sunset and last at least 3 h. All levels of the forest (from 0 to 20 m) should be scanned to detect eye-shine. Animals are most easily spotted about 4 m up either on lianas or tree trunks, but they also use tangles of vegetation and tree crowns in which they are difficult to detect. Strong flashlights (3D-cell Maglites) and good binoculars (WP FP 10 × 50 minimum) aid identification. I suggest that the best period to see *A. trichotis* is either before or after the drier, colder winter season (i.e., before May or after August).

This pilot study allows several predictions on the methodological aspects of a long-term field study of this species. Firstly, my results suggest the species is highly insectivorous, which could create problems for animal captures as they will not easily be attracted to traps which are difficult to bait with live flying insects. I therefore suggest capturing individuals by hand, with nets or from their tree holes, if these can be located. These methods were successful in previous captures of this species (Meier and Albignac 1991; Rakotoarison et al. 1997; Goodman and Raselimanana 2002). Secondly, since, once located, animals often remain out of sight and are easily lost when they move through the canopy, radio-tracking will prove invaluable to

enable uninterrupted follows. Finally, finding a GPS unit that works under dense canopy cover would be very useful.

Conclusion

My study confirmed the presence of the rare and endangered hairy-eared dwarf lemur in Analamazaotra Special Reserve and Forest Station and demonstrated the feasibility of studying the species in its natural habitat. Methodological improvements in capture techniques, radio-tracking and visualization of animals for behavioral observations will enable a better understanding of the species activity cycle, diet, home range and habitat use.

Acknowledgments The study was funded by the Primate Society of Great Britain and Primate Conservation, Inc. MICET helped with research permits, visas and logistics in Madagascar. The local ANGAP and Association Mitsinjo in Andasibe helped with logistics, access to the field sites and support staff. Field assistants included Mr Rakotonirina Laingo from the Department of Paleontology and Biological Anthropology at the University of Antananarivo; Richard and Theodore from the local ANGAP office and Play, Nasoavina, Pierre and Justin-Claude from Association Mitsinjo. The project was conducted as part of my doctoral research at Oxford Brookes University and I thank my supervisors Anna Nekaris and Simon Bearder for their support and advice throughout the study and for comments and reviews on this chapter.

References

Andriamasimanana RH, Rabenandrasana MN, Raminoarisoa V, Virginie MC, Ratelolahy FJ, Rakotonirainy EO (2001) Effets de la fragmentation de la forêt humide sur les populations d'oiseaux et de lémuriens dans le corridor Mantadia-Zahamena. Lemur News 6:18–22

Dolch R (2003) Andasibe (Perinet): are current efforts sufficient to protect Madagascar's biodiversity hot spot? In: Goodman SM, Benstead JP (eds) The natural history of Madagascar. University of Chicago Press, Chicago, pp 1480–1485

Garbutt N (2001) Brief observations of hairy-eared dwarf lemur (*Allocebus trichotis*) in Analamazaotra Special Reserve, Eastern Madagascar. Lemur News 6:37

Goodman SM, Raselimanana AP (2002) The occurrence of *Allocebus trichotis* in the Park National de Marojejy. Lemur News 7:21–22

IUCN (2008) IUCN Red list of threatened species. Available at http://www.iucnredlist.org/

Meier B, Albignac R (1989) Hairy-eared dwarf lemur rediscovered (*Allocebus trichotis*). Primate Conserv 10:27

Meier B, Albignac R (1991) Rediscovery of *Allocebus trichotis* Guenther 1875 (Primates) in northeast Madagascar. Folia Primatol 56:57–63

Petter J-J, Albignac R, Rumpler Y (1977) Genre *Allocebus*. In: Faune de Madagascar 4: Mammifères. Lémuriens (Primates Prosimiens). Orstrom and CNRS, Paris, pp 96–100

Rakotoarison N, Zimmermann H, Zimmermann E (1997) First discovery of the hairy-eared dwarf lemur (*Allocebus trichotis*) in a highland rain forest of eastern Madagascar. Folia Primatol 68:86–94

Schuetz H, Goodman S (1998) Photographic evidence of *Allocebus trichotis* in the Reserve Speciale d'Anjanaharibe-Sud. Lemur News 3:21–22

Chapter 14
Venus in Fur: Female Power in Mouse Lemurs *Microcebus murinus* and *M. griseorufus*

Fabien Génin

Abstract Female power is a characteristic peculiar to lemurs, involving dominance in agonistic interactions, and other strategies enabling priority of access to resources. I investigated three strategies of power used by the females of two mouse lemur species, both in captivity and in the wild. In both species, most agonistic encounters involved intersexual dyads, and the females won most of the observed agonistic interactions, expressing unambiguous female dominance. I observed female priority of food access on both species, the males usually avoiding interactions with females on the resources. In 3/4 resource trees and in 4/10 supplemented food sources, the 7 males I observed in the vicinity of the resources (<10 m) never consumed them. Moreover, animals found in sleeping associations (11/14 females and 7/12 males) showed higher body masses, larger home ranges, and higher proportions of fruit foraging than isolated animals.

Résumé Le pouvoir des femelles sur les mâles est une curieuse caractéristique des lémuriens, qui implique une dominance inférée par les interactions agonistiques, et d'autres stratégies conduisant à une priorité d'accès aux ressources. Cette étude a porté sur trois stratégies de pouvoir employées par deux espèces de microcèbes en captivité et en conditions naturelles. Chez les deux espèces, la plupart des rencontres agonistiques ont impliqué des dyades intersexuées, et les femelles ont remporté la plupart des conflits, exprimant une claire dominance femelle. Chez les deux espèces, les femelles ont montré une priorité d'accès aux ressources en conditions naturelles seulement, les mâles évitant généralement d'interagir avec les femelles à proximité des ressources. Sur 3/4 arbres-ressources et 4/10 ressources expérimentales, 7 mâles observés à proximité (< 10 m) n'ont jamais consommé la ressource. De plus, les

F. Génin (✉)
Department of Zoology and Entomology, University of Fort Hare,
Private Bag X1314, Alice 5700, South Africa
e-mail: FGenin@ufh.ac.za; fabien.genin@free.fr

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_14,

animaux observés dans des groupes d'association diurnes (11/14 femelles et 7/12 mâles) ont montré une plus grande masse corporelle, de plus grands domaines vitaux, et consommé une plus grande proportion de fruits que les animaux isolés.

Introduction

Female dominance is a peculiar characteristic of many lemurs that has inspired an abundant literature (Dunham 2008; Jolly 1984; Hemelrijk et al. 2008; Kappeler 1990; Richard and Nicoll 1987; Tilden and Oftedal 1995; Young et al. 1990). The concept of dominance, however, is confusing (Lewis 2002) and should only be used to refer to hierarchical dominance based on the frequency of agonistic interactions. Lewis (loc. cit.) suggested a more general term, power, which also includes feeding priority.

Female dominance in mouse lemurs (*Microcebus*) has been known for a long time but is poorly documented (Perret 1982; Radespiel and Zimmermann 2001; Génin 2004). Mouse lemur social organization is described as solitary (Kappeler and van Schaik 2002) but involves a complex network of relationships (Kappeler et al. 2002). Animals associate in sleeping sites, chiefly involving related females and less frequently males (Radespiel 2000; Radespiel et al. 2001). In *M. murinus*, found in the west and the south of Madagascar, the higher body mass of females, found in most mouse lemur species, has been interpreted as a result of their dominance (Génin et al. 2005) or their feeding priority (Génin 2004). However, because of their cryptic habits and nocturnality, the social behavior of mouse lemurs has essentially been studied in captivity (Andrès et al. 2003; Radespiel and Zimmermann 2001), whereas most field studies involve indirect observations based on capture–recapture and sleeping associations recorded during the daytime (Radespiel et al. 2001; Schmid and Kappeler 1998). Moreover, many newly (re)discovered mouse lemur species, like *Microcebus griseorufus* of the south, still await more detailed studies (Génin 2008).

This study, conducted both in captivity and in the field, aimed to examine the respective roles of three strategies of power involved in male–female relationships in two mouse lemur species, *Microcebus murinus* and *M. griseorufus* (1) female dominance based on agonistic interactions, (2) female feeding priority, and (3) cooperative control of space and/or local resources or information sharing by associated females.

Methods

For behavioral observations, animals were individually marked by clipping the hairs of the tail, except for observations of wild *M. murinus* (Génin 2004). I considered three categories of behaviors involved in contests for food: tolerance (animals forage together), avoidance (one animal replaces the other on a feeding tree), and

agonism (chases and bites). Social interactions were agonistic or sociable. For *M. murinus*, I used the results of a study conducted in the western deciduous forest in Kirindy in 1999 (54 h of observation; Génin 2004), and unpublished results of a study I conducted in the laboratory at Brunoy (Génin 2002). The captive conditions are described elsewhere (Génin et al. 2005). Animals were exposed to a short photoperiod (SP: 10–14; i.e., "winter"), resulting in seasonal fattening. I compared the body masses of individuals found in sleeping associations and individuals always found alone in their nest boxes for 38 individuals (22 males and 16 females) in 13 groups of 2–8 individuals.

To assess the establishment of dominance, I conducted dyadic encounters on animals transferred to experimental cages. I divided cages ($1.5 \times 0.5 \times 0.5$ m) into two identical compartments opened for observations. The nest boxes were checked twice and animals were considered sleeping separately if they slept alone at least once. I performed 56 h of observation in 28 independent dyads (12 male–male dyads, 9 female–female dyads, and 7 male–female dyads). The animals were observed during the first hour of darkness using a red light.

For *M. griseorufus*, the methods used for capture and radio-tracking are described by Génin (2008). I conducted this study in the spiny forest of the Berenty Private Reserve between 2000 and 2008. I radio-tracked 26 individuals (12 males and 14 females) to assess home range size (minimum convex polygon method), and gum and fruit foraging durations (total 210 h of follows). I weighed the animals within the month of radio-tracking. I also conducted focal observations of a gum tree *Commiphora orbicularis* (12 h), three fruiting *Viscum* plants (12 h), and ten opened traps baited with banana (20 h).

Results

Female Dominance in Agonistic Interactions

In both species, agonistic interactions were most frequent in male–female encounters and usually won by the females (Table 14.1). In dyadic encounters, dominants exhibited more frequent urine washing and spent longer in the neighbor's compartment and nest box than subordinates (respectively, $F1/17 = 13.6$, $P < 0.005$; $F1/17 = 8.5$, $P < 0.01$; and $F1/17 = 16.5$; $P < 0.001$). In wild *M. griseorufus*, females won agonistic interactions in 9/12 dyads (16 male–female interactions out of 34 agonistic encounters), and three heavy resident males won contests over subadult females.

Female Feeding Priority

In wild *M. murinus*, in 379 encounters I observed 36 cases of resource monopolization on seven different gum trees (*Terminalia* spp.). The oldest female trapped (92 g

Table 14.1 Focal observations on natural resource trees and trees supplemented with banana

	Microcebus murinus	*Microcebus griseorufus*	
	Terminalia mantaliopsis	Natural resources ($N=4$)	Supplemented with banana ($N=10$)
Effective observation (h)	17	24	20
Total adult males	3	5	6
Total adult females	2	15	14
Total juveniles	1	5	5
Maximum together	5	4	2
Female pairs	1	6	3
Tolerance by females	6	15	3
Replacements[a]	0	6	0
Displacements[b]	0	8	2
Chases by males	0	3	0
Chases by females	6	8	4
Deferring males	3	3	4
Deferring females	0	0	0

[a]Replacements: females briefly forage together
[b]Displacements: animals do not forage together

and at least 5 years old) was observed six times out of 17 focal observations on the focal gum tree (Table 14.1). Each time she chased one or several males but tolerated other females. In captive animals, because of *ad libitum* feeding, feeding priority was only observed in rare cases of social exclusion, consisting of exclusion from nest boxes and sometimes from food. In *M. griseorufus*, fruit foraging averaged 91 ± 24 min/night in females ($N=14$), significantly longer than in males ($N=12$) in which it averaged 13 ± 10 min/night ($t=2.9$, df $=24$, $P=0.008$). Focal observations revealed a pattern of monopolization of fruiting trees by associated females (Table 14.1).

Sleeping Associations

In captive *M. murinus*, body mass was lower in individuals excluded from sleeping associations than in associated individuals, corresponding to inhibition of seasonal fattening, independent of sex (association: $F1/46=6.2$, $P=0.017$; sex: $F1/46=1.6$, $P=0.2$; and association × sex: $F1/46=0.0$, $P=0.8$; Table 14.2). The same pattern was observed in wild *M. griseorufus*: animals found in sleeping associations had higher body masses, larger home ranges, and spent more time foraging on fruit than isolated animals (respectively, $t=2.2$, df $=24$, $P=0.036$; $t=2.1$, df $=24$, $P=0.046$; and $F1/23=4.3$, $P=0.049$). Focal observations confirmed that fruits are monopolized by associated females, often with offspring, the adult females replacing each other in the fruit trees after foraging briefly together (Table 14.1). In both species I

Table 14.2 Effect of sleeping association on captive *Microcebus murinus* (body mass: 13 groups of 3–8 individuals, behaviors: 28 dyads) and wild *Microcebus griseorufus* (12 males and 14 females)

Species		*Microcebus murinus*		*Microcebus griseorufus*	
Sleeping association[b]		Associated	Nonassociated	Associated	Nonassociated
Body mass (g)		111 ± 3 (N = 36)	92 ± 8 (N = 14)	57 ± 2	49 ± 3
Home range size (ha)				0.74 ± 0.07	0.48 ± 0.10
Feeding/fruit foraging		11 ± 2 min/h	6 ± 3 min/h	67 ± 21 min/night	30 ± 18 min/night
Interactions	Agonistic	1.6 ± 0.6 /h	11.5 ± 7.6/h	1.3 ± 0.5[a]/night	1.3 ± 0.4/night
	Sociable	6.3 ± 1.0/h	3.3 ± 1.2/h	6.2 ± 1.0/night	4.7 ± 1.0/night
N		19	9	18	8

[a]Only nonassociated dyads
[b]Male–female dyads that slept together (1/7), groups of association involving both sexes (3/12)

observed occasional male–female associations in which the male groomed the female and called to her, emitting a mating call (trill call), including cases that occurred out of the mating season. In both species, males associated with females tended to be lighter than males associated with other males, confirming that associating with females provides an advantage in mating competition (Génin 2008).

I compared the frequencies of stable sleeping associations (i.e., associations maintained over at least 3 months) observed in adult radio-tracked *M. murinus* (15 males and 15 females) and *M. griseorufus* (12 males and 14 females). There was no specific difference in the frequency of sleeping association (G-test: $G1 = 0.0$, $P = 1.0$). In both species, sleeping association was more frequent in females (78 % in *M. griseorufus* and 87 % in *M. murinus*) than in males ($G1 = 22.1$, $P < 0.0001$), but the proportion of associated males was higher in *M. griseorufus* (50 %) than in *M. murinus* (20 %) ($G1 = 6.2$, $P = 0.01$).

Discussion

In both *Microcebus murinus* and *M. griseorufus*, female power involved dominance based on rare agonistic interactions. A pattern of spatial exclusion was also observed, with most males deferring to females, as already observed in *M. murinus* (Perret 1982; Radespiel and Zimmermann 2001; Génin 2004) and other lemurs (White et al. 2006). In both species, females had priority of access to food and higher body masses. Feeding priority was observed on defendable, profitable resources: a gum tree *Terminalia mantaliopsis* for *M. murinus* and sparse fruiting trees for *M. griseorufus*.

In *M. griseorufus*, another strategy of power consisted of the co-operative control of resources by females, occasionally with resident males. Associated animals had larger home ranges, fed more on fruit, and exhibited higher body masses than isolated animals. Associated females, in particular, replaced each other on fruiting trees after foraging together briefly (observed in six female pairs). Similarly, in captive *M. murinus*, animals were heavier when they shared their nest boxes with other individuals. Moreover, some individuals, generally males, were socially excluded, a situation that may result in spatial exclusion or migration in wild animals.

References

Andrès M, Solignac M, Perret M (2003) Mating system in mouse lemurs: theories and facts, using analysis of paternity. Folia Primatol 74:355–366

Dunham AE (2008) Battle of the sexes: cost asymmetry explains female dominance in lemurs. Anim Behav 76:1435–1439

Génin F (2004) Female dominance in competition for gum trees in the grey mouse lemur. Rev Ecol 58:397–410

Génin F (2002) Economie et conservation de l'énergie au cours du cycle saisonnier chez un primate, *Microcebus murinus*: approches physiologique, comportementale et écologique. Unpublished PhD thesis, University of Paris 13, Paris

Génin F (2008) Life in unpredictable environments: first investigation of the natural history of *Microcebus griseorufus*. Int J Primatol 29:303–321

Génin F, Schilling A, Perret M (2005) Social inhibition on seasonal fattening in wild and captive grey mouse lemurs. Physiol Behav 86:185–194

Hemelrijk CK, Wantia J, Isler K (2008) Female dominance over males in primates: self-organisation and sexual dimorphism. PLoS One 3(7):e2678. doi:10.1371/ journal.pone.0002678

Jolly A (1984) The puzzle of female feeding priority. In: Small M (ed) Female primates: studies by women primatologists. Alan R. Liss, New York, pp 197–216

Kappeler PM (1990) Female dominance in *Lemur catta*: more than just female feeding priority? Folia Primatol 55:92–95

Kappeler PM, van Schaik CP (2002) Evolution of primate social systems. Int J Primatol 23:707–740

Kappeler PM, Wimmer B, Zinner D, Tautz D (2002) The hidden matrilineal structure of a solitary lemur: implications for primate social evolution. Proc R Soc Lond B 269:1755–1763

Lewis RJ (2002) Beyond dominance: the importance of leverage. Q Rev Biol 77:149–164

Perret M (1982) Influence du groupement social sur la femelle de *Microcebus murinus* (Miller, 1777). Z Tierpsychol 60:47–65

Radespiel U (2000) Sociality in the gray mouse lemur (*Microcebus murinus*) in northwestern Madagascar. Am J Primatol 51:21–40

Radespiel U, Sarikaya Z, Zimmermann E, Bruford MW (2001) Sociogenetic structure in a free-living nocturnal primate population: sex-specific differences in the grey mouse lemur (*Microcebus murinus*). Behav Ecol Sociobiol 50:493–502

Radespiel U, Zimmermann E (2001) Female dominance in captive gray mouse lemurs (*Microcebus murinus*). Am J Primatol 54:181–192

Richard AF, Nicoll ME (1987) Female social dominance and basal metabolism in a Malagasy primate, *Propithecus verreauxi*. Am J Primatol 12:309–314

Schmid J, Kappeler PM (1998) Fluctuating sexual dimorphism and differential hibernation by sex in a primate, the grey mouse lemur (*Microcebus murinus*). Behav Ecol Sociobiol 43: 125–132

Tilden DC, Oftedal OT (1995) The bioenergetics of reproduction in prosimian primates: is it related to female dominance? In: Alterman L, Doyle GA, Izard MK (eds) Creatures of the dark: the nocturnal prosimians. Plenum, New York, pp 119–131

White FJ, Overdorff DJ, Keith-Lucas T, Rasmussen MA, Kallam WE, Forward Z (2006) Female dominance and feeding priority in a prosimian primate: experimental manipulation of feeding competition. Am J Primatol 69:295–304

Young AL, Richard AF, Aiello LC (1990) Female dominance and maternal investment in strepsirhine primates. Am Nat 135:473–488

Chapter 15
Group Size, Composition and Stability in a Wild Population of Blue-Eyed Black Lemurs (*Eulemur flavifrons*) at Ankarafa, Sahamalaza National Park

Guy Hermas Randriatahina and Jean-Jacques Roeder

Abstract Four groups of blue-eyed black lemurs (*Eulemur flavifrons*) were under continuous observation over a 3-year period. Data on group composition and dynamics were regularly recorded. Groups were multimale, multifemale ranging in size from six to eleven individuals, including three to seven adults. The number of resident individuals (those remaining in the same social group for the duration of the study) varied between groups, but any given group never contained more than three adult females. Both male and female migrations occurred, but only males were seen immigrating to a foreign social group. Sex ratio at birth varied strongly between years and could be male biased.

Resume Quatre groupes de lemurs noirs (*Eulemur flavifrons*) ont fait l'objet d'un suivi continu sur une période de trois ans. Des données concernant la composition des groupes et leur stabilité ont pu être collectées régulièrement. Les associations sont de type multimâles-multifemelles. La taille des groupes oscille entre six et 11 individus, le nombre d'adultes variant de trois à sept. Le nombre d'individus résidents (présents dans un groupe donné tout au long de l'étude) varie en fonction des groupes. Toutefois, le nombre de femelles adultes présentes dans un groupe ne dépasse jamais trois. Les migrations concernent aussi bien les mâles adultes que les

G.H. Randriatahina (✉)
Département de Paléontologie et d'Anthropologie Biologique, Université d'Antananarivo, Association Européene pour l 'Etude et la Conservation des Lemuriens (AEECL), Lot IVH 169N Ambohimanandray, Ambohimanarina, Antananarivo 101, Madagascar

Association Européene pour l 'Etude et la Conservation des Lemuriens (AEECL), Antananarivo 101, Madagascar
e-mail: guyhrand@hotmail.com

J.-J. Roeder
DEPE, UMR 7178, 23 rue Becquerel, 67000, Strasbourg, France
e-mail: jeanjacques.roeder@c-strasbourg.fr

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_15,

femelles adultes, mais seul les mâles semblent immigrer dans de nouveaux groupes. Le sexe ratio à la naissance varie selon les années et peut présenter un biais en faveur des mâles.

Introduction

The blue-eyed black lemur (*Eulemur flavifrons*) is one of the most threatened lemur species, classified as Critically Endangered in the latest IUCN red list. This subspecies is found in a small area (about 2,700 km^2) located south of the Andranomalaza, north of the Maevarano, and west of the Sandrakota rivers (Mittermeier et al. 1994, Randriatahina and Rabarivola 2004) in north-western Madagascar. The actual population is unknown but has been estimated to be between 700 and 3,500 by Meier et al. (1996) and between 100 and 1,000 individuals by Mittermeier et al. (1992). The most recent estimate of the Sahamalaza peninsula population is 450–2,300 individuals (Rakotondratsima 1999). These records indicate the urgent need to establish conservation programs and to increase our knowledge about the socioecology of the blue-eyed black lemur.

Black lemurs (*E. macaco* and *E. flavifrons*) are of special interest for understanding lemur societies. Although they are genetically closely related to brown lemurs (*Eulemur fulvus*), they share the same social organization based on female dominance (Digby and Kahlenberg 2002, Fornasieri et al. 1993) with a more genetically distant species, the ring-tailed lemur (*Lemur catta*). Moreover, ecological features (e.g. resource availability) differ among the three species: ring-tailed lemurs live in the south of Madagascar (semiarid region with drastic changes in food availability), while brown and black lemurs occupy the middle and north of the island (where food availability is more constant over seasons). Therefore, no theoretical explanation based on female needs or on common evolutionary traits seems sufficient to explain the observed variation in lemur social organization.

Studies on demography and social behavior have mainly focused on ring-tailed lemurs (*Lemur catta*) (e.g. Gould et al. 2003, Jolly et al. 2002) and brown lemurs (*Eulemur fulvus*) (e.g. Overdorff et al. 1999, Ostner and Kappeler 1999). Few studies have investigated black lemur population dynamics in the wild. Andrews (1990) recorded the size and composition of 27 groups in various habitats but did not carry out long-term surveys of these groups. Bayart and Simmen (2005) reported demographic data on four groups at different periods but no continuous survey. The only long-term continuous survey of black lemurs (four social groups) was carried out by Colquhoun (1993) over a 15-month field study in various forest habitats. These studies provide demographic data (group size, group composition and sex ratio) but give no information at the individual level (e.g. the number of resident individuals, which individuals migrate, genetic relatedness between individuals). Furthermore, these studies focused on the species *Eulemur macaco.* Here we provide the first data based on a long-term continuous survey of well-known individuals belonging to clearly identified social groups of the critically endangered *Eulemur flavifrons*.

Methods

The study was carried out in Ankarafa, a forest area surrounding Ambolobozo village in Sahamalaza (Iles Radama) National Park. The park is located 13°52′–14°46′S and 47°38′E–47°46′E in the north-west of Madagascar. The Sahamalaza Peninsula is about 590 km^2 in extent and includes several forest fragments which shelter the largest connected population of blue-eyed lemurs.

In September 2004, 27 individuals were captured, making it possible to identify individuals, to carry out cutaneous biopsies and blood sampling for genetic analyses (done at the Institut d'Embryologie de l'Université de Strasbourg, Fausser L.) and to collar the animals to facilitate the collection of the demographic data and behavioral observations that follow. The animals were darted using a Telinject blowgun and anesthetised with 2 ml Ketalar by IM or IV route. Once captured, the individual was examined in order to evaluate its general health. Morphometric data were collected (sex, weight and dimensions of the body, tail and upper canines), and its age was estimated from its teeth and general health. Three age-classes were determined:

- Infants: Individuals aged less than 1 year.
- Sub-adults: Individuals between 1 and 2.5 years old, sexually immature (weight < 1,400 g).
- Adults: Individuals with fully erupted canines, weight > 1,400 g, descended testicles for males, nipples that were ±0.5 cm in length for females.

Groups were identified according to the colors of plastic collars fitted to selected individuals: Blue Group (BG), Green Group (GG), Pink Group (PG) and Yellow Group (YG). Individuals were identified by specific badges attached to the collars. Groups were habituated to the presence of humans over a 1-month period, after which it was possible to approach the individuals without eliciting flight or signs of tension.

Groups were followed between October 2004 and December 2007. Focal animal observations were conducted during this period in order to analyse social relationships in each group. Focal animals were chosen by rotation, so that a particular group was under observation for a complete week. Group composition was recorded once for the three other groups during this period. Observations were performed between 07:30 and 12:00, and from 13:30 to 17:30.

Results

Morphometric Data

All morphometric data were collected in September 2004. We found minor sex differences in both size and weight (weight: ±200 g, size: ±2 cm), with female body size and weight being significantly higher than those of males (Mann–Whitney: $n_1 = 9$, $n_2 = 12$, $U = 23$, $p = 0.029$; $U = 8$ and $p = 0.001$; Table 15.1). Although weight

Table 15.1 Mean body sizes and weights (and standard deviations) of adult female and adult male blue-eyed black lemurs

	Body size (cm)	Tail (cm)	Upper canines (mm)	Weight (kg)
Females				
$N=9$	43 ± 0.5	53.4 ± 1.9	9.14 ± 0.7	2.04 ± 0.7
Males				
$N=12$	41.8 ± 1.3	51.6 ± 1.5	9.5 ± 0.8	1.87 ± 0.9

Body size = length from the head to the base of the tail

differences can be explained by the season in which the animals were captured (i.e. during pregnancy), the reason for the size differences remains unclear.

Group Size and Reproduction

At the onset of the study (September 2004), our population contained 27 individuals (9 adult females, 14 adult males and 4 juveniles and infants; Fig. 15.1). Between November 2004 and December 2007 the population size fluctuated between 30 and 37 individuals, comprising four social groups which ranged in size from 6 to 11 individuals (mean group size: 7.68 ± 1.59, $N=24$) with 3 to 7 adults (mean number of adults: 5.04 ± 0.8). All groups were multimale, multifemale. On average, each group contained 2.42 ± 0.51 adult females and 2.92 ± 0.2 adult males during mating and 2.06 ± 0.44 adult females and 2.88 ± 0.89 adult males during weaning. The adult sex ratio ranged between 1 and 2.5 M:F with a mean of 1.43 ± 0.44.

Birth rates (number of newborns/number of sexually mature females) were 44.4 % in 2004 and 100 % in 2005 and 2006. Sex ratio at birth fluctuated greatly. In 2005, the number of males was nearly equivalent to that of females (four males and five females). However, in 2006, we recorded seven infant males and only one female (Figs. 15.2, 15.3, 15.4).

Group Dynamics

The number of resident individuals (individuals who were present in the same group for the duration of the study) varied between groups: BG: one female and one male, GG: one female and three males and YG and PG: two females and two males. Genetic analyses (unpublished data) revealed that adult females belonging to a group were not “closely related” (mother and daughters or sisters). In three groups (BG, GG and YG), one adult female was associated with her infant daughter (Fig. 15.1).

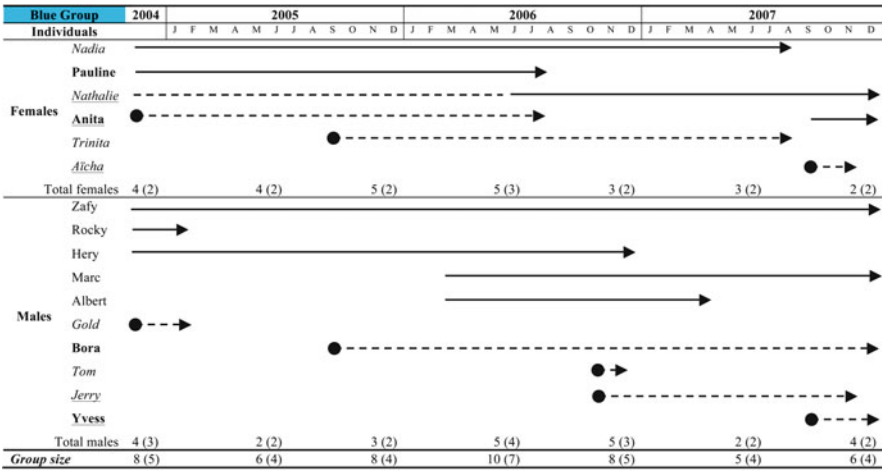


Fig. 15.1 Group composition and stability, Blue group. *Arrow*: adult; *dashed arrow*: juveniles/infants; *filled circle*: birth; number within *parentheses*: number of adults; *italics/bold*: individuals belonging to the same lineage

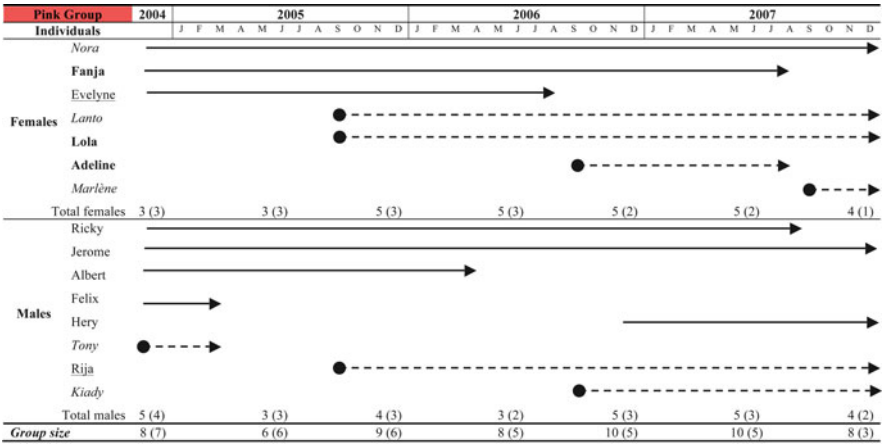


Fig. 15.2 Group composition and stability, Pink group. Legend as for Fig. 15.1

A group never contained more than three adult (sexually mature) females. In two groups (BG and GG), when one female's daughter became sexually mature, the unrelated female migrated. In YG (which had an association between two adult females), one female's daughter dispersed when she reached sexual maturity. In the last group (PG), composed of three adult females, the female without offspring migrated. Female migration and dispersal occurred in August and September (Table 15.2), close to the birth season. Migrating females were classified as "erratic"

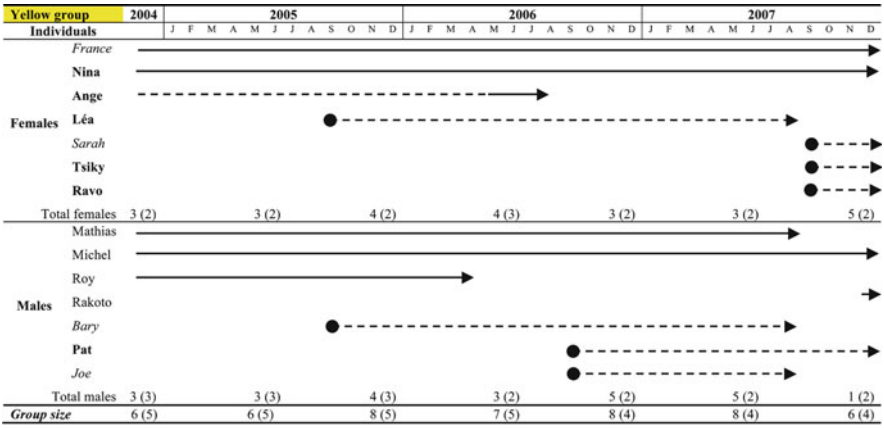


Fig. 15.3 Group composition and stability, Yellow group. Legend as for Fig. 15.1

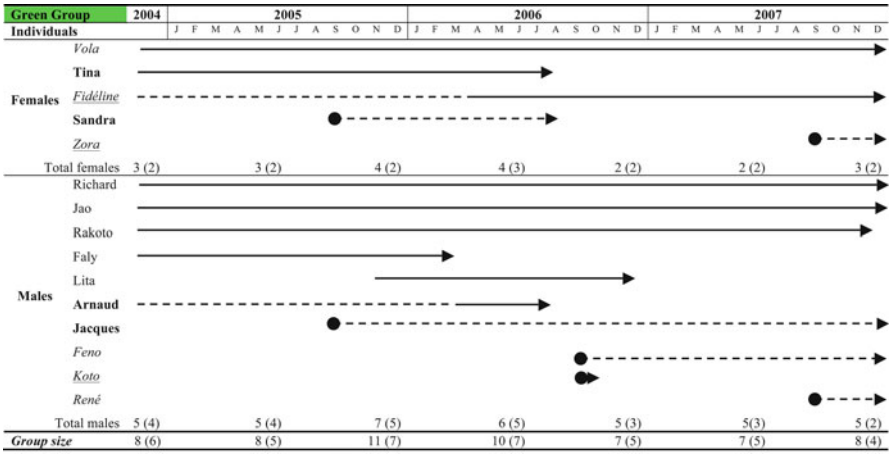


Fig. 15.4 Group composition and stability, Green group. Legend as for Fig. 15.1

(seen several times alone and not associated with another group). We did not observe foreign females entering a social group.

The number of adult males per group varied over the study, ranging from two to five. Male intergroup movements were recorded and, over the course of the study, we observed a total of 12 male migrations. In five cases, males were seen entering a new group. One male (Lita), coming from an unknown group, joined GG, where he remained for 1 year before leaving again. Two males (Albert and Hery) were seen entering neighboring groups (Fig. 15.1). Male migrations occurred mainly before the mating season (Table 15.2) and only adult individuals were involved in intergroup movements.

Table 15.2 Intergroup movements of collared blue-eyed black lemurs during the study period (September 2004–March 2007)

Sex	Individual	Group	Emigrant	Immigrant	Date
Females	Ange	Yellow	?		August 2006
	Tina	Green	Erratic		August 2006
	Pauline	Blue	Erratic		September 2006
	Evelyne	Pink	Erratic		September 2006
	Nadia	Blue	?		August 2007
	Anita	Bue	?	Blue	September 2007
	Fanja	Pink	?		September 2007
Total	7				
Males	Rocky	Blue		?	February 2005
	Felix	Pink		?	March 2005
	Lita	?		Green	December 2005
	Faly	Green		?	February 2006
	Albert	Pink		Blue	March 2006
	Roy	Yellow		?	March 2006
	Lita	Green		Erratic	March 2006
	Marc	?	Blue		December 2006
	Hery	Blue	Blue	Pink	January 2007
	Mathias	Yellow			August 2007
	Ricky	Pink			September 2007
	Rakoto	Green		Yellow	December 2007
Total	12				

Erratic refers to individuals observed alone several times

Encounters between groups generally occurred at feeding places and at resting sites. Although we observed males from different groups resting together, female interactions were almost always agonistic (Randriatahina, personal observation). Groups did not mix and each social group returned to its own home range.

Discussion

Our study reveals that blue-eyed black lemurs live in relatively stable groups comprising both resident males and females. The most salient conclusion of our data is that blue-eyed black lemur groups never contained more than three adult females. Only two studies of *Eulemur macaco* (see Table 15.3) reveal a higher number of females per group, and these studies were not continuous over time. Different groups may occasionally forage in the same area at the same time; in disturbed environments, where the resource areas are fragmented and isolated due to human activities, group size may increase temporarily.

Table 15.3 Comparison between group size and composition obtained from different studies

	Andrews (1990)	Colquhoun (1993)	Bayart and Simmen (2005)	Volampeno et al. (2010)	Present study
Species studied	*E. macaco*	*E. macaco*	*E. macaco*	*E. flavirons*	*E. flavifrons*
Study duration	Census	1 year	7 months 3 weeks	Census	3 years
Group size	2–12	5–12	4–17	4–11	16–11
Number of adults	2–8	3–7	2–12	?	3–7
Adult males	1–4	1–4	1–7	?	2–5
Adult females	1–4	2–3	1–5	?	2–3
Sex ratio	1.06	0.96	1.08	Male biased?	1.43

This result is in accordance with previous observations of captive *Eulemur macaco* (J.-J. Roeder, in preparation). When three adult females were present in a group, the youngest daughter belonging to the second lineage excluded agonistically the unrelated female. This exclusion occurred generally when the latter reached sexual maturity. In our study, the same phenomenon was recorded twice, but, in two groups, it was the youngest females who dispersed. Females appeared to leave their group without suffering targeted aggression (Randriatahina and Roeder, in preparation).

From a socioecological point of view, female dispersal may reduce intrasexual competition for access to food resources. As females are dominant over males (Digby and Kahlenberg 2002, Fornasieri et al. 1993), both male-biased sex ratios (observed in 2006) and limitation of the number of females per group may ensure female fitness in this species.

Several questions remain to be answered. For example:

- What is the degree of genetic relatedness between females belonging to the same social group? What are the proximates cue that induce female migration?
- What is the fate of migrating females? Do they always start new social groups?
- Do resident females establish special relationships with resident males?
- What is the reproductive success of resident males compared with that of immigrant males?

These questions underline the need for further continuous, long-term surveys of black lemur populations.

Acknowledgments We acknowledge the Department of Paleontology and Biological Anthropology, University of Antananarivo and l'Association Nationale pour la Gestion des Aires Protégées. Special thanks to Christoph and Nora Schwitzer and the guides. This study was supported by l'Association Européenne pour l'Etude et la Conservation des Lémuriens, and the Centre de Primatologie de l'Université Louis Pasteur de Strasbourg. We are grateful to A. Ruiz for correcting the English.

References

Andrews JR (1990) A preliminary survey of black lemurs, *Lemur macaco* in North West Madagascar. Royal Geographic Society reports, London

Bayart F, Simmen B (2005) Demography, range use, and behaviour in Black lemurs (*Eulemur macaco macaco*) at Ampasikely, North western Madagascar. Am J Primatol 67:299–312

Colquhoun IC (1993) The sociology of *Eulemur macaco*: a preliminary report. In: Kappeler PM, Ganzhorn JU (eds) Lemur social systems and their ecological basis. Plenum, New York, pp 11–23

Digby LJ, Kahlenberg SM (2002) Female dominance in blue-eyed black lemurs (*Eulemur macaco flavifrons*). Primates 43:191–199

Fornasieri I, Caubere M, Roeder JJ (1993) Social dominance and priority of access to drinking in *Lemur macaco*. Aggress Behav 19:455–464

Gould L, Sussman RW, Sauther ML (2003) Demographic and life-history patterns in a population of ring-tailed lemurs (*Lemur catta*) at Beza Mahafaly Reserve, Madagascar: a 15-year perspective. Am J Phys Anthropol 120:182–194

Jolly A, Dobson A, Rasamimanana HM, Walker J, O'Connor S, Solberg M, Perle V (2002) Demography of *Lemur catta* at Berenty Reserve, Madagascar: effects of troop size, habitat and rainfall. Int J Primatol 23:327–354

Meier B, Lonina A, Hahn T (1996) Expeditionsbericht Sommer 1995- Schaffung eines neuen Nationalparks in Madagascar. Z Kölner Zoo 39:61–72

Mittermeier RA, Konstant WR, Nicoll ME, Legrand O (1992) Lemurs of Madagascar: an action plan for their conservation. 1993–1999. IUCN/SSC Primate Specialist Group, Gland, Switzerland

Mittermeier RA, Tattersall I, Konstant WR, Meyers DM, Mast RB (1994) Lemurs of Madagascar. Conservation International, Washington, DC

Overdorff DJ, Merenlender AM, Talata P, Telo A, Forward ZA (1999) Life history of *Eulemur fulvus rufus* from 1988–1998 in southeastern Madagascar. Am J Phys Anthropol 108:295–310

Ostner J, Kappeler PM (1999) Central males instead of multiple pairs in redfronted lemurs, *Eulemur fulvus rufus* (Primates, Lemuridae)? Anim Behav 58:1069–1078

Rakotondratsima M (1999) Etude quantitative de *Eulemur macaco flavifrons* dans la presqu'île Radama. In: Wildlife Conservation Society Madagascar Country Program: Evaluation de l'état de l'environnement naturel terrestre de la presqu'île Radama. WCS, Antananarivo, pp 15–29

Randriatahina GH, Rabarivola JC (2004) Inventaire des lémuriens dans la partie nord-ouest de Madagascar et distribution d'*Eulemur macaco flavifrons*. Lemur News 9:7–9

Volampeno MSN, Masters JC, Downs CT (2010) A population estimate of blue-eyed black lemurs in Ankarafa forest, Sahamalaza-Iles Radama National Park, Madagascar. Folia Primatol 81:305–314

Chapter 16
Eviction and Troop Reconstruction in a Single Matriline of Ring-Tailed Lemurs (*Lemur catta*): What Happened When "Grandmother" Died?

Takayo Soma and Naoki Koyama

Abstract Eviction of subordinate females is well known in female-dominated ring-tailed lemur society. In almost all cases, evictions result from a dominant matriline targeting aggression towards subordinate matrilines. Here, we report an eviction in a large, single matrilineal troop after the death of the troop's "Grandmother." Although the troop contained ≥18 individuals and 8 females over several years, no evictions occurred while the Grandmother was alive. After her death, a newly dominant female and her younger sisters evicted their nieces whose higher-ranking mother had already died. The younger relatives of the evicted females did not follow their mother and sisters but stayed in the natal troop. We suggest (1) the presence of certain females like Grandmother may function as a deterrent to eviction among descendants; (2) if eviction occurs within a single matriline, aggressors evict the most distant kin; (3) a newly dominant female may form a subgroup with her younger and subordinate sisters rather than older and higher-ranking ones to circumvent intragroup competition; and (4) the juveniles of evicted female kin do not always follow the nomadic evictees but may choose the safer strategy of remaining within their natal troop.

Resume L'éviction de femelles subordonnées dans des groupes sociaux dominés par les femelles est bien connue chez le Lémur catta. Dans presque tous les cas, les évictions font suite à des agressions ciblées dirigées d'une lignée dominante vers une lignée subordonnée. Nous rapportons ici un cas d'éviction dans une troupe constituée d'une seule lignée matrilinéaire qui a fait suite à la mort de la « Grand-mère ». Bien que la troupe contienne ≥ 18 individus et 8 femelles depuis plusieurs années, aucun cas d'éviction n'a été observé tant que Grand-mère était en vie. Après sa mort, une nouvelle femelle dominante et ses jeunes sœurs ont évincé leurs nièces dont la mère, de rang élevé, était morte auparavant. Les jeunes apparentés aux

T. Soma (✉) • N. Koyama
The Center for African Area Studies, Kyoto University,
46 Shimoadachi-cho, Yoshida, Sakyo-ku, Kyoto 606-8501, Japan
e-mail: soma@jambo.africa.kyoto-u.ac.jp; mv2z67@bma.biglobe.ne.jp

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_16,

femelles évincées n'ont pas suivi leurs mères et sœurs mais sont restés dans la troupe natale. Nous suggérons que (1) la présence de certaines femelles telles que Grand-mère pourrait inhiber les évictions entre ses descendants; (2) quand une éviction se produit au sein d'un groupe matrilinéaire, les agresseurs évincent les individus qui leur sont le moins apparentés; (3) une nouvelle femelle dominante pourrait former un sous-groupe composé de sœurs plus jeunes qui leur sont subordonnées, plutôt que de femelles de haut rang et plus âgées, afin de diminuer la compétition entre groupes; (4) les jeunes apparentés aux femelles évincées ne suivent pas toujours les femelles évincées, mais peuvent choisir la stratégie plus sûre consistant à demeurer dans leur groupe natal.

Introduction

Female ring-tailed lemurs (*Lemur catta*) are dominant over males (Jolly 1966; Kappeler 1990; Sauther 1993). Eviction of females from their natal troops has been observed in troops with ≥16 individuals, at least 7–8 of whom are adult females (Jolly et al. 2002; Ichino and Koyama 2006), as a result of targeting aggression (intense and persistent aggression from one or more females to one or more subordinate individuals; Vick and Pereira 1989; Koyama et al. 2002; Ichino and Koyama 2006).

Almost all previous descriptions of female eviction have involved aggression by dominant kin groups towards subordinate ones, suggesting that female eviction and troop fission occur between matrilineal groups to reduce intratroop competition (Koyama et al. 2002; Ichino and Koyama 2006). We report a sequence of observations from targeting aggression and female eviction to troop fission in a single matriline after the death of their "Grandmother." In our terminology, *troops* have at least one adult male while *groups* have no adult males (Koyama 1991). The terms *nomadic troop* and *nomadic group* describe troops/groups that do not maintain exclusive core areas (Jolly and Pride 1999). *Troop fission* refers to the separation of troop members into permanent new social troops with secure ranges (Vick and Pereira 1989; Hood and Jolly 1995; Koyama et al. 2002).

Study Site and Troop History

Our study was conducted in the Berenty Private Reserve adjacent to the Mandrare River in southern Madagascar (see Chap. 39). The reserve is approximate 240 ha, and composed of gallery forest, scrub forest, and spiny forest (Jolly 1966; Jolly and Pride 1999). Individuals in the seven study troops have been systematically identified and named by Koyama and his colleagues since 1989 (Chap. 42). Every female has her own code name; e.g., ME89♀ refers to the daughter born to mother ME♀ in the year 1989 and ME8993♀ is the granddaughter of ME♀ born to ME89♀ in 1993.

The composition of C1 troop over 2 years (2004 and 2005) is shown in Table 16.1. Individuals ≥3 years of age were considered adult. Rank was determined by submissive behaviors like spat calls. C1 troop split from the original C troop in 1989, sharing its original core area with the neighboring CX troop. When observations commenced in September 2004, C1 comprised 21 individuals including 8 adult females and 5 adult males. Their territory, which they defended in confrontations with other troops, was 4.19 ha, situated in the gallery forest, and included the tourist bungalow area. A map showing the territories of these and adjacent troops can be found in Koyama et al. (2006) and in Chap. 42 (Fig. 42.4).

Methods

The study formed part of a broader investigation into feeding ecology that spanned 13 months (September 16, 2004–February 15, 2005; April 10–November 20, 2005) and focused on two ring-tailed lemur troops, C1 and CX. Observations were conducted from 6:00 to 18:00 in the dry season and from 5:00 to 19:00 in the rainy season. We used focal animal sampling (Altmann 1974) and 5-min instantaneous point sampling to collect data on proximity of individuals (≥2 m). When targeting aggression, eviction or other special behaviors occurred, and we collected data ad libitum, including time, behavior, and place.

Results

We observed the following sequence of events.

1. Rank change and emergence of subgroups before September 2004
   Troop C1 was composed of the descendants of one female, "Grandmother" ME89♀. She gave birth to 11 offspring, 8 of whom were still living at the time of the study (6 females and 2 males). From September 2000 to 2006, the troop contained 18–21 individuals and 6–8 adult females. The female dominance hierarchy generally reflected birth order, with the older daughters being more dominant. In September 2003, ME89♀'s fourth daughter ME8998♀ became the second-ranked female after her mother. ME89♀ was not very active but still dominant. Both ME89♀ and her second daughter ME8994♀ died sometime between December 2003 and August 2004.

   By September 2004, C1 troop contained 21 individuals (Table 16.1). After the death of Grandmother ME89♀, ME8998♀ (6 years old) became the Alpha female. She and her three younger sisters without offspring, ME8900♀, ME8901♀, and ME8999♀, formed a subgroup (proximity rate = 21.6, 18.4, and 10.6 % respectively, $N = 2$ days). The oldest sister (ME8993♀) was Beta-ranked and associated with her two sons, ME899302♂ and ME899303♂ (24.7 and 36.1 %, $N = 2$ days). Older, middle-ranked ME8997♀ associated often with her

Table 16.1 Age–sex composition and names of individuals in C1 troop over the study

Rank	(a) Names of individuals (September 2004)					(b) Names of individuals (September 2005)				
Order	Class	Female	Age	Male	Age	Class	Female	Age	Male	Age
1	Ad	ME8998♀	6	TUR♂	Unknown	Ad	ME8998♀	7	TUR♂	Unknown
2		ME8993♀	11	SEN♂	Unknown		ME8997♀	8	SEN♂	Unknown
3		ME8997♀	7	FUJ♂	Unknown		ME8901♀	4	FUJ♂	Unknown
4		ME8900♀	4	GRZ ♂→	Unknown		ME8900♀	5	↓GRI♂	Unknown
5		ME8901♀	3	KTN♂	Unknown		ME8993♀	12	↓FTM♂	Unknown
6		ME899499♀	5				ME8999♀	6	ME8902♂	3
7		ME899401♀	3						ME899702♂	3
8		ME8999♀	5						ME899302♂	3
9									KTN♂	Unknown
10									↓TUN♂	Unknown
	Sad	ME899402♀	2	ME899702♂	2	Sad	ME899403♀	2	ME8903♂	2
				ME899302♂	2				ME899303♂	2
				ME8902♂	2				ME89949903♂	2
	J	ME899403♀	1	ME8903♂	1	J			ME890004♂	1
				ME89949903♂	1					
				ME899303♂	1					
	I	ME899804♀	0	ME890004♂	0	I			ME890005♂	0
				ME890104♂	0				ME890105♂	0
				ME89949904♂	0				ME899805♂	0
Troop C1 = 21 + 4NI						Troop C1 = 21 + 3NI				
Adult females N = 8						*Adult females N* = 6				
→:Emigration							Evicted		Left C1 troop	
↓:Immigration							ME899499♀	6	ME899402♀	3
							ME899401♀	4		

Ad: Adult, Sad: Subadult, J: Juvenile, I:Infant

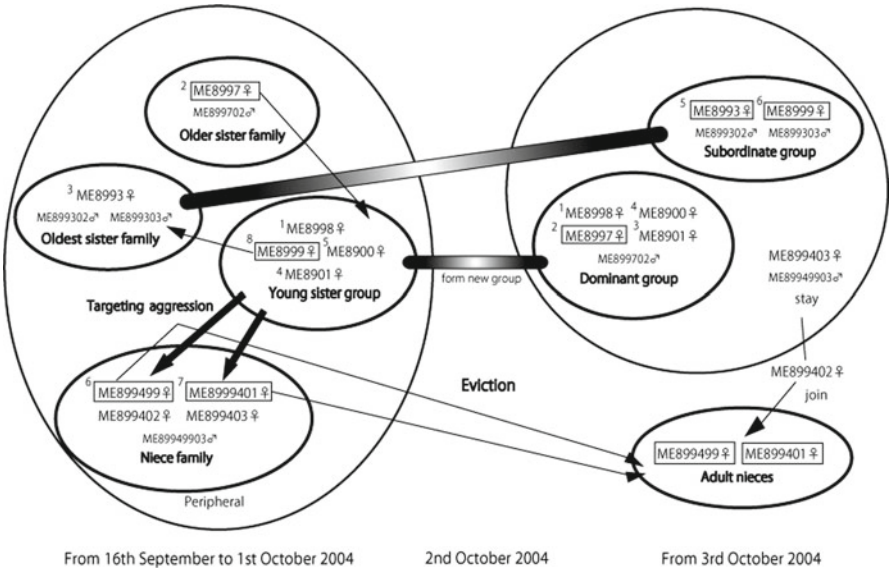


Fig. 16.1 Diagram of social changes in the C1 troop before and after the evictions

subadult son, ME899702♂. ME8994♀'s daughters, ME899499♀, ME899401♀, ME899402♀, and ME899403♀, who had not stayed in the troop center near the Alpha female, kept their distance from the other females on September 17. ME899499♀ had also not remained near the Alpha (0 %) and other females (2.8–6.8 %) but stayed with her sisters (36.8 %) on October 18. Thus, there were four female subgroups in September 2004 (1) the Alpha female and her younger sisters, (2) the older sister family, (3) the oldest sister family, and (4) the niece family (Fig. 16.1).

2. Targeting aggression and eviction, late September to early October 2004
   The Alpha female (ME8998♀) and ME8900♀ began targeting aggression at ME8994♀'s adult daughters in mid-September 2004 (5 times in 3 days). ME8998♀, ME8900♀, ME8999♀ (lost on September 18), and ME899401♀ had infants during this period. At 15:00 on October 2, ME899499♀ and ME899401♀ were chased by the Alpha subgroup and ran away, crossing the territories of two other troops into A2 territory. After this eviction, whenever C1 troop encountered ME8994♀'s adult daughters, three of the Alpha subgroup (ME8998♀, ME8900♀, and ME8901♀) pursued their adult nieces aggressively, while ME8993♀, ME8997♀, and ME8999♀ did not.

   The older ME8997♀ began to participate in the Alpha female subgroup after the eviction. ME8993♀, the oldest sister, fell in rank from Beta to second lowest female. Subordinate ME8999♀ left the Alpha female group and moved with ME8993♀. The new subgroups were (1) the dominant group, (2) the subordinate group, and (3) the adult nieces outside the troop (Fig. 16.1). The subordinate

group was not aggressive to ME899499♀ and ME899401♀ when they encountered each other on the C1 boundary.

The second daughter of ME8994♀, ME899401♀, had a male infant when the eviction occurred. The infant fell from his mother and was found in a weakened condition near the boundary of the neighboring YF troop on October 3. The dominant group was not aggressive towards the immature ME899402♀ and ME899403♀, and even though their older sisters had been chased, they were allowed to return to C1 troop. ME899402♀ sometimes stayed with her sisters but most often returned to C1 troop. However, she joined her older sisters on October 15 and remained with them.

3. Juveniles remained in their natal troop, early October
   There were two juveniles in the evicted niece family. The youngest, ME899403♀, tried to follow her sisters, but when ME899499♀ and ME899401♀ fled, she could not keep up and lost track of them. On October 15, when the C1 troop encountered ME899499♀ and ME899401♀ at the A2/C1 boundary, they were attacked by the Alpha female; ME899402♀ followed her sisters but ME899403♀ could not, emitting loud "lost calls," and ceased following her sisters from that time. ME899499♀'s son, ME89949903♂, did not follow his mother but stayed in C1 troop. He spent time with his mother outside the C1 territory three times, when he groomed and moved with his family, but returned to C1 in the evening. Although he became less active and lost weight and condition, he survived and was not subjected to aggression by troop members.
4. Formation of a nomadic troop after the mating season, April 2005
   From November to December 2004, the adult nieces avoided the C1 home range, although they were seen in the neighboring CX range. However, from the end of January 2005, when the top-ranking food plant *Azadirachta indica* was fruiting, they entered the C1 range several times quietly to feed on fruits. Whenever they were discovered by the dominant group, they were chased vehemently.

   In the April 2005 mating season, we frequently found the adult nieces near the C1/A2 boundary with two accompanying males (5 times in 9 days). One A2 male joined them temporarily during the mating season, but another 6-year-old male, CW9094♂ from the neighboring CX troop, remained with them beyond this period. Hence, the adult nieces formed a new troop (Koyama 1991). The dominant group continued to chase them, but the adult nieces resisted their aggression, fighting back on the confrontation line. ME8993♀ and ME8999♀ did not attack the nieces in the absence of the dominant group members. Although they were still nomadic (Ichino and Koyama 2006), they intruded frequently into the C1, A2, and CX home ranges, from April through the dry season to November.

   By the September 2005 birth season, the adult nieces had gained a sleeping site on the A1/A2 boundary. However, they did not often win confrontations with other troops, and ME899499♀ dropped her infant when they retreated on October 11. They did not succeed in establishing a territory. On October 31, 2005, their male consort (CW909499♂) was found dead from unidentified causes, and the adult nieces again became a nomadic group.

Discussion

Troop Hierarchy Change After the Death of Grandmother

Almost all cases of eviction described previously at Berenty and Beza Mahafaly were carried out by dominant matrilineal groups against subordinate matrilines (Koyama 1991; Hood and Jolly 1995; Jolly and Pride 1999; Gould et al. 2003; Ichino and Koyama 2006). In the T2 troop, a similar classic eviction occurred in September 2003 ($N = 18$, 8 adult females comprised of 6 dominant kin and 2 subordinate kin, 5 adult males, dominant kin group = 11, subordinate kin group = 3). Ichino and Koyama (2006) proposed that female eviction occurred when the troop contained ≥16 individuals (mean = 22.5, range 16–28) and the number of adult females was ≥7 (mean = 8.4, range 7–10), while Jolly et al. (2002) favored ≥8 females. When C1 contained more than two matrilineal groups in 2000, ME89♀ and her daughters evicted another kin group.

In C2A troop, two females were evicted in October 2009 when the number of adult females reached 7; the Alpha female, her daughters, and granddaughter evicted her cousin's daughters. In the A2 troop, which lacked a Grandmother figure, 3 adult females were evicted in October 2012 when the adult female number was 10 (our observations).

In the case we have described, all the females in C1 troop were daughters or granddaughters of Grandmother ME89♀, who retained the Alpha rank until she died. Although C1 troop comprised more than 16 individuals and 8 females, there were no evictions and the dominance hierarchy was stable. After Grandmother's death, hierarchy stability crumbled and targeting aggressions led to evictions. The presence of an old matriarch thus may deter evictions when all the troop's females are her descendants.

Choice of Eviction Targets and Allies

If a dominant female evicts other females within the same matriline to avoid food competition, nieces would be more appropriate targets than sisters because of their more distant relationship; this was the case in our study.

ME8998♀ initially formed a subgroup with her younger sisters rather than the older, stronger ones with offspring. Among cercopithecine monkeys, adult sisters usually rank in inverse order of age (Japanese macaque: Koyama 1970; Nakamichi et al. 1995; long-tailed macaque: Netto and van Hooff 1986), female dominance ranks remain stable over considerable periods, and daughters acquire ranks immediately below those of their mothers (Nakamichi et al. 1995). In ring-tailed lemurs, however, daughters are not invariably ranked immediately below their mothers, and adult sisters are dominant over younger sisters (Nakamichi and Koyama 1997). Moreover, dominance relations change frequently in both sexes (Jolly 1966; Taylor

and Sussman 1985; Nakamichi et al. 1997) and are largely determined by attributes like age, size, fighting ability, and social skills (Nakamichi and Koyama 1997). When ME8998♀ became an adult, her older sisters, ME8993♀ and ME8994♀, were higher ranking. ME8998♀ emitted submissive "spat" calls and was displaced by them, while her younger sisters were not aggressive towards her. She chose to form a subgroup with her more compliant younger sisters in intragroup contests, ultimately depriving her older sisters of their high ranks. Moreover, targeting her nieces for eviction could increase ME8998♀'s inclusive fitness.

Juvenile Strategies to Cope with the Eviction of Close Kin

Although their close kin, including their mothers, were evicted, the juveniles chose to stay in C1 troop. They groomed and moved with their mothers and sisters for a few hours when they met them, indicating they did not forget their close kin.

When a female of CX troop died, her female juvenile did not have any kin with whom to groom and huddle. She did not feed well and died 2 weeks after the death of her mother (Soma 2006). ME89♀'s last offspring, ME8903♂, also became markedly unhealthy after his mother's death. However, ME899403♀ and ME899403♂ had juvenile ($N=2$) and subadult males ($N=3$) and adult females from the same matriline with whom they could groom and huddle, and the dominant subgroup members were not especially aggressive towards them. The adult females were tolerant and groomed the juveniles. Later, when ME8990♀ was evicted by the returned adult nieces in 2006, her son ME899005♂ did not follow his mother and remained in C1 troop.

Juveniles face potential costs in following nomadic kin as opposed to staying in their natal troops. They might not be able to follow the adults when they intrude into another territory and are chased by the proprietors. Juveniles left alone in unfamiliar territories are vulnerable to predation, and October may be a time of especially high vulnerability for infant ring-tailed lemurs, because this period coincides with the nesting season of both harrier hawks and buzzards, which have increased nutritional needs for egg laying and incubation (Sauther 1989). A subadult male of the T1B troop was preyed upon by a Madagascar buzzard, *Buteo brachypterus*, in September 2003 (Jolly and Soma, personal observation). In May 2005, a male juvenile of CX troop ($N=10$, 5 adult females and 3 adult males) was eaten by a feral dog, even though he was moving with his mother in the troop (Soma, personal observation). Juveniles may be less vulnerable than infants but still face danger moving alone, making it safer for them to stay in the natal troop with its enhanced capacity for predator detection.

When C1 and CX troops split, Koyama et al. (2002) found the juveniles initially stayed in the natal C1 troop and did not follow their mother and sisters. However, once their kin succeeded in establishing a territory, the juveniles joined their kin. Hence, ME899403♀ and ME89949903♂ may join the adult nieces' troop when they establish a stable territory.

Conclusions

1. The existence of a matriarch like Grandmother in a ring-tailed lemur troop may deter evictions when all the troop's females are her descendants.
2. If eviction occurs within a single matriline, targeting the most distantly related kin could increase the inclusive fitness of the dominant and high-ranking antagonists.
3. The dominant female may form a subgroup with her younger and subordinate sisters rather than the older and higher-ranking ones to circumvent intragroup competition.
4. Juveniles of evicted females may not follow their closest nomadic kin, preferring the relative safety of their natal troops.

Acknowledgments We thank Jean de Healme and family for their hospitality and for allowing us to conduct research in Berenty Reserve, and the Government of Madagascar and the Botanical and Zoological Park of Tsimbazaza for research permission. TS is grateful to Alison Jolly for advice and encouragement.

References

Altmann J (1974) Observational study of behaviour: sampling methods. Behaviour 49:227–267

Gould L, Sussman RW, Sauther ML (2003) Demographic and life-history patterns in a population of ring-tailed lemurs (*Lemur catta*) at Beza Mahafaly Reserve, Madagascar: a 15-year perspective. Am J Phys Anthropol 120:182–194

Hood LC, Jolly A (1995) Troop fission in female *Lemur catta* at Berenty Reserve, Madagascar. Int J Primatol 16:997–1015

Ichino S, Koyama N (2006) Social change in a wild population of ringtailed lemurs (*Lemur catta*) at Berenty, Madagascar. In: Jolly A, Sussman RW, Koyama N, Rasamimanana H (eds) Ringtailed lemur biology: *Lemur catta* in Madagascar. Springer, New York, pp 233–244

Jolly A (1966) Lemur behavior. University of Chicago Press, Chicago

Jolly A, Pride Y (1999) Troop histories and range inertia of *Lemur catta* at Berenty, Madagascar: a 33-year perspective. Int J Primatol 20:359–373

Jolly A, Dobson A, Rasamimanana HM, Walker J, O'Conner S, Solberg M, Perel V (2002) Demography of *Lemur catta* at Berenty Reserve, Madagascar: effects of troop size, habitat and rainfall. Int J Primatol 23:327–353

Kappeler PM (1990) Female dominance in *Lemur catta*: more than just female feeding priority? Folia Primatol 55:92–95

Koyama N (1970) Changes in dominance rank and division of a wild Japanese monkey troop in Arashiyama. Primates 11:335–390

Koyama N (1991) Troop division and inter-troop relationships of ring-tailed lemurs (*Lemur catta*) at Berenty, Madagascar. In: Ehara A, Kimura T, Takenaka O, Iwamoto M (eds) Primatology today. Elsevier, Amsterdam, pp 173–176

Koyama N, Nakamichi N, Ichino S, Takahata Y (2002) Population and social dynamics changes in ring-tailed lemur troops at Berenty, Madagascar between 1989–1999. Primates 43:291–314

Koyama N, Soma T, Ichino S, Takahata Y (2006) Home ranges of ringtailed emur troops and the density of large trees at Berenty reserve, Madagascar. In: Jolly A, Sussman RW, Koyama N, Rasamimanana H (eds) Ringtailed lemur biology: *Lemur catta* in Madagascar. Springer, New York, pp 86–101

Nakamichi M, Itoigawa N, Imakawa S, Machida S (1995) Behavioral characteristics of old female Japanese monkeys in a free-ranging group of Japanese monkeys at Katsurayama. Primates 25:192–203

Nakamichi M, Rakototiana MLO, Koyama N (1997) Effects of spatial proximity and alliances on dominance relations among female ring-tailed lemurs (*Lemur catta*) at the Berenty Reserve, Madagascar. Primates 38:331–340

Nakamichi M, Koyama N (1997) Social relationships among ring-tailed lemurs (*Lemur catta*) in two free-ranging troops at Berenty Reserve, Madagascar. Int J Primatol 18:73–93

Netto WJ, van Hooff JARAM (1986) Conflict interference and the development of dominance relationships in immature *Macaca fasicularis*. In: Else JG, Lee PC (eds) Primate ontogeny, cognition and social behaviour. Cambridge University Press, Cambridge, pp 291–300

Sauther ML (1989) Antipredator behavior in troops of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. Int J Primatol 10:595–606

Sauther ML (1993) Resource competition in wild populations of ringtailed lemurs (*Lemur catta*): implications for female dominance. In: Kappeler PM, Ganzhorn JU (eds) Lemur social systems and their ecological basis. Plenum, New York, pp 135–152

Soma T (2006) Tradition and novelty: *Lemur catta* feeding strategy on introduced tree species at Berenty Reserve. In: Jolly A, Sussman RW, Koyama N, Rasamimanana H (eds) Ringtailed lemur biology: *Lemur catta* in Madagascar. Springer, New York, pp 141–159

Taylor L, Sussman RW (1985) A preliminary study of kinship and social organization in a semi-free-ranging group of *Lemur catta*. Int J Primatol 6:601–614

Vick GL, Pereira ME (1989) Episodic targeting aggression and the histories of *Lemur catta* social groups. Behav Ecol Sociobiol 25:3–12

Part IV
Dietary Ecology

Chapter 17
Coprolites Associated with *Archaeolemur* Remains in North-Western Madagascar Suggest Dietary Diversity and Cave Use in a Subfossil Prosimian

Natalie Vasey, David A. Burney, and Laurie R. Godfrey

Abstract Subfossil fecal pellets associated with *Archaeolemur* cf. *edwardsi* skeletal material from Anjohikely Cave in north-western Madagascar were probably derived from this large extinct lemur. Pellets were photographed, measured, and dissected. One of the pellets dates to 830 ± 60 years BP. Pellets contain a wide variety of items indicative of omnivory, including fibrous fruit exocarps and seeds; bat, rodent, frog, and lizard bone; gastropod shell; and crustacean and arthropod exoskeletons—all within a matrix of comminuted vegetation. Pollen contents from inside intact pellets support other paleoecological evidence that recent feeding had taken place in wooded grassland habitat. This diet is consistent with ethnohistorical data and anatomical studies that indicate hard-object feeding in *Archaeolemur*. *Archaeolemur* may have deliberately entered caves to forage, although caves would also have offered water, abundant shade, cool conditions, cryptic sleeping sites, and refuge from predators. Cave-exploring behavior is rare in primates, but consistent with anatomical evidence that *Archaeolemur* was well adapted for terrestrial locomotion as well as arboreal climbing.

N. Vasey (✉)
Department of Anthropology, Portland State University, Portland, OR 97207, USA
e-mail: nvasey@pdx.edu

D.A. Burney
National Tropical Botanical Garden, 3530 Papalina Road, Kalaheo, HI 96741, USA
e-mail: dburney@ntbg.org

L.R. Godfrey
Department of Anthropology, University of Massachusetts, 240 Hicks Way,
Amherst, MA 01003, USA
e-mail: lgodfrey@anthro.umass.edu

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_17,

Resume Les pelotes fécales associées aux squelettes de *Archaeolemur* cf. *edwardsi* trouvés dans la grotte de Anjohikely, au nord-ouest de Madagascar peuvent être attribuées à ce grand lémurien aujourd'hui éteint. Des pelotes ont été photographiées, mesurées, et disséquées. L'âge de l'une d'entre elles a été estimé à 830 ± 60 ans. Les pelotes contiennent des éléments variés indicateurs d'un régime omnivore, tels que des exocarpes de fruits fibreux et des graines, des os de chauves-souris, de rongeurs, de grenouilles et de lézards, des coquilles de gastéropodes et des exosquelettes de crustacés et d'arthropodes – tous enveloppés dans une matrice végétale. Les pollens contenus dans les pelotes intactes confirment d'autres travaux paléo-écologiques et suggèrent que les animaux se sont récemment nourris dans un habitat de prairies boisées. Ce résultat confirme aussi les données ethno-historiques et anatomiques qui suggèrent qu'*Archaeolemur* se nourrissaient d'objets durs. *Archaeolemur* pourrait avoir pénétré dans ces grottes délibérément pour se nourrir, et ces grottes pourraient également avoir offert de l'eau, de l'ombre, des températures fraiches, des gîtes diurnes abrités, et des refuges contre les prédateurs. L'utilisation de grottes est rare chez les primates, mais possible pour *Archaeolemur* qu'on sait avoir été partiellement terrestre.

Introduction

Subfossil fecal pellets from Anjohikely Cave in north-western Madagascar are believed, from association with *Archaeolemur* cf. *edwardsi* skeletal material, to be derived from this large extinct lemur (26.5 kg; Jungers et al. 2008). Anjohikely is a shallow limestone cave with several horizontal entrances and numerous sinkholes. Its passages total just over 2.5 km, divided into three areas—Anjohikely 1, 2, and 3 (Laumanns et al. 1991). In 1992, 30 pellets were collected from a single site in Anjohikely 2 (Burney et al. 1997), and in 2004 we recovered another 29 pellets from two sites in Anjohikely 3. Coprolites have not been reported previously in the literature on Malagasy subfossils, and our sample potentially provides unique and direct insights into *Archaeolemur*'s paleoecology.

Material and Paleontological Context

At site 1-1 in Anjohikely 2, a small rimstone dam filled with moist sand yielded 30 pellets along with an intact, nearly complete juvenile *Archaeolemur* skeleton and the bones of a small extant lemur (*Eulemur* cf. *fulvus*). Most of the pellets are pinched off at one or both ends, indicating they had been extruded. Pellet contents include masticated fragments of the cave-roosting bat *Hipposideros commersoni*, pollen of grassland plants, plant fibers, and small seeds (Burney et al. 1997). Further examination of loose matrix from partially disintegrated pellets reveals crustacean carapaces, rodent bones, bat bones, and woody exocarp. The pellets do not resemble those of

Table 17.1 Measurements (mm) of coprolites from different sites in Anjohikely Cave, including means ± one standard deviation, observed ranges, and sample size (*n*)

	Anjohikely 2: 1-1 Pockets 1 and 2[a,b]	Anjohikely 3: 15-2 Pocket 1[a,c]	Anjohikely 3: 15-2 Pocket 5[b]	Anjohikely 3: 16-1[b]
	$n=6$	$n=6$	$n=3$	$n=7$
Length	19.24 ± 3.63	–	34.07 ± 5.79	27.65 ± 4.9
	14.41–22.54	–	27.48–38.34	20.39–34.14
Width	13.34 ± 0.9	11.26 ± 2.55	17.19 ±1.5	14.93 ± 2.33
	11.97–14.66	8.84–15.05	15.6–18.59	12.49–17.92

[a]Pellets associated with *Archaeolemur* remains
[b]We measured only whole pellets showing clear evidence of extrusion (pinched off at one or both ends). Pellets collected whole but partially disintegrated after collection could not be measured
[c]Length measurements not possible due to fragmentation after collection; pellets may not have been extruded

E. fulvus. Rather, they are similar to most of those from Anjohikely 3, and from site 16-1 in particular, in form (elliptical), content (shell, vertebrate bone, and plant fiber matrix), color (grayish-brown), and state of preservation (powdery and dry) (Table 17.1). One of the pellets from Anjohikely 2 yielded a radiocarbon date of 1041–1280 AD (830 ± 60 year BP). If these subfossil pellets are indeed derived from *Archaeolemur*, this is the latest dated occurrence for the genus (Burney et al. 2004).

At site 15-2 in Anjohikely 3, we collected seven pellets and some fragments from several small, dry rimstone dams located approximately 2 m above the cave floor (pocket 1 in Table 17.1) as well as an adult *Eulemur* maxilla, and infant *Archaeolemur* skull fragments and teeth. In a set of rimstone dams directly adjacent, forming graduated levels along the wall of the cave (pocket 2), we recovered additional *Archaeolemur* remains, including more skull fragments, ribs, an ilium, a calcaneum, and a talus. The individual had a full deciduous dentition, with M^1 erupted and M^{2-3} partly formed within crypts. We found no duplicate elements. At floor level 10 m from these deposits (pocket 5 in Table 17.1) were another four coprolites lying at the edge of a rimstone pool that contained moist sand and gravel.

The first seven pellets from site 15-2 (pocket 1) contained reddish-brown chitin in addition to fine, partially digested plant material and sand. They were distinguished from other pellets in our sample by their narrower width (Table 17.1), a higher density of gastropod shell fragments and arthropod exoskeletons, absence of bone, and by the fact that none appeared pinched off. They may be the colon contents of a very young individual, based on skeletal age of the associated *Archaeolemur* remains. If so, this suggests the animal died *in situ*. The remaining four pellets from site 15-2 (pocket 5) were extruded and are larger (Fig. 17.1a, Table 17.1). One selected for dissection contained gastropod shell fragments, arthropod exoskeletons, microchiropteran and frog bone, and fur, enmeshed in a fibrous matrix.

At site 16-1 in Anjohikely 3, we collected 18 whole pellets and some large fragments in a small cavern with flowstone walls, approximately 3 m × 4 m in diameter. We scooped the coprolites out of soft, dry sediment that had accumulated on the floor to a depth of 4 cm. Sixteen of the pellets were pinched off at one or both ends

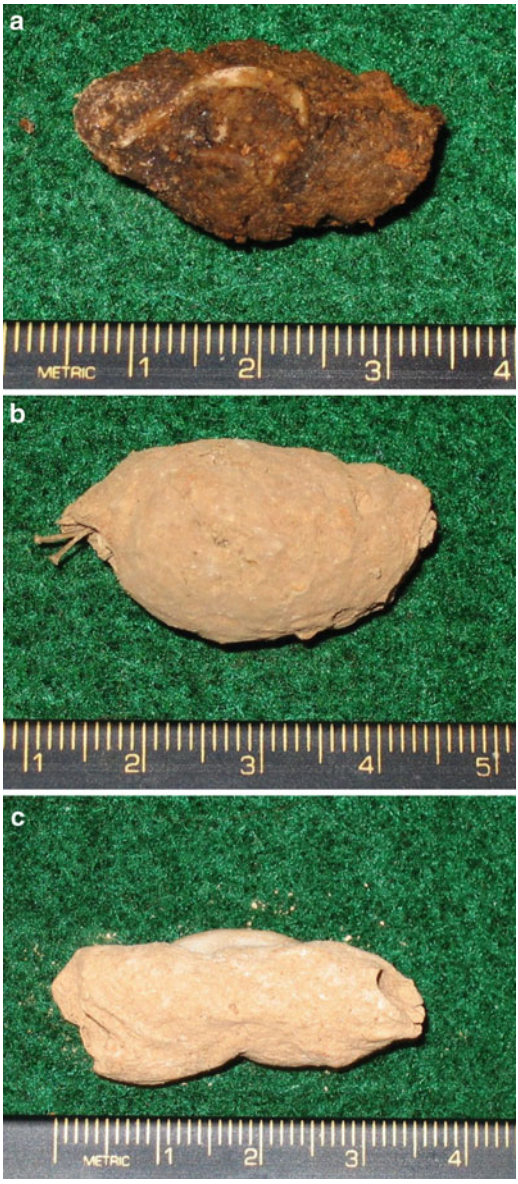


Fig. 17.1 Representative subfossil fecal pellets with pinched off ends from (**a**) Anjohikely 3, site 15-2: pocket 5 and (**b**) Anjohikely 3, site 16-1. A pellet illustrative of those that appear to have been colon contents is shown in (**c**) from Anjohikely 2, site 1-1

(Fig. 17.1b), while two others were not. The latter had flattened ends and were more elongate, bearing impressions of the soft tissues of the GI tract. They are possibly the colon contents of an individual that died *in situ*. One of the extruded pellets selected for dissection contained gastropod shell, insect wings, microchiropteran bones, and chunks of plant fiber resembling dried fruit pulp. Grayish-brown matrix from some of the coprolites that partially disintegrated in transit contained bat,

lizard, and frog bones, and some tiny seeds. The content of unpinched pellets did not appear to differ from those bearing evidence of extrusion.

Discussion

The context and content of the pellets suggest several different scenarios concerning how and why their bearers entered the cave. *Archaeolemur* has been reconstructed as both arboreal and terrestrial (Godfrey et al. 1997), and it is plausible that they walked or climbed into the cave seeking food (gastropods, crustaceans, bats, and frogs). However, even if *Archaeolemur* deliberately sought out these resources, caves would have comprised just part of their foraging range, as pellets also contained abundant plant material from outside the cave. Pollen spectra from speleothems at Anjohibe Cave (2 km distant) depicted a grassland with endemic grasses, satra palms, and trees adapted to a long dry season and periodic fires at <4 Kya—a habitat that persists in the region today (Burney et al. 1997). *Archaeolemur* may also have entered the cave for some of the same reasons that extant primates do—to obtain water, micronutrients (via geophagy), security, and/or thermoregulatory benefits (McGrew et al. 2003).

Cave use has rarely been reported in extant primates, with the exception of baboons. At De Hoop Nature Reserve in Western Cape Province, South Africa, chacma baboons habitually use limestone caves for sleeping, more often during colder months (Barrett et al. 2004). At Uitkomst Cave in the highveld, Brain (1981) reported that baboons regularly slept overnight on huge fallen roof blocks where an extensive deposit of their feces had accumulated. This conforms to what Simons (1966) observed in the Mount Suswa cave system of Kenya, where baboons experience heavy predation by leopards. Cave use by chimpanzees at Fongoli in Senegal may provide a better comparison in some respects. This savanna woodland is one of the hottest and driest habitats that chimpanzees presently occupy, and they use caves as shelters during the hottest times of year (Pruetz 2007). However, caves at Fongoli are very small, and so in other respects, primates inhabiting karst topography where caves contain extensive dark passages provide better comparisons. Observations of cave use by extant lemurs are rare, and none involve use of long, dark passages. In the Ankarana limestone massif in northern Madagascar, crowned lemurs enter Second River Cave to drink during the dry season (Wilson et al. 1989). At Tsimanampesotse, a dry coastal zone in south-western Madagascar, ring-tailed lemurs enter small limestone fissures, evidently to avoid both high and low temperatures and to evade predators (Cuozzo and Sauther, personal communication). In south-eastern Madagascar, we have observed ring-tailed lemurs feeding and taking daytime shelter in Andrahomana Cave by entering through tree tops that emerge at ground level from a sunken forest within the cave.

It is also possible that *Archaeolemur* fell in through sinkholes, getting injured, trapped or disoriented, and dying as a result. If the water table were higher than present levels, or experienced a temporary surge caused by storm water run-off, the likelihood of getting trapped in a section of the cave would be high, regardless of

whether an individual entered deliberately through a horizontal passage or accidentally through a sinkhole. Presumably the five *Archaeolemur* individuals collected at the sides of two caverns in Anjohikely 2 had crawled up to die after entrapment. One of these (a juvenile) was associated with 30 subfossil pellets (site 1-1; Burney et al. 1997). The cavern where we collected many pellets at Anjohikely 3 (site 16-1) bears a close resemblance to the Anjohikely 2 localities, having crawl spaces partway up the walls. Because all pellets may not have been extruded at Anjohikely 3 site 16-1 (suggesting death *in situ*), and because pellets were found in association with an *Archaeolemur* skeleton at Anjohikely 2 site 1-1 (indicating death *in situ*), accidental entry or entrapment are likely scenarios.

A third scenario, albeit one that is less likely, is that *Archaeolemur* was brought into the cave by predators large enough to transport them. If this were the case, their skeletal material would simply be the remains of carnivore meals, and we would not expect to find extruded lemur fecal pellets or intact lemur bones, let alone near-complete skeletons, as at Anjohikely 2 site 1-1. We would also expect to find predator scat. We compared the scat of an endemic carnivore (*Cryptoprocta ferox*) and two viverrids (*Suricata suricatta* and *Bassariscus astutus*) with the subfossil pellets. Neither form nor content of the subfossil pellets resembles the scats of these carnivores (see also Burney et al. 1997). Carnivore scat is cylindrical and variable in length (not elliptical and pellet-shaped) and does not contain abundant remains of masticated vegetation. Furthermore, the subfossil pellets contain bones only of small vertebrates, whereas we would expect *Cryptoprocta ferox* to take larger prey items, including lemurs. It remains a possibility that some *Archaeolemur* skeletal elements belong to individuals that encountered predators after entering the cave. However, none of the *Archaeolemur* bones associated with pellets at Anjohikely show signs of carnivore or scavenger damage.

We intend to analyze the subfossil pellets for ancient DNA as another means of determining which species left them behind and which plants and animals it fed on, a feat accomplished with coprolites of extinct ground sloths (Poinar et al. 1998). For now, we are restricted to examining the pellet contents. The coprolites contain a wide variety of items, indicative of omnivory: fibrous fruit exocarps and seeds, bones of small vertebrates, gastropod shell and crustacean and arthropod exoskeletons, all within a matrix of comminuted vegetation. No living lemur has this array of items in its diet. The reconstructed diet of *Archaeolemur*, on the other hand, is compatible with these dietary items. Several microstructural features indicate that *Archaeolemur* was a capable processor of hard objects (Godfrey et al. 2004). When a suite of microwear variables was analyzed, *Archaeolemur* clustered with extant frugivorous seed predators and omnivores, including *Cebus apella*, *Chiropotes satanas, Cacajao melanocephalus*, and *Daubentonia*. Furthermore, *Archaeolemur* has highly decussated enamel with thickness on a par with *Paranthropus* and thick-enameled Miocene apes (Godfrey et al. 2005). Lucas et al. (2008) argued that thick, heavily decussated enamel is ideal for a diet of small and large hard objects exerting high forces on teeth, and a recent biomechanical analysis lends additional support to hard object processing by *Archaeolemur* (Dumont et al. 2011). Various gross features

of *Archaeolemur*'s skull also indicate it was capable of powerful mastication and shearing (Tattersall 1973; Jungers et al. 2002).

Ethnohistorical data collected in the hinterland of western Madagascar complement the direct dietary evidence from the pellets and anatomical reconstructions. Burney and Ramilisonina (1998) equated *Archaeolemur* with an animal known in the Belo-sur-Mer region as the *kindoky*, based on consistent ethnohistorical descriptions of the *kindoky*'s body size and partly terrestrial locomotion, which resembles no living or subfossil lemur except *Archaeolemur* or *Hadropithecus*. Ethnohistorical data collected in this region in 2004 by N. Vasey further revealed that the *kindoky* foraged for crabs in the mangroves that blanket the coast. The high incidence of large pits and hypercoarse scratches found on their molar teeth (Godfrey et al. 2005) probably arose not only just from seed predation and the processing of small vertebrates but also from crustaceans.

Conclusions

Coprolites from Anjohikely Cave may offer a new perspective on aspects of *Archaeolemur*'s paleoecology. *Archaeolemur* was omnivorous and may have entered caves to forage, although these refuges would also have offered water in the dry season, abundant shade, cool conditions, cryptic sleeping sites, and protection from predators. Cave-exploring behavior is consistent with anatomical evidence that *Archaeolemur* was adapted for arboreal and terrestrial locomotion. Clearly there are risks involved in entering caves; some individuals never left Anjohikely. However, the benefits may have outweighed the risks, and some *Archaeolemur* subfossils found in caves may be viewed as minor casualties of cave-exploring behavior in a primate generally adept at entering and exiting them.

Acknowledgments This research was conducted under collaborative agreements with the Département de Paléontologie et d'Anthropologie Biologique, University of Antananarivo and supported by a CLAS Grant from Portland State University to N. Vasey and NSF BCS-0129185 to D.A. Burney, L.R. Godfrey and William L. Jungers. Thanks to Callan Cohen for images of *Cryptoprocta* scat and the Oregon Zoo for providing scat of ring-tailed cat and meerkat.

References

Barrett L, Gaynor D, Rendall D, Mitchell D, Henzi SP (2004) Habitual cave use and thermoregulation in chacma baboons (*Papio hamadryas ursinus*). J Hum Evol 46:215–222

Brain CK (1981) The hunters or the hunted. An introduction to African Cave Taphonomy. University of Chicago Press, Chicago

Burney DA, Ramilisonina (1998) The *kilopilopitsofy, kidoky,* and *bokyboky*: accounts of strange animals from Belo-sur-mer, Madagascar, and the megafaunal "extinction window". Am Anthropol 100:957–966

Burney DA, James HF, Grady FV, Rafamantanantsoa J, Ramilisonina, Wright HT, Cowart JB (1997) Environmental change, extinction, and human activity: evidence from caves in NW Madagascar. J Biogeogr 24:755–767

Burney DA, Burney LP, Godfrey LR, Jungers WL, Goodman SM, Wright HT, Jull AJT (2004) A chronology for late prehistoric Madagascar. J Hum Evol 47:25–63

Dumont ER, Ryan TM, Godfrey LR (2011) The *Hadropithecus* conundrum reconsidered, with implications for interpreting diet in fossil hominins. Proc R Soc B 278:3654–3661

Godfrey LR, Jungers WL, Wunderlich RE, Richmond BG (1997) Reappraisal of the postcranium of *Hadropithecus* (Primates, Indroidea). Am J Phys Anthropol 103:529–556

Godfrey LR, Semprebon GM, Jungers WL, Sutherland MR, Simons EL, Solounias N (2004) Dental use wear in extinct lemurs: evidence of diet and niche differentiation. J Hum Evol 47:145–169

Godfrey LR, Semprebon GM, Schwartz GT, Burney DA, Jungers WL, Flanagan EK, Cuozzo FP, King SJ (2005) New insights into old lemurs: the trophic adaptations of the Archaeolemuridae. Int J Primatol 26:825–854

Jungers WL, Godfrey LR, Simons EL, Wunderlich RE, Richmond BG, Chatrath PS (2002) Ecomorphology and behavior of giant extinct lemurs from Madagascar. In: Plavcan JM, Kay RF, Jungers WL, van Schaik CP (eds) Reconstructing behavior in the primate fossil record. Kluwer Academic/Plenum, New York, pp 371–411

Jungers WL, Demes B, Godfrey LR (2008) How big were the "giant" extinct lemurs of Madagascar? In: Fleagle JG, Gilbert CG (eds) Elwyn Simons, a search for origins. Springer, New York, pp 343–360

Laumanns M, Burgsmüller J, Geuke W (1991) Höhlenkundliche Aktivitäten HuK Nordrhein nordöstlich Majunga und südlich Antsirabe. Mitteilungen des Verbandes der deutschen Höhlen- und Karstforscher 37:68–73

Lucas P, Constantino P, Wood B, Lawn B (2008) Dental enamel as a dietary indicator in mammals. BioEssays 30:374–385

McGrew WC, McKee JK, Tutin CEG (2003) Primates in caves: two new reports of *Papio* spp. J Hum Evol 44:521–526

Poinar HN, Hofreiter M, Spaulding WG, Martin PS, Stankiewicz BS, Bland H, Evershed RP, Possnert G, Pääbo S (1998) Molecular coproscopy: dung and diet of the extinct ground sloth *Nothrotheriops shastensis*. Science 281:402–406

Pruetz JD (2007) Evidence of cave use by savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal: implications for thermoregulatory behavior. Primates 48:316–319

Simons JW (1966) The presence of leopard and a study of the food debris in the leopard lairs of the Mount Suswa cave Kenya. Bull Cave Explor Group East Afr 1:51–69

Tattersall I (1973) Cranial anatomy of the Archaeolemurinae (Lemuroidea, Primates). Anthropol Pap Am Mus Nat Hist 52:1–110

Wilson JM, Stewart PD, Ramangason G-S, Denning AM, Hutchings MS (1989) Ecology and conservation of the crowned lemur, *Lemur coronatus*, at Ankarana N. Madagascar. Folia Primatol 52:1–26

Chapter 18
The Dental Ecology of Ring-Tailed Lemurs (*Lemur catta*)

Frank P. Cuozzo and Michelle L. Sauther

Abstract Ring-tailed lemurs (*Lemur catta*) are among the best-known primates. Long-term study of their behavior, ecology and dentition at a single locality, the Beza Mahafaly Special Reserve, Madagascar, has enabled a detailed understanding of their dental ecology. Patterns of dental pathology including tooth wear, tooth loss and abscessed canines correspond to use of specific resources and habitats and differ from patterns seen in sympatric primate species. Regular use of tamarind fruit (*Tamarindus indicus*) likely leads to a distinct pattern of severe tooth wear and tooth loss, suggesting a "mismatch" between dental morphology and the animals' primary fallback food.

Resume Le lémur catta (*Lemur catta*) est l'un des primates les mieux connus. Une étude à long-terme de son comportement, son écologie, et sa dentition dans un site unique, la Réserve Spéciale de Beza Mahafaly a permis une meilleure compréhension des détails de son écologie dentaire. Les pathologies dentaires observées chez cette espèce, mais pas chez d'autres espèces sympatriques, notamment l'usure et la perte de dents et les abcès observés au niveau des canines correspondent à l'utilisation d'habitats et de ressources spécifiques. La consommation régulière de fruits de tamariniers (*Tamarindus indicus*) conduit probablement à une usure sévère et à une perte de dents qui suggèrent une mal-adaptation de la morphologie dentaire et de cette importante ressource secondaire.

F.P. Cuozzo (✉)
Department of Anthropology, University of North Dakota, Box 8374,
Grand Forks, ND 58202-8374, USA
e-mail: frank.cuozzo@und.nodak.edu

M.L. Sauther
Department of Anthropology, University of Colorado, Campus Box 233,
Boulder, CO 80309-0233, USA
e-mail: michelle.sauther@colorado.edu

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_18,

Introduction

Ring-tailed lemurs (*Lemur catta*) are among the best-known and most studied prosimian primates (Sauther et al. 1999; Gould 2006; Jolly et al. 2006), and the breadth and temporal depth of ring-tailed lemur research rivals that of the best-known anthropoids, chimpanzees and baboons (Cuozzo and Sauther 2006a). In addition to extensive behavioral, ecological and demographic studies (Sauther et al. 1999; Gould 2006), the dentition of this species ranks among the most thoroughly studied of any extant primate (reviewed in Cuozzo and Yamashita 2006). Over the past decade, detailed information on dental variation, morphology and function (Yamashita 1998, 2003; Sauther et al. 2001), disease and pathology (Sauther et al. 2002, 2006; Cuozzo and Sauther 2006b), tooth size change over time (Cuozzo and Sauther 2006a) and tooth wear (Cuozzo and Sauther 2004, 2006b; Cuozzo et al. 2010) has been published, focusing on ring-tailed lemurs inhabiting the tamarind-dominated gallery forest in the Beza Mahafaly Special Reserve (BMSR), southern Madagascar (Sauther et al. 1999, 2006; Cuozzo and Sauther 2004, 2006b). Comparative data on ring-tailed lemur tooth wear and oral health have also been collected in the limestone spiny forest at Tsimanampetsotse National Park (TNP), Madagascar (Cuozzo et al. 2008; Sauther and Cuozzo 2008).

We review ring-tailed lemur dental ecology, defining this, in part, as the study of patterns of dental pathology (i.e. abscessed teeth, tooth loss and dental damage) and tooth wear, as a reflection of feeding ecology, behavior and habitat variation, including the exploitation of areas affected by anthropogenic disturbance (i.e. forest fragmentation and/or areas with introduced plants). This approach allows us to study ecological change over time, as (1) teeth provide a direct record of individual life histories; (2) overall tooth wear as well as pathologies such as maxillary canine abscesses reflect long-term exploitation of particular foods, thus recording habitat use and (3) dental data are accessible in living individuals and correlate with specific behaviors and ecological variables. Since teeth are often preserved in the fossil record, data on dental ecology in living animals can be extrapolated to primate fossils, providing a comparative context for interpreting primate paleobiology (Cuozzo and Sauther 2006b; Millette et al. 2009).

Ring-Tailed Lemur Dental Pathology

Among extant primates, BMSR gallery forest ring-tailed lemurs display an exceptionally high frequency of severe tooth wear and antemortem tooth loss (Cuozzo and Sauther 2004, 2006a, b) (Fig. 18.1; Table 18.1), largely as a result of exploiting tamarind fruit (*Tamarindus indicus*), a major fallback food relied upon during the dry season (Sauther 1992, 1998; Yamashita 1998, 2002; Cuozzo and Sauther 2004, 2006a, b; Gould 2006; Gemmill and Gould 2008; Sauther and Cuozzo 2009). The fruit is mechanically challenging (Yamashita 2008), large with a tough exocarp,

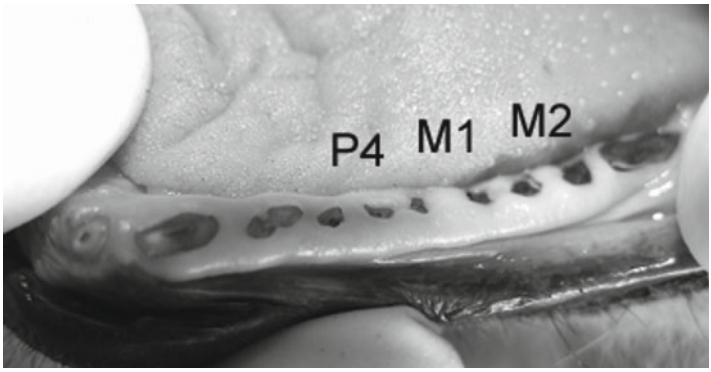


Fig. 18.1 Severe dental wear and antemortem tooth loss in a living ring-tailed lemur from the gallery forest at Beza Mahafaly (Blue 138). Note that the fourth premolar (P4) and the first and second molars (M1 and M2) retain only worn roots, worn to below the gumline, thus "functionally absent" as defined by Cuozzo and Sauther (2004, 2006b)

Table 18.1 Frequency of dental pathologies compared between two living, wild ring-tailed lemur populations in Madagascar

		Antemortem Tooth Loss		Maxillary Canine Abscesses	
Location[a]	*n*[b]	*n*	%	*n*	%
Beza Mahafaly	167	38	22.8	6	3.6
Tsimanampetsotse	24	1	4.2	0	0.0

[a]Beza Mahafaly is a gallery forest; Tsimanampetsotse is a limestone spiny forest (see text)
[b]Adults only (3 years and older)

and is the hardest food eaten by *L. catta* in the BMSR gallery forest (Yamashita 2000). Regular processing of the fruit leads to frequent and rapid wear of the thin-enameled crowns used to open it (posterior premolars and anterior molars; see Fig. 18.1). This dramatic pattern of tooth wear indicates a discordance between the dental morphology of *L. catta* (thin enamel, elongated shearing crests; Cuozzo and Sauther 2006b; Yamashita 2008) and their primary fallback food in the BMSR gallery forest (Cuozzo and Sauther 2006b; Sauther and Cuozzo 2009).

BMSR gallery forest *Lemur catta* also suffer from maxillary canine abscesses, which present as open wounds on the muzzle (Sauther et al. 2006) and are detectable in skeletal specimens (Fig. 18.2a, b; Table 18.1). Notably, all known cases occur in areas of severe anthropogenic impact, either where the forest understory has been removed through domestic livestock grazing or where ring-tailed lemurs exploit crops and/or other introduced plants that border on the reserve (Sauther et al. 2006). In contrast to sympatric Verreaux's sifaka (*Propithecus verreauxi*), in which a high frequency of canine abscesses (~30 % of the BMSR skeletal sample) appears related to processing tamarind fruit with their maxillary canines, canine abscesses in *L. catta* (3.6 %) are likely caused by tooth breakage as a result of processing other foods in disturbed areas in and around BMSR.

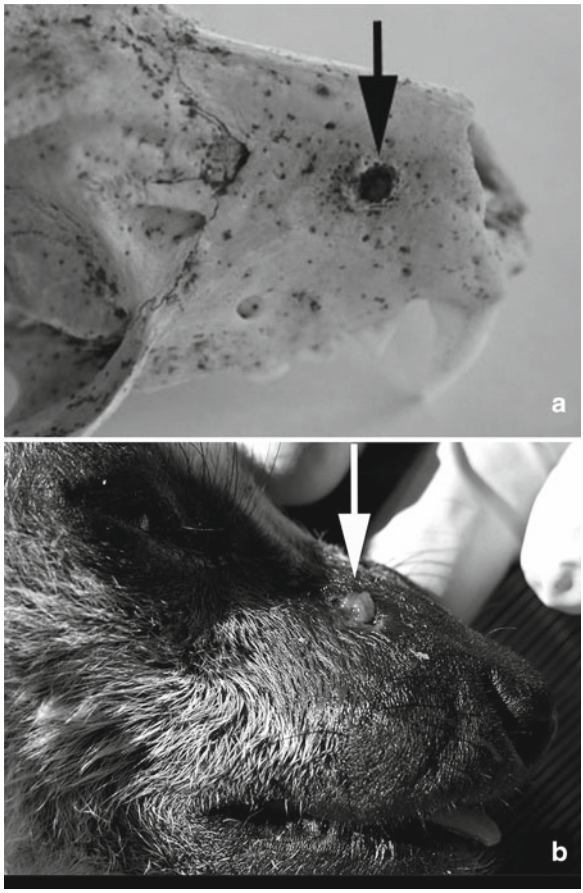


Fig. 18.2 Apical, maxillary canine abscesses in gallery forest Beza Mahafaly ring-tailed lemurs. (**a**) Bone damage at the apex of the right maxillary canine (*black arrow*) on the muzzle of a ring-tailed lemur skeletal specimen from Beza Mahafaly. (**b**) Open wound at the apex of the right maxillary canine (*white arrow*) on the muzzle of a living individual at Beza Mahafaly (Blue 127)

Comparative data on lemur salivary pH indicate long-term adjustments by ring-tailed lemurs to food resources with high acidity including *T. indicus* (Cuozzo et al. 2008). Comparing data from wild ring-tailed lemurs at BMSR and TNP, as well as a captive population, reveals that the extreme acidity of tamarind fruit is buffered by the oral chemistry of ring-tailed lemurs, which have high salivary pH. At BMSR, the folivorous Verreaux's sifaka (*Propithecus verreauxi*) consumes less acidic foods and has more acidic salivary pH.

Behavioral Responses to Dental Impairment

Combining long-term behavioral and ecological research with studies of dental pathology and tooth wear (e.g. Sauther et al. 1999; Gould 2006) is important for a comprehensive understanding of *L. catta* dental ecology. At BMSR ring-tailed

lemurs with severe dental wear and tooth loss compensate behaviorally for their impairment. Stable isotope values measured for $\delta^{13}C$ and $\delta^{15}N$ showed significant differences between dentally impaired individuals and other troop members, implying use of different resources (Loudon et al. 2007). In addition, individuals with marked tooth loss (>10 %) displayed different daily activity patterns, often feeding during periods when individuals without tooth loss were resting or engaging in social activities like grooming (Millette et al. 2009). These impaired individuals also engaged in interspecific coprophagy, i.e. the consumption of the feces of domestic animals and sometimes humans, which is a rare behavior among wild vertebrates (Fish et al. 2007). Our data are among the first to illustrate significant behavioral adjustments to dental pathologies among mammals and provide a comparative context for interpreting the dental ecology of living and fossil lemurs, as well as other primates including hominins (Cuozzo and Sauther 2004, 2006b; Millette et al. 2009).

Conclusions

Since the initial 1972 conference on prosimian primates (Martin et al. 1974), and subsequent congresses and their publications (Alterman et al. 1995; Harcourt et al. 1998), our understanding of prosimian teeth has advanced beyond the studies of dental morphology, metrics and development included in these earlier volumes. As a result of long-term prosimian field research (e.g. Jolly 1966; Sussman 1991; Richard et al. 1993; Sauther and Cuozzo, loc. cit.), we can now begin to synthesize a comprehensive picture of prosimian dental ecology. For example, King et al. (2005) used long-term behavioral and ecological data, combined with environmental data (rainfall patterns), to explore the relationship between tooth wear and reproductive success in *Propithecus edwardsi* at Ranomafana National Park, Madagascar. Building on such studies, including the synopsis of ring-tailed lemur dental studies described here, we can achieve the holistic understanding of the prosimian dentition envisaged by Seligsohn and Szalay (1974) in the first prosimian volume.

Acknowledgements We thank the many individuals, institutions and organizations acknowledged in previous publications (Sauther et al. 2001, 2002, 2006; Cuozzo and Sauther 2004, 2006a, b) for their support, field assistance and/or collaboration. We also thank two anonymous reviewers for their comments. Research at Beza Mahafaly (2003–2010) and Tsimanampetsotse (2006–2008) was supported by the St. Louis Zoo (FRC 06-1), the University of North Dakota (SSAC; Faculty Research Seed Money Council; Arts, Humanities and Social Sciences Committee), North Dakota EPSCoR, Primate Conservation Inc., the American Society of Primatologists (Conservation Grant), the International Primatological Society, the Lindbergh Fund, the John Ball Zoo Society, the National Geographic Society, the University of Colorado-Boulder (IGP, CRCW) and the National Science Foundation (BCS 0922465). Data collection at Beza Mahafaly and/or Tsimanampetsotse from 2003 to 2010 received approval from and followed standard animal handling guidelines and protocols of the Institutional Animal Care and Use Committees (IACUC) of the University of North Dakota and the University of Colorado.

References

Alterman L, Doyle GA, Izard MK (eds) (1995) Creatures of the dark: the nocturnal prosimians. Plenum, New York

Cuozzo FP, Sauther ML (2004) Tooth loss, survival, and resource use in wild ring-tailed lemurs (*Lemur catta*): implications for inferring conspecific care in fossil hominids. J Hum Evol 46:625–633

Cuozzo FP, Sauther ML (2006a) Temporal change in tooth size among ring-tailed lemurs (*Lemur catta*) at the Beza Mahafaly Special Reserve, Madagascar: effects of an environmental fluctuation. In: Jolly A, Sussman RW, Koyama N, Rasmimanana H (eds) Ring-tailed lemur biology. Springer, New York, pp 343–366

Cuozzo FP, Sauther ML (2006b) Severe wear and tooth loss in wild ring-tailed lemurs (*Lemur catta*): a function of feeding ecology, dental structure, and individual life history. J Hum Evol 51:490–505

Cuozzo FP, Yamashita N (2006) Impact of ecology on dental adaptations of extant lemurs: a review of tooth function, variation, and life history. In: Gould L, Sauther ML (eds) Lemurs: ecology and adaptations. Springer, New York, pp 69–98

Cuozzo FP, Sauther ML, Yamashita N, Lawler RR, Brockman DK, Godfrey LR, Gould L, Jacky Youssouf IA, Lent C, Ratsirarson J, Richard AF, Scott JR, Sussman RW, Villers LM, Weber MA, Willis G (2008) A comparison of salivary pH in sympatric wild lemurs (*Lemur catta* and *Propithecus verreauxi*) at Beza Mahafaly Special Reserve, Madagascar. Am J Primatol 70:363–371

Cuozzo FP, Sauther ML, Gould L, Sussman RW, Villers LM, Lent C (2010) Variation in dental wear and tooth loss in known-aged, older ring-tailed lemurs (*Lemur catta*): a comparison between wild and captive individuals. Am J Primatol 72:1026–1037

Fish KD, Sauther ML, Loudon JE, Cuozzo FP (2007) Coprophagy by wild ring-tailed lemurs (*Lemur catta*) in human-disturbed locations adjacent to the Beza Mahafaly Special Reserve, Madagascar. Am J Primatol 69:713–718

Gemmill A, Gould L (2008) Microhabitat variation and its effects on dietary composition and intragroup feeding interactions between adult female *Lemur catta* during the dry season at Beza Mahafaly Special Reserve. Int J Primatol 29:1511–1533

Gould L (2006) *Lemur catta* ecology: what we know and what we need to know. In: Gould L, Sauther ML (eds) Lemurs: ecology and adaptations. Springer, New York, pp 255–274

Harcourt CS, Crompton RH, Feistner ATC (eds) (1998) Biology and conservation of prosimians. Folia Primatol 69(Suppl 1)

Jolly A (1966) Lemur behavior. University of Chicago Press, Chicago

Jolly A, Sussman RW, Koyama N, Rasmimanana H (eds) (2006) Ring-tailed lemur biology: *Lemur catta* in Madagascar. Springer, New York

King SJ, Arrigo-Nelson SJ, Pochron ST, Semprebon GM, Godfrey LR, Wright PC, Jernvall J (2005) Dental senescence in a long-lived primate links infant survival to rainfall. Proc Natl Acad Sci USA 102:16579–16583

Loudon JE, Sponheimer M, Sauther ML, Cuozzo FP (2007) A study of intraspecific variation in hair $\delta^{13}C$ and $\delta^{15}N$ of ring-tailed lemurs (*Lemur catta*) with known individual histories, behavior and feeding ecology. Am J Phys Anthropol 133:978–985

Martin RD, Doyle GA, Walker AC (eds) (1974) Prosimian biology. Duckworth, London

Millette JB, Sauther ML, Cuozzo FP (2009) Behavioral responses to tooth loss in wild ring-tailed lemurs (*Lemur catta*) at the Beza Mahafaly Special Reserve, Madagascar. Am J Phys Anthropol 140:120–134

Richard AF, Rakotomanga P, Schwartz M (1993) Demography of *Propithecus verreauxi* at Beza Mahafaly, Madagascar: sex ratio, survival, and fertility, 1984–1988. Am J Phys Anthropol 84:307–322

Sauther ML (1992) Effect of reproductive state, social rank and group size on resource use among free-ranging ring-tailed lemurs (*Lemur catta*) of Madagascar. Unpublished PhD thesis, Washington University, St. Louis

Sauther ML (1998) The interplay of phenology and reproduction in ring-tailed lemurs; implications for ring-tailed lemur conservation. Folia Primatol 69(Suppl 1):309–320
Sauther ML, Cuozzo FP (2008) Somatic variation in living, wild ring-tailed lemurs (*Lemur catta*). Folia Primatol 79:55–78
Sauther ML, Cuozzo FP (2009) The impact of fallback foods on wild ring-tailed lemur biology within an anthropogenically disturbed habitat. Am J Phys Anthropol 70:363–371
Sauther ML, Sussman RW, Gould L (1999) The socioecology of the ring-tailed lemur: thirty-five years of research. Evol Anthropol 8:120–132
Sauther ML, Cuozzo FP, Sussman RW (2001) Analysis of dentition of a living, wild population of ring-tailed lemurs (*Lemur catta*) from Beza Mahafaly Madagascar. Am J Phys Anthropol 114:215–223
Sauther ML, Sussman RW, Cuozzo FP (2002) Dental and general health in a population of wild ring-tailed lemurs: a life history approach. Am J Phys Anthropol 117:122–132
Sauther ML, Fish K, Cuozzo FP, Miller DS, Hunter-Ishikawa M, Culbertson H (2006) Patterns of health, disease and behavior among wild ring-tailed lemurs, *Lemur catta*: effects of habitat and sex. In: Jolly A, Sussman RW, Koyama N, Rasmimanana H (eds) Ring-tailed lemur biology. Springer, New York, pp 313–331
Seligsohn D, Szalay FS (1974) Dental occlusion and the masticatory apparatus in *Lemur* and *Varecia*: their bearing on the systematics of living and fossil Primates. In: Martin RD, Doyle GA, Walker AC (eds) Prosimian biology. Duckworth, London, pp 543–561
Sussman RW (1991) Demography and social organization of free-ranging *Lemur catta* in the Beza Mahafaly Reserve, Madagascar. Am J Phys Anthropol 84:43–58
Yamashita N (1998) Functional dental correlates of food properties in five Malagasy lemur species. Am J Phys Anthropol 106:169–188
Yamashita N (2000) Mechanical thresholds as a criterion for food selection in two prosimian primate species. In: Proceedings of the 3rd plant biomechanics conference, Freiburg-Badenweiler, Thieme Verlag, Stuttgart, pp 590–595
Yamashita N (2002) Diets of two lemur species in different microhabitats in Beza Mahafaly special reserve, Madagascar. Int J Primatol 23:1025–1051
Yamashita N (2003) Food procurement and tooth use in two sympatric lemur species. Am J Phys Anthropol 121:125–133
Yamashita N (2008) Food physical properties and their relationship to morphology: the curious case of kily. In: Vinyard C, Ravosa MJ, Wall CE (eds) Primate craniofacial function and biology. Kluwer, New York, pp 387–446

Chapter 19
Exudates and Animal Prey Characterize Slow Loris (*Nycticebus pygmaeus, N. coucang* and *N. javanicus*) Diet in Captivity and After Release into the Wild

Ulrike Streicher, Angelina Wilson, Rebecca L. Collins, and K. Anne-Isola Nekaris

Abstract We present dietary data for individuals of three species of slow loris rescued from the pet trade: *Nycticebus pygmaeus* released and radio-tracked in Vietnam and *N. coucang* and *N. javanicus* held in captivity in Indonesia. Contrary to popular belief that slow lorises are frugivores, our data support recent studies that slow lorises are one of few primates specialized for regular extractive gouging of plant exudates, and capable of consuming insect prey containing secondary compounds. These behaviors are present in juveniles as young as 4 months. This specialized diet should be considered when maintaining captive individuals, and when planning reintroduction programs.

Resume Nous présentons des données sur le régime alimentaire de trois espèces de loris lents, obtenues sur des individus vendus sur les marchés locaux: *Nycticebus pygmaeus*, relâchés et radio-pistés au Vietnam, et captifs *N. coucang* et *N. javanicus* en Indonésie. Contrairement à la croyance populaire qui voit ces animaux comme frugivores, nos donnés indiquent que les loris lents sont parmi les rares primates spécialisés dans l'extraction d'exudats, et capables de consummer des insectes contenant des produits toxiques. Ces comportements sont déjà observés chez les juvéniles de quatre mois. Ce régime alimentaire spécialisé devrait être pris en considération dans les élevages captifs, et les plans de réintroduction.

U. Streicher (✉)
Endangered Primate Rescue Center, Cuc Phuong National Park,
Nho Quan District, Ninh Binh Province, Vietnam
e-mail: uli@mail.hut.edu.vn

A. Wilson • R.L. Collins • K.A.-I. Nekaris
Nocturnal Primate Research Group, School of Social Sciences and Law,
Oxford Brookes University, Oxford OX3 0BP, UK
e-mail: Angelina.Wilson@traffic.org; collir678@yahoo.com; anekaris@brookes.ac.uk

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_19,

Introduction

Slow lorises (Lorisidae: *Nycticebus*) are nocturnal primates ranging throughout Southeast Asia. All five *Nycticebus* species have recently been discovered to feed regularly on exudates that they obtain through active gouging (*N. bengalensis*, Swapna et al. 2010; *N. coucang*, Wiens et al. 2006; *N. javanicus*, Nekaris et al. 2010; *N. menagensis*, Nekaris and Munds 2010 and *N. pygmaeus*, Starr et al. 2011). These same studies reveal that nectar, insects (including those containing secondary toxic compounds) and fruit also form part of their diets.

These new findings have not yet been applied to the dietary regimes of captive slow lorises, which have classically been modeled on that of the mainly frugivorous potto (*Perodicticus*) (Charles-Dominique 1977; Fitch-Snyder et al. 2001), a genus that can be up to six times heavier than the smallest slow lorises (Nekaris and Bearder 2007). In captivity, slow lorises are usually maintained on fruit and vegetables, with some insects (Fitch-Snyder et al. 2001). Opportunities to access gum are usually presented only through enrichment devices (Craig and Reed 2003), and zoo keepers report that slow lorises can cause considerable damage to the wood in their enclosures (Streicher 2004). Inappropriate captive diets may be linked to dental disease, obesity and low reproductive output (Streicher 2004). Furthermore, no data are available as to how diet develops ontogenetically in slow lorises, although youngsters seem to learn about food resources directly from their parents, either through active (visual) or passive (olfactory) observation (Wiens and Zitzmann 2003; Nekaris et al. 2010).

An understanding of the feeding behavior of slow lorises is crucial, as they are amongst the most common primates in the Southeast Asian pet trade (Nekaris and Nijman 2007). To improve their suitability as pets, many slow lorises have their anterior incisors and canines removed by traders (Nekaris and Munds 2010). Juvenile lorises are prevalent in the trade, and both adults and juveniles may be confiscated many miles from their capture localities and released into areas with unfamiliar food resources. If animals survive transport to one of South-east Asia's many rescue centers, it is common practice to release them directly into the wild without a period of adjustment (Collins and Nekaris 2008). Knowledge of how rescued slow lorises select their captive diet, whether all age classes gouge, and what they eat when released is hitherto lacking. To address these issues, we present data on the diet of three slow loris species (*N. pygmaeus, N. coucang* and *N. javanicus*) confiscated from the pet trade.

Methods

Released Slow Lorises: Vietnam

Streicher collected dietary data from four reintroduced *N. pygmaeus* individuals that had been held in captivity for several months at the Endangered Primate Rescue Center (EPRC), Cuc Phuong, Vietnam. All animals were captured as adults, so all had previous experience of wild food sources. Full details of their release are

described in Streicher and Nadler (2003). The individuals were equipped with radio transmitters. Before dusk, an observer arrived at the sleeping site and observed *N. pygameus* from a distance of 5–15 m from the beginning of the active period for a few minutes to 2 h over 163 days. Each animal was radio tracked for 4–6 weeks from the date of release. Data were collected *ad libitum* (Altman 1974).

Captive Slow Lorises: Sumatra

The other authors collected data from 2 April to 17 June 2007 at Pusat Penyelamatan Satwa (PPS), Lampung, Sumatra on twelve *N. coucang* (two adults and ten juveniles) and one adult *N. javanicus*. The *N. coucang* had been rescued from the pet trade 2 weeks prior to the study, and the *N. javanicus* had been at PPS for 3 months. By the third week, all juveniles ate solid food. The outdoor enclosure was comprised of two neighboring chambers (2 m × 2 m × 2 m), with *N. javanicus* in one and *N. coucang* in the second. It had an open floor with natural ground and foliage and was thickly furnished with natural branches at all levels. Slow lorises were fed six times nightly. In addition to insects and reptiles that entered the enclosure naturally, 23 types of food were offered (Table 19.1). We recorded all dietary selections and

Table 19.1 Food items presented to *N. javanicus* and *N. coucang*, and their reactions to these items: ++ instantly accepted; + accepted with hesitation; −− refused

Food type	*N. javanicus*	*N. coucang*
Fruits		
Duku	++	++
Banana	++	++
Ripe kiwi	++	++
Orange	+	++
Green grape	−−	+
Red grape	+	−−
Guava	−−	+
Corn	−−	−−
Raisin	−−	−−
Avocado	−−	−−
Animals		
Moths	++	++
Crickets	++	++
Yellow-vented bulbul	++	++
Mealworms	+	+
Millipede	++	−−
Chicken eggs (raw)	++	−−
Quail eggs (raw)	−−	++
Cooked chicken	−−	−−
Ants	−−	−−
Other		
Honey	−−	+
Yoghurt	−−	−−
Peanuts	−−	−−
Baby formula	+	+

modeled food tests after Hladik (1979). We recorded observations nightly from 19:00 to 05:00 over 153 h.

Results

Released Slow Lorises

Streicher recorded 27 feeding bouts by solitary *N. pygmaeus*. Eleven observations (40%) involved insect prey, including Hymenoptera and Hemiptera. Insect feeding occurred at heights <10 m. *Nycticebus pygmaeus* fed on gum eight times (30%) and on unidentifiable plant exudates eight times (30%); seven of these bouts occurred at heights over 8 m. Feeding on fruit was never observed.

Nycticebus pygmaeus searched for animal prey by moving slowly along branches with their noses near the substrate. They caught insects with one or both hands, clinging with both legs to the branch or standing bipedally. Pygmy lorises licked some smaller insects, including ants, off branches. Larger insects were eaten head first, the wings were dropped and other parts were disposed of by fierce head shaking. Head shaking also followed when an *N. pygmaeus* was bitten by its prey. Hunting in general was a rapid event. Only when a pygmy loris found a large insect or a number of insects in the same place did it spend several minutes feeding (e.g. the devouring of a large cricket required 20 min).

Whilst feeding on gum, pygmy lorises remained stationary while intensely licking a single trunk or branch for 1–20 min. They consumed exudates from *Spondias axillaris* (Anacardiaceae), *Sapindus* sp. (Sapindaceae), *Vernicia montana* (Euphorbiaceae) and *Saraca dives* (Fabaceae). When animals licked the branches of *S. dives*, no sounds were audible, suggesting the food sources were on the surface. For all other species, gum scraping was accompanied by intense sounds of scratching and breaking bark. Animals fed with the body orthograde, clinging with all four extremities to the tree. One pygmy loris returned to the same site several times.

In full blossom *S. dives* carried large bundles of orange flowers. Pygmy lorises inspected these intensively and probably consumed the nectar. Of the few observations of wild pygmy lorises at Cuc Phuong National Park, two were made in *S. dives* in bloom (Roberton, personal communication).

Captive Slow Lorises

Results of food tests are presented in Table 19.1. Both *N. javanicus* and *N. coucang* consumed animal prey eagerly. Slow lorises caught prey by stalking it and rapidly lunging forward to grab it with one or two hands. They caught yellow-vented bulbuls (*Pycnonotus goiavier*) within 30–50 s, instantly killed them by biting the neck

and consumed all parts, including the bones and beak. Four juveniles grouped together to catch one bird that escaped but was swiftly killed by the adult female, who then shared it with them. Interestingly, although *N. coucang* rejected ants as food, they allowed them to crawl onto their hands, feet and limbs and shook or rubbed them off.

Nycticebus javanicus and *N. coucang* accepted fruit, especially duku (*Lansium domesticum*) and banana (*Musa* sp.). Fruit was consumed slowly, and even if instantly accepted, animals only ate small pieces, returning to it throughout the night. Sharing of fruit and animal prey occurred with no aggression.

Although no exudates could be derived from the timber of their enclosures or from fresh branches that were placed there daily, both species of all age classes gouged and chewed daily at a rate of 2.9 times per hour (see also Nekaris et al. 2010). Gouging was accompanied by audible bark breaking and could be heard even when animals entered dense foliage. Gouging resulted in deep holes measuring on average 2.5-cm diameter and 0.6-cm deep in the substrate (Fig. 19.1).

Discussion

Nycticebus has previously been assumed to be largely frugivorous (Chivers and Hladik 1980). Our study contributes to the growing volume of literature that fruits form only part of slow loris diets. Released *N. pygmaeus* did not consume any fruit during the observation period. Before their release at EPRC, *N. pygmaeus* (350–600 g) chose invertebrates over other food items and mostly rejected fruit, boiled eggs and vegetables (Streicher 2004). In the case of the larger *N. javanicus* (650–1,000 g) and *N. coucang* (600–750 g), some fruits were consumed, but animal prey was always preferred. These differences could be a result of physiological requirements. Hladik (1979) postulated that strepsirhines in this size range must utilize a variety of food sources, since they are too large to be able to maintain themselves merely on insects, which they consumed with far more enthusiasm and familiarity in our study.

Based on its sympatry with *N. bengalensis* and on morphological characteristics, Ratajszczak (1998) and Ravosa (1998) suggested that *N. pygmaeus* is insectivorous. Although Wiens et al. (2006) viewed insects as unimportant to *N. coucang*, invertebrates including ants were nevertheless present in >90% of feces they analysed, including up to 20 ants in a single sample. The closely related slender loris is mainly faunivorous, and its capture mode is identical to that observed in slow lorises (Nekaris and Rasmussen 2003). All slow lorises in our study captured insects single handedly or bimanually with stereotyped movements typical for prosimians and specifically adapted to catch rapidly moving or flying insects (see also Hladik 1979; Nekaris and Rasmussen 2003). Feeding similarities between slender and slow lorises extend to the consumption of noxious prey including Hymenoptera, usually avoided by other strepsirhines (Hladik 1979). Although our captive slow lorises did not consume ants, it is possible they were engaging in passive “anting”. Common in

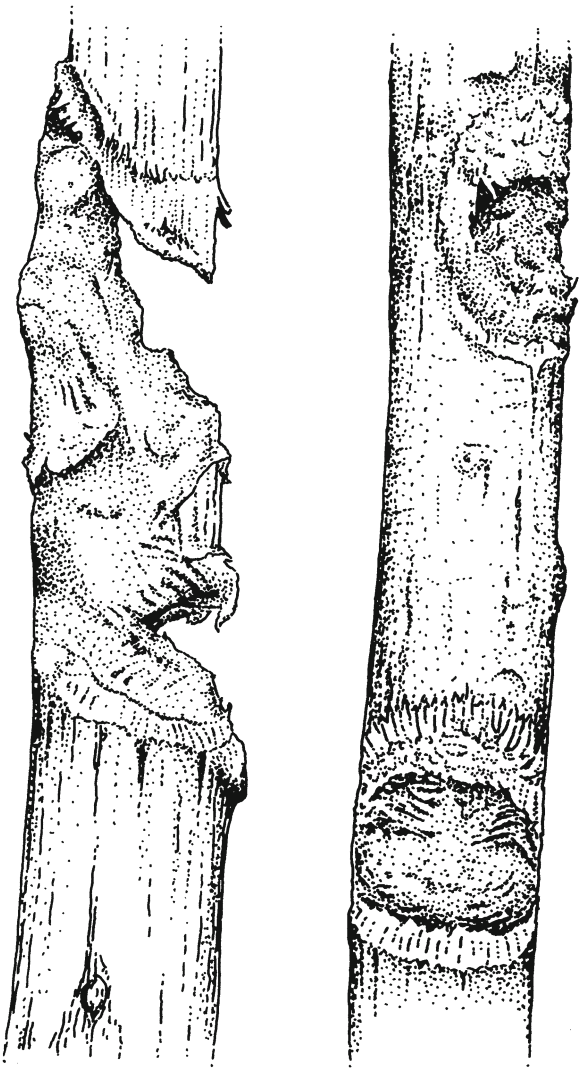


Fig. 19.1 Examples of branches gouged by *N. coucang*, showing the typical gnawing pattern for this genus (drawing by H. Schulze)

birds and some monkeys (Weldon 2004), several species of *Loris* and *Nycticebus* have now been observed to allow ants to crawl over their limbs (Kumara et al. 2005) and even to rub ants into their fur before consuming them (Nekaris personal observation). One use of secondary compounds may be to keep the body free of ticks. Indeed, no loris in the Sumatra study had any ectoparasites, and of a sample of 51 *N. pygmaeus* studied at EPRC, only one animal was infested with lice (Streicher 2004). How lorises use the secondary compounds sequestered from their noxious prey deserves further study.

Gum and plant exudates, extracted through active gouging, were also essential foods for the slow lorises observed in this study. Exudates were the foods most

frequently consumed by *N. pygmaeus*. Captive wild-caught Sumatran *N. coucang* began "practising" gouging behavior from 4 months of age; the fact that the branches did not contain gum supports the interpretation of gouging as a stereotyped behavior and implies that exudate consumption in the wild begins at an early age (Hladik 1979). Active stimulation of exudate flow by gouging trees has previously been documented for some callitrichines, *Cebuella* and *Callithrix* (Coimbra-Filho and Mittermeier 1978) and the fork-marked lemur, *Phaner (furcifer) pallescens* (Petter et al. 1971). Stimulating exudate flow by scraping gum at the same location every night maintains a renewable food supply. Gum contains high concentrations of carbohydrates (Bearder and Martin 1980; Hladik 1979) and some strepsirhines, such as the lesser bushbaby (*Galago moholi*) and the thick-tailed bushbaby (*Otolemur crassicaudatus*), are able to subsist on gum alone when other foods are scarce (Bearder 1987). Being available all year round, gum is a reliable food, and consumption of exudates has now been observed year round for three slow loris species (Nekaris et al. 2010). Consequently, when considering a slow loris reintroduction project, sites containing gum-producing trees should be chosen, and only slow lorises with teeth should be reintroduced.

Nycticebus pygmaeus in this study foraged alone, whereas *N. coucang* shared food peacefully. However, *N. pygmaeus* housed together at Cuc Phuong Rescue Centre also engaged in food sharing. Captive slow lorises are normally held alone or in pairs, mainly due to fear of fighting (Fitch-Snyder et al. 2001). Knowing that some slow lorises can be housed together without aggression is important for captive management, especially as numbers of animals confiscated from the pet trade are increasing. Providing ample live prey and gouging opportunities may facilitate social grouping.

Slow lorises clearly show numerous morphological and physiological adaptations for processing animal prey and harvesting and consuming plant exudates. The myth that these animals are frugivores should at last be quashed for the sake of their health in captivity and for designing reintroduction programs.

Acknowledgments We thank J. Masters, J. Ratsimbazafy and C. Scheepers for organizing the Prosimians International Congress. The following people helped with the study: Vietnam, T. Nadler, Dao Van Khuong, Truong Quang Bich, Do Huu Lap, Nguyen Manh Hiep and Le Thien Duc; Indonesia, P. Agus, F. den Haas, A. Knight, E. Rahadian, K. Sanchez and K. Sudaryatmo. The Eva-mayr-Stihl Foundation, Andreas Stihl Stiftung, International Animal Rescue Indonesia and Oxford Brookes University provided financial support. Comments from two reviewers improved the manuscript.

References

Altman J (1974) Observational study of behaviour: sampling methods. Behaviour 49:227–267

Bearder SK (1987) Lorises, bushbabies and tarsiers: diverse societies in solitary foragers. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 11–24

Bearder SK, Martin RD (1980) *Acacia* gum and its use by bushbabies, *Galago senegalensis* (Primates: Lorisidae). Int J Primatol 1:103–128

Charles-Dominique P (1977) Ecology and behaviour of the nocturnal primates. Prosimians of equatorial West Africa. Duckworth, London
Chivers DL, Hladik CM (1980) Morphology of the gastrointestinal tracts in primates: comparisons with other animals in relation to diet. J Morphol 166:337–386
Coimbra-Filho AF, Mittermeier RA (1978) Tree-gouging, exudate-eating and the "short-tusked" condition in *Callithrix* and *Cebuella*. In: Kleimann DG (ed) The behaviour and conservation of the Callithrichidae. Smithsonian Institution Press, Washington, pp 41–46
Collins R, Nekaris KAI (2008) Release of greater slow lorises (*Nycticebus coucang*), confiscated from the pet trade, to Batutegi Protected Forest, Sumatra, Indonesia. In: Soorae PS (ed) IUCN Global re-introduction perspectives. IUCN/SSC Reintroduction Specialist Group, Abu Dabhi, UAE, pp 192–195
Craig J, Reed C (2003) Diet-based enrichment ideas for small primates. Int Zoo News 50(1):16–20
Fitch-Snyder H, Schulze H, Larson L (2001) Management of lorises in captivity. A husbandry manual for Asian lorisines (*Nycticebus* & *Loris* ssp.). Center for Reproduction in Endangered Species (CRES), Zoological Society of SanDiego, San Diego
Hladik CM (1979) Diet and ecology of prosimians. In: Doyle GA, Martin RD (eds) The study of prosimian behaviour. Academic, New York, pp 307–357
Kumara HN, Kumar S, Singh M (2005) A novel foraging technique observed in slender loris (*Loris lydekkerianus malabaricus*) feeding on red ants in the Western Ghats. India Folia Primatol 76:116–118
Nekaris KAI, Bearder SK (2007) The strepsirrhine primates of Asia and mainland Africa: diversity shrouded in darkness. In: Campbell C, Fuentes A, MacKinnon K, Panger M, Bearder SK (eds) Primates in perspective. Oxford University Press, Oxford, pp 24–45
Nekaris KAI, Munds RA (2010) Using facial markings to unmask diversity: the slow lorises (Primates: Lorisidae: *Nycticebus*) of Indonesia. In: Gursky S, Supriatna J (eds) The primates of Indonesia. Springer, New York, pp 383–396
Nekaris KAI, Nijman V (2007) CITES proposal highlights rarity of Asian nocturnal primates (Lorisidae: *Nycticebus*). Folia Primatol 78:211–214
Nekaris KAI, Rasmussen DT (2003) Diet and feeding behaviour of the Mysore slender loris. Int J Primatol 24:33–46
Nekaris KAI, Starr CR, Collins RL, Navarro-Montes A (2010) Comparative ecology of exudate feeding by Asian slow lorises (*Nycticebus*). In: Burrows A, Nash L (eds) The evolution of exudativory in primates. Springer, New York, pp 155–168
Petter J-J, Schilling A, Pariente G (1971) Observations eco-ethologiques sur deux lemuriens malgaches nocturnes: *Phaner furcifer* et *Microcebus coquereli*. Terre Vie 118:287–327
Ratajszczak R (1998) Taxonomy, distribution and status of the lesser slow loris *Nycticebus pygmaeus* and their implications for captive management. Folia Primatol 69(suppl 1):171–174
Ravosa MJ (1998) Cranial allometry and geographic variation in slow lorises (*Nycticebus*). Am J Primatol 45:225–243
Starr CR, Nekaris KAI, Streicher U, Leung L (2011) Field surveys of the threatened pygmy slow loris (*Nycticebus pygmaeus*) using local knowledge in Mondulkiri Province, Cambodia. Oryx 45:135–142
Streicher U (2004) Aspects of the ecology and conservation of the pygmy loris *Nycticebus pygmaeus* in Vietnam. Unpublished PhD thesis. Ludwig-Maximilians Universität, Germany
Streicher U, Nadler T (2003) Re-introduction of pygmy lorises in Vietnam. Reintroduction News 23:37–40
Swapna N, Radakrishna S, Gupta AK, Kumar A (2010) Exudativory in the Bengal slow loris in Trishna Wildlife Sanctuary, Tripura, northeast India. Am J Primatol 72:113–121
Weldon PJ (2004) Defensive anointing: extended chemical phenotype and unorthodox ecology. Chemoecology 14:1–4
Wiens F, Zitzmann A (2003) Social dependence of infant slow lorises to learn diet. Int J Primatol 24:1008–1021
Wiens F, Zitzmann A, Hussein NA (2006) Fast food for slow lorises: is low metabolism related to secondary compounds in high-energy plant diet? J Mammal 87:790–798

Chapter 20
Isotopic Variability and Lemur Diet in a Dry Madagascan Forest: A Cautionary Tale

Brooke E. Crowley and Laurie R. Godfrey

Abstract With the increasing use of carbon and nitrogen stable isotope variations in studies of prosimian diets, it is essential to understand the full extent of this variation in food plants. Our goal here is to characterize the $\delta^{13}C$ and $\delta^{15}N$ values of plants and modern and subfossil lemurs in and near Beza Mahafaly Special Reserve, south-western Madagascar. The region is characterized by a long dry season and a shorter monsoon season. In general, we found a high degree of variability both intra- and interspecifically. Furthermore, some of the general assumptions of isotopic ecology were not supported by our results. We suggest that researchers should be cautious when interpreting isotope values, especially when the conclusions are used to model paleocommunities or to inform conservation policies.

Resume Avec l'utilisation accrue des profils d'isotopes stables de carbone et d'azote dans les études portant sur les régimes alimentaires des prosimiens, il est essentiel que les variations des profils observés chez les plantes consommées soient comprises pleinement. Notre but est ici de mesurer les teneurs en $\delta^{13}C$ et $\delta^{15}N$ chez les plantes et les lémuriens actuels et sub-fossiles trouvés dans la Réserve Spéciale de Beza Mahafaly et ses environs. Cette région est caractérisée par une longue saison sèche et une plus brève saison de moussons. En général, nous avons constaté

B.E. Crowley (✉)
Department of Geology, University of Cincinnati, Cincinnati, OH 45221, USA

Department of Anthropology, University of Cincinnati, Cincinnati, OH 45221, USA
e-mail: brooke.crowley@uc.edu

L.R. Godfrey
Department of Anthropology, University of Massachusetts, 240 Hicks Way,
Amherst, MA 01003, USA
e-mail: lgodfrey@anthro.umass.edu

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_20,

une importante variation aussi bien au niveau intra-spécifique qu'au niveau interspécifique. De plus, certaines des règles fondamentales de l'écologie des isotopes ne sont pas vérifiées par nos résultats. Les chercheurs doivent rester prudents dans l'interprétation des données isotopiques, plus particulièrement lorsque de telles conclusions sont appliquées à la paléo-écologie des communautés et à la conservation.

Introduction

Stable isotopes have become increasingly important tools in ecological research. Natural variation in the abundance of stable isotopes of light elements (e.g., nitrogen, carbon, hydrogen, and oxygen) can be used to identify physiological and dietary differences among individuals and species. Stable isotopes can also be used to recognize seasonal shifts in an animal's metabolism or diet and to reconstruct ancient habitats and communities. Isotopes of an element have different numbers of neutrons and differ in mass and thermodynamic and kinetic properties. This leads to isotopic partitioning or fractionation during physical and chemical reactions. Fractionation, in turn, results in different materials having discrete isotopic ratios, reflecting their proportions of lighter and heavier isotopes. Since the absolute ratio of heavy to light isotopes is very small, isotopic abundance is expressed with reference to an international standard in parts per thousand (‰) using a standardized "δ" notation, where $\delta = ((R_{sample}/R_{standard}) - 1) \times 1{,}000$ and $R = {}^{13}C/{}^{12}C$, ${}^{15}N/{}^{14}N$, and so on. The standard is Pee Dee Belemnite for carbon and air for nitrogen.

Carbon isotope variation in plants relates to both physiology and environment. For example, plants using C3 versus C4 photosynthetic pathways differ in their stable carbon isotope ($\delta^{13}C$) values. Succulents often use the Crassulacean acid metabolism (CAM) photosynthetic pathway, which increases water use efficiency (e.g., Winter et al. 2005), and can result in $\delta^{13}C$ values that are intermediate between those of C3 and C4 plants. Moreover, both genetic differences and microhabitat differences in light, aridity, soil composition, and drainage can result in large intraspecific variations within a locality (Heaton 1999). In most terrestrial systems, plants obtain their nitrogen from soil nitrate and ammonium, and their $\delta^{15}N$ values are greater than air (~0‰). Legumes and other plants with symbiotic bacteria tend to have $\delta^{15}N$ values close to 0‰ because the bacteria fix nitrogen directly from the atmosphere (Ambrose 1991; Schulze et al. 1991). Thus, an animal whose diet is dominated by N-fixing legumes should display relatively low $\delta^{15}N$ values. Nitrogen isotopes also vary with trophic level (DeNiro and Epstein 1981; Ambrose 1991). In an isotopically simple world, herbivore bone collagen exhibits $\delta^{15}N$ and $\delta^{13}C$ values that are 3–5‰ and ~5‰ higher, respectively, than the plants they consume (DeNiro and Epstein 1981; Krueger and Sullivan 1984; Fox-Dobbs et al. 2007).

Yet these general principles tend to break down in coastal and arid systems. Although high $\delta^{15}N$ values in animal tissues tend to indicate consumption of

animal matter, such inferences may be tenuous without a proper understanding of vegetation and source $\delta^{15}N$ variation of a site (Handley et al. 1994; Högberg 1997). For example, the $\delta^{15}N$ values of some plants can be so elevated that their utility for assessing trophic level may be compromised (e.g., Sealy et al. 1987; Ambrose 1991). Interpretations based on $\delta^{13}C$ values can also be compromised unless environmental and physiological variables that influence vegetation $\delta^{13}C$ values are considered.

Here we examine isotopic variability in plants and animals in the Beza Mahafaly Special Reserve (BMSR), south-west Madagascar. Our goal is to determine the usefulness of certain isotopic "rules" for interpreting variation in a unique tropical dry forest. BMSR is characterized by a long dry season and the presence of four lemur species (*Propithecus verreauxi*, *Lemur catta*, *Lepilemur leucopus*, and *Microcebus griseorufus*). A few kilometers away from BMSR is a Holocene subfossil site, Taolambiby, with the remains of these extant species as well as extinct *Megaladapis edwardsi*, *M. madagascariensis*, *Archaeolemur majori*, *Pachylemur insignis*, and *Palaeopropithecus ingens.* Given that the diets of the four surviving lemurs at BMSR are well characterized (Nash 1998; Yamashita 2002), the site is ideally suited for an isotopic analysis of lemur communities through time. For this project, we sampled nonsucculent woody plants with an emphasis on legumes. Although *P. verreauxi* and *L. leucopus* consume some succulent CAM plants, C3 plants (particularly leguminous species) tend to be preferred (e.g., *Tamarindus indicus* is consumed in varying extents by *L. catta*, *L. leucopus*, and *P. verreauxi*, see Chap. 17).

Materials and Methods

BMSR is divided into two parcels. Parcel 1 is a riparian gallery forest on unconsolidated flood sediments. It is bordered to the east by the seasonally dry Sakamena River, which floods annually and provides a year-round water supply for nearby deep-rooted trees and wells. Within Parcel 1 there is a shift in vegetation structure and diversity as one moves westward from the Sakamena River (Sussman and Rakotozafy 1994; Yamashita 2002). Parcel 2 is classified as deciduous dry scrubland on sandstone and is further from the river. Its vegetation is dominated by xerophytic plants (Du Puy and Moat 1998).

We collected approximately 50 mature leaf specimens from a broad taxonomic sample of herbaceous and woody plants during the dry season of October 2006 (Table 20.1). Plants were identified by vernacular name on site and later identified to family level at the Parc Botanique et Zoologique de Tsimbazaza. To confirm that the isotopic ranges seen in our broad taxonomic sample are similar to those in known food species, we collected mature leaf samples from *Tamarindus indica* (Fabaceae), *Marsdenia verrucosa* (Asclepiadaceae), and *Pentopetia androsaemifolia* (Asclepiadaceae) from Parcel 1 in July 2007 (Table 20.2). The isotopic values of these plants are expected to approximate dietary inputs for *L. catta*, *L. leucopus*, and

Table 20.1 Extant lemur species and their food plant families at BMSR

Species	Tissue	*N*	Mean $\delta^{13}C‰$	SD	Range	Mean $\delta^{15}N‰$	SD	Range	Important plant families
Modern									
Lemur catta[a]	Fur	30	−24.31	0.60	−25.30 −23.20	6.71	0.81	5.10, 8.00	Asclepiadaceae[b], Combretaceae[b], Convolvulaceae, Euphorbiaceae[b], Fabaceae[b], Meliaceae, Salvadoraceae, Tiliaceae[b,c]
Lepilemur leucopus[d]	Fur	9	−21.30	0.80	−22.40 −20.10	5.50	1.00	4.20, 7.30	Asclepiadaceae[b], Fabaceae[b], Euphorbiaceae[b,e]
Propithecus verreauxi[f]	Bone	4	−21.38	0.67	−22.3 −20.82	6.85	0.73	6.11, 7.85	Asclepiadaceae[b], Burseraceae, Capparidaceae[b], Combretaceae[b], Convolvulaceae, Euphorbiaceae[b], Fabaceae[b], Meliaceae, Salvadoraceae, Tiliaceae[b]
Subfossil[g]									
Lemur catta	Bone	3	−21.15[h]	0.32	−21.4 −20.79	7.32	2.79	4.26, 7.99	
Lepilemur leucopus	Bone	2	−19.90[h]	1.87	−21.22 −18.57	9.20	0.92	8.55, 9.85	
Propithecus verreauxi	Bone	8	−20.82[h]	1.30	−23.57 −19.10	8.69	2.08	6.80, 13.54	

[a]Loudon et al. (2007)
[b]Families sampled for this study
[c]Yamashita (2002). Important plant families are families consumed by more than one lemur species
[d]Schoeninger et al. (1998)
[e]Nash (1998)
[f]Beza Mahafaly Osteologic Collection, BMOC #91, 94, 96, 97
[g]Alan Walker Taolambiby Collection (UMASS)
[h]Subfossil values corrected −1.22‰ to accommodate industrial changes in atmospheric CO_2 (Chamberlain et al. 2005)

Table 20.2 Coefficients of variation for three species of food plants at BMSR

Species	*N*	$\delta^{13}C$	$\delta^{15}N$
Marsdenia verrucosa	11	0.05	0.27
Tamarindus indica	67	0.06	0.32
Pentopetia androsaemifolia	11	0.03	0.19

P. verreauxi (Schoeninger et al. 1998; Yamashita 2002). We recognize that bone collagen isotope values reflect larger windows of time than our leaf samples. However, because we sampled leaves during the dry season, when plants are most stressed, we are likely to have captured the maximum amount of foliar isotopic variability within and between species at this site, which in turn can be used to infer the maximum amount of foliar isotopic variability in the lemurs' diets.

Leaf specimens were dried and ground into a fine powder. Approximately 5 mg of each powdered sample were weighed into a tin boat and analyzed for $\delta^{13}C$ and $\delta^{15}N$ values on a ThermoElectron (Finnigan) Delta+XP continuous flow system connected to an Elemental Analyzer (EA) using standardized methods at the University of California, Santa Cruz (UCSC) Stable Isotope Lab. Analytical precision (±1 SD) based on 11 IAEA Acetanilide replicates is −29.1 ± 0.05‰ for carbon and 1.7 ± 0.1‰ for nitrogen.

Collagen from the BMSR osteologic collection and subfossil extant lemurs from Taolambiby was isolated and analyzed following standardized procedures (Fox-Dobbs et al. 2006): ~100 mg of bone was cleaned, fragmented, decalcified in EDTA, rinsed in ultrapure water, and gelatinized in 0.01 N HCl. The gelatin solution was filtered using a 1.5-μm glass fiber filter and dried under vacuum, and 0.5 mg of collagen was weighed into tin boats and analyzed at UCSC. Collagen samples were excluded if their atomic C:N ratios were greater or less than 2.3–3.5. These data were then combined with published values compiled from the literature (Table 20.1). We combined results from fur and bone because the isotopic offset between keratin and collagen is expected to be small (<1‰) compared to the overall range in $\delta^{13}C$ and $\delta^{15}N$ values (Crowley et al. 2010).

Results and Discussion

We tested three isotopic "rules" (1) animal nitrogen isotopes reveal trophic level, (2) nitrogen-fixing leguminous plants (Fabaceae) have lower $\delta^{15}N$ values than sympatric nonleguminous plants, and (3) nonsucculent plants (including legumes) show no evidence for CAM photosynthesis and therefore have low $\delta^{13}C$ values. The combination of these rules suggests that if a lemur consumes nonsucculent plants including lots of legumes, its $\delta^{15}N$ and $\delta^{13}C$ values should be relatively low. If animal foods are important, then higher $\delta^{15}N$ values should be observed, and if CAM or C4 foods are important, then lemur $\delta^{13}C$ values should be high.

Rule 1: Nitrogen Isotopes Can Be Used to Infer Trophic Level

This rule is problematic. Lemur δ^{15}N values were variable; in general, the δ^{15}N values of subfossil samples were higher than those in modern samples (Table 20.1). This difference is unlikely to be the result of isotopic differences between bone and fur. On average, the δ^{15}N values of primate keratin are only ~0.8‰ lighter than bone (Crowley et al. 2010).

Foliar δ^{15}N values ranged from –0.9 to 12.8‰ (mean = 5.6‰) (Fig. 20.1a, b). N-cycles, especially in arid systems, can be complex and variability among different nitrogen sources (e.g., different N-fixing bacteria vs. variable soil nitrogen pools) could contribute to this observed variation (Handley et al. 1994; Högberg 1997). Although we attempted to minimize isotopic variability by sampling only fully mature leaves over a brief interval of time during the dry season, some variation in source N is likely to remain. Additionally, some Euphorbiaceae and Asclepiadaceae have extremely high δ^{15}N values, suggesting that alternatives to omnivory must be considered as explanations for high δ^{15}N values in some lemur tissues. We used a one-way ANOVA with Tukey's posthoc test of Honestly Significant Differences (HSD) to ascertain the significance of differences between δ^{15}N values for our selected plant food species, modern lemurs at BMSR, and subfossil extant and extinct lemurs at Taolambiby. Given an allowance for a positive trophic shift of 3‰ for δ^{15}N values between plant and animal tissue, all modern lemur values can be explained by variation in the food plants sampled (Tukey's HSD $p = 0.89$). However, the subfossil samples have significantly higher δ^{15}N values than do modern plants or extant lemurs ($F_{2,152} = 39.99$, $p < 0.001$, Tukey's HSD $p < 0.001$). This pattern holds for the subset of extant subfossil species ($t = -4.388$, df = 64, $p < 0.001$). Such a shift suggests a modification in diet or factors that influence the δ^{15}N values of plants like changes in aridity, urea content of the soil (higher levels in the past), or degree of burning (higher levels today) (Sealy et al. 1987; Cook 2001; Crowley et al. 2011).

Rule 2: Nitrogen Can Be Used to Assess Preference for Legumes

This rule is somewhat problematic. Average Fabaceae δ^{15}N values (2.2‰) are significantly lower than nonleguminous δ^{15}N values (6.3‰) ($t = 2.6$, df = 31, $p = 0.01$). On the whole, these values fit well with the principle that nitrogen fixing legumes should exhibit δ^{15}N values that are ~2‰ or more lower than sympatric nonfixing species. However, not all legumes have N-fixing bacteria, and some species show substantial variability (Schulze et al. 1991, Handley et al. 1994; Codron et al. 2005). Such variability is evident at BMSR, where *T. indica* can have surprisingly high δ^{15}N values (Fig. 20.1c). In addition to Fabaceae, other plant families are known to have N-fixing bacteria, and some of the Euphorbiaceae and Asclepiadaceae samples in our data set have values suggestive of nitrogen fixation (Fig. 20.1a). Thus, low δ^{15}N values from animal tissues may not necessarily indicate the heavy consumption of legumes, and high values do not preclude the heavy consumption of certain legumes such as *T. indica.*

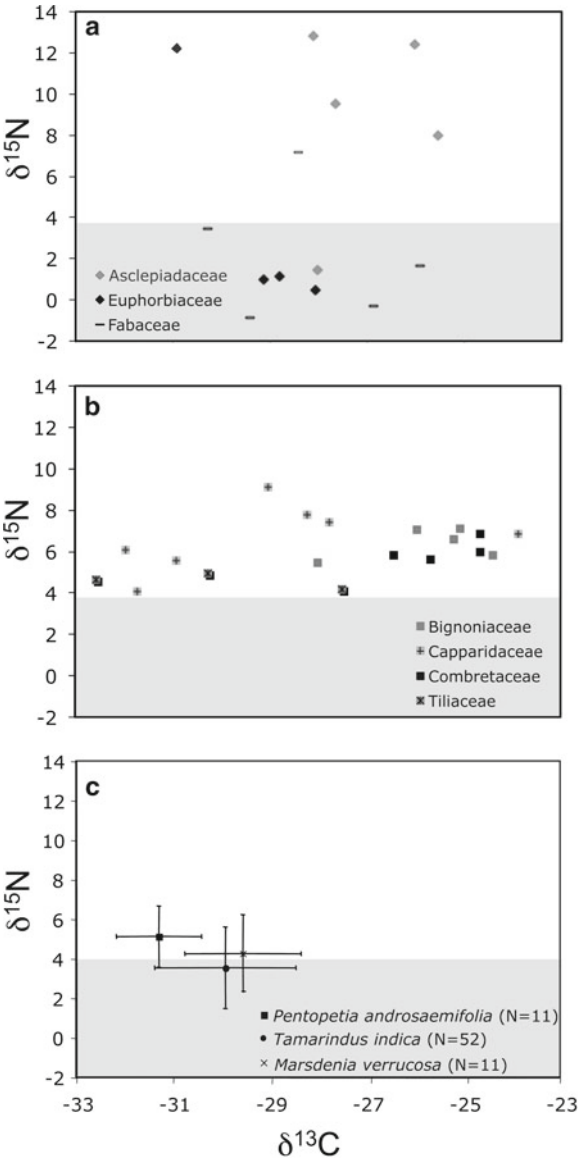


Fig. 20.1 Carbon and nitrogen isotope values for plant families at Beza Mahafaly. (**a**) Plant families exhibiting high δ^{15}N variance. (**b**) Plant families with low δ^{15}N variance. (**c**) Food plants that approximate nonsucculent dietary input. The *gray shaded* region shows the δ^{15}N range for plants with N-fixing bacteria (Fry 1991). *Error bars* indicate ±1 standard deviation

Rule 3: Carbon Can Be Used to Assess Preference for C3 Plants

Our results are consistent with this rule. The minimum and maximum δ^{13}C values for leaf samples were −32.6 and −23.5‰ (mean = −27.8‰) (Fig. 20.1a, b). Our three food species ranged from −33.4 to −27.6‰. The highest foliar δ^{13}C

value (−23.5‰) was within the anticipated range for C3 plants and outside of the range for obligate CAM plants. Some CAM plants can change their photosynthetic behavior depending on water availability. However, because we collected samples during the dry season, the likelihood of identifying nonsucculent facultative CAM plants was maximized. Our results suggest that if lemurs have high $\delta^{13}C$ values, some consumption of succulents, C4 plants, or animal resources may be inferred.

Overall, the observed $\delta^{13}C$ values of plants were unexpectedly negative for a dry deciduous forest. Aridity is usually linked to higher $\delta^{13}C$ values (Farquhar et al. 1989). We used ANOVA with Tukey's HSD to compare food plant values ("corrected" by 5‰ to allow for trophic effects) to those of lemurs (subfossil and modern samples treated separately). The three groups were all significantly different ($F_{2,154}=93.67$, $p<0.001$, Tukey's HSD $p<0.001$ for each). This holds for a subsample including only extant species ($t=-6.675$, df = 64, $p<0.001$). Because subfossil $\delta^{13}C$ values are significantly higher than those of modern lemurs, and modern lemur $\delta^{13}C$ values are significantly higher than those for our selected food plants, it stands to reason that the diets of lemurs at BMSR today, and to a greater extent, of lemurs in the region in the past, included some succulent plants. Indeed, we know this to be true of today's lemurs. Without sampling the vegetation of BMSR, we might have assumed that $\delta^{13}C$ values were as high as −21‰, and that subfossil lemurs were consuming only C3 plants (Crowley et al. 2011).

It is noteworthy that the food plants that we intensively sampled differ significantly from each other in their $\delta^{13}C$ ($F_{2,63}=6.343$, $p=0.003$) but not their $\delta^{15}N$ values ($F_{2,63}=2.406$, $p=0.098$). These differences are attributed to large intraspecific variability in $\delta^{15}N$ among the three food plant species (Table 20.2).

Conclusion

We conclude with a note of caution. As the plant isotope values of BMSR demonstrate, some common assumptions in the isotope literature may not hold true for every site. With few exceptions (e.g., Handley et al. 1994; Codron et al. 2005, 2006), researchers have come to rely on limited plant isotope data to make inferences about primate diets (e.g., Schoeninger et al. 1998; Loudon et al. 2007). Ideally, samples of plant and animal tissues should be drawn from the same sites, and intra- as well as interspecific isotopic variability of plants should be evaluated.

Acknowledgments We thank the chief of the Reserve, Andry Randrianandrasana, as well as Ibrahim Antho Jacky-Youssouf, Joachim Randriamahefa, Olivier Razanajafy, Elahavelo Efitroharany, Retala, Edward, and Emilienne Rasoazanabary for their exceptional field assistance, and E. Rasoazananbary for translating our abstract, Jeannin Ranaivonasy and Lalao Andriamahefarivo for handling our permits, Leanne Nash and Margaret Schoeninger for *L. leucopus* data, and Nathaniel Dominy, Paul Koch and Matt Sponheimer for comments on this chapter.

References

Ambrose SH (1991) Effects of diet, climate and physiology on nitrogen isotope abundances in terrestrial foodwebs. J Archaeol Sci 18:293–317

Chamberlain CP, Waldbauer JR, Fox-Dobbs K, Newsome SD, Koch PL, Smith DR, Church ME, Chamberlain SD, Sorenson KS, Risebrough R (2005) Pleistocene to recent dietary shifts in California condors. Proc Natl Acad Sci USA 102:16707–16711

Codron J, Codron D, Lee-Thorp JA, Sponheimer M, Bond WJ, de Ruiter D, Grant R (2005) Taxonomic, anatomical, and spatio-temporal variations in the stable carbon and nitrogen isotopic compositions of plants from an African savanna. J Archaeol Sci 32:1757–1772

Codron D, Lee-Thorp JA, Sponheimer M, de Ruiter D, Codron J (2006) Inter- and intrahabitat dietary variability of chacma baboons (*Papio ursinus*) in South African savannas based on fecal $\delta^{13}C$, $\delta^{15}N$, and %N. Am J Phys Anthropol 129:204–214

Cook GD (2001) Effects of frequent fires and grazing on stable nitrogen isotope ratios of vegetation in northern Australia. Austral Ecol 26:630–636

Crowley BE, Carter ML, Karpanty SM, Zihlman AL, Koch PL, Dominy NJ (2010) Stable carbon and nitrogen isotope enrichment in primate tissues. Oecologia 164:611–626

Crowley BE, Godfrey LR, Irwin MT (2011) A glance to the past: subfossils, stable isotopes, seed dispersal, and lemur species loss in southern Madagascar. Am J Primatol 73: 25–37

DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. Geochim Cosmochim Acta 45:341–351

Du Puy DJ, Moat JF (1998) Vegetation mapping and classification in Madagascar (using GIS): implications and recommendations for the conservation of biodiversity. In: Huxley CR, Lock JM, Cutler DF (eds) Chorology, taxonomy and ecology of the floras of Africa and Madagascar. Royal Botanic Gardens, Kew

Farquhar GD, Ehleringer JR, Hubick KT (1989) Discrimination and photosynthesis. Annu Rev Plant Physiol 40:503–537

Fox-Dobbs K, Stidman TA, Bowen GJ, Emslie SD, Koch PL (2006) Dietary controls on extinction versus survival among avian megafauna in the late Pleistocene. Geology 34:685–688

Fox-Dobbs K, Bump JK, Peterson RO, Fox DL, Koch PL (2007) Carnivore-specific stable isotope variables and variation in the foraging ecology of modern and ancient wolf populations: case studies from Isle Royale, Minnesota, and La Brea. Can J Zool 85:458–471

Fry B (1991) Stable isotope diagrams of freshwater food webs. Ecology 72:2293–2297

Handley LL, Odee D, Scrimgeour CM (1994) $\delta^{15}N$ and $\delta^{13}C$ patterns in savanna vegetation: dependence on water availability and disturbance. Funct Ecol 8:306–314

Heaton THE (1999) Spatial, species, and temporal variations in the $^{13}C/^{12}C$ ratios of C_3 plants: implications for palaeodiet studies. J Archaeol Sci 26:637–649

Högberg P (1997) Tansley Review No. 95 – ^{15}N natural abundance in soil-plant systems. New Phytol 137:179–203

Krueger HW, Sullivan CH (1984) Models for carbon isotope fractionation between diet and bone. In: Turnlund J, Johnson PE (eds) Stable isotopes in nutrition, vol 258, ACS symposium series. American Chemical Society, Washington, DC

Loudon JE, Sponheimer M, Sauther ML, Cuozzo FP (2007) Intraspecific variation in hair $\delta^{13}C$ and $\delta^{15}N$ values of ring-tailed lemurs (*Lemur catta*) with known individual histories, behavior, and feeding ecology. Am J Phys Anthropol 183:978–985

Nash LT (1998) Vertical clingers and sleepers: seasonal influences on the activities and substrate use of *Lepilemur leucopus* at Beza Mahafaly Special Reserve, Madagascar. Folia Primatol 69(suppl 1):204–217

Schoeninger MJ, Iwaniec UT, Nash LT (1998) Ecological attributes recorded in stable isotope ratios of arboreal prosimian hair. Oecologia 113:222–230

Schulze ED, Gebauer G, Ziegler H, Lange OL (1991) Estimates of nitrogen fixation by trees on an aridity gradient in Namibia. Oecologia 88:451–455

Sealy JV, Van der Merwe NJ, Lee Thorp JA, Lanham JL (1987) Nitrogen isotopic ecology in southern Africa: implications for environmental and dietary tracing. Geochim Cosmochim Acta 51:2707–2717

Sussman RW, Rakotozafy A (1994) Plant diversity and structural analysis of a tropical dry forest in southwestern Madagascar. Biotropica 26:241–254

Winter K, Aranda J, Holtum JAM (2005) Carbon isotope composition and water-use efficiency in plants with crassulacean acid metabolism. Funct Plant Biol 32:381–388

Yamashita N (2002) Diets of two lemur species in different microhabitats in Beza Mahafaly Special Reserve, Madagascar. Int J Primatol 23:1025–1051

Part V
Physiological Ecology

Chapter 21
Variable Energetic Strategies in Disturbed and Undisturbed Rain Forests: *Eulemur rubriventer* Fecal Cortisol Levels in South-Eastern Madagascar

Stacey R. Tecot

Abstract Habitat disturbance in Madagascar is pervasive. Researchers have assessed anthropogenic impacts on lemurs from alterations in locomotion, behavior, diet, distribution, and density. Such strategies may help lemurs cope with environmental change, but the underlying mechanisms facilitating such flexibility remain poorly understood. To document a physiological response to ecological stress, I investigated stress hormones in wild adult *Eulemur rubriventer*, the red-bellied lemur, in disturbed and undisturbed rain forests in south-eastern Madagascar over 17 months, from November 2003 to March 2005. My goals were to compile *E. rubriventer* cortisol excretion profiles, observe *E. rubriventer*'s response to food fluctuations, and compare these responses among groups in disturbed and undisturbed sites. Fecal glucocorticoid metabolite levels (fGCs) did not differ by sex and were lowest during the prebreeding season when fruit was abundant and highest during parturition and early lactation when fruit was scarce. Though fGC patterns were similar across sites, levels were significantly higher in the undisturbed site, contrary to expectations. fGCs were invariable in the disturbed site, despite lower and less seasonal fruit availability. A severely attenuated response to known environmental challenges, coupled with high infant mortality in the disturbed site, indicates that this population may be at risk of decline.

Resume Les perturbations d'habitat à Madagascar se généralisent. Des chercheurs ont commencé à estimer l'impact des perturbations anthropogéniques sur les lémuriens, mettant en évidence des différences intra spécifiques de locomotion, comportement, régime alimentaire, distribution et densité. Ces différentes stratégies aident les lémuriens à faire face aux changements environnementaux, mais les mécanismes

S.R. Tecot (✉)
School of Anthropology, University of Arizona, 1009 E. South Campus Drive, P.O. Box 210030, Tucson, AZ 85721, USA
e-mail: stecot@email.arizona.edu

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_21,

sous jacents, permettant une telle flexibilité restent mal compris. Afin d'appréhender la réponse physiologique à un stress écologique, j'ai étudié les hormones de stress chez *Eulemur rubriventer*, le lémur à ventre rouge en forêts humides perturbées ou non au sud ouest de Madagascar pendant 17 mois, de novembre 2003 à mars 2005. Mon but était de créer des profils de cortisol des excrétions de *E. rubriventer*, de déterminer les réponses d'*E. rubriventer* aux fluctuations de nourriture et comparer ces réponses entre groupes de sites perturbés et non-perturbés. The niveaux de métabolites glucocorticoïdiques fécaux (fGCs) ne différent pas selon les sexes, sont les plus bas pendant la saison pre-reproductuive lorsque les fruits sont abondants et les plus hauts en période de parturition et début de lactation lorsque les fruits sont rares. De plus, et contrairement à ce qui était attendu, les niveaux de fGC sont significativement plus forts dans les sites non perturbés. Le niveau de FGC est peu variable dans les sites perturbés, malgré la fluctuation en disponibilité des fruits. Cette réponse atténuée aux changements environnementaux, associée à une haute mortalité infantile dans les sites perturbés indiquent que ces populations pourraient montrer un plus fort risque de déclin.

Introduction

Madagascar's habitats are generally energetically poor, with low fruit quality and soil fertility, long fruiting periodicity, slow tree growth, and small tree crown diameters (Overdorff 1996a; Wright 1999). The climate is harsh, with recurrent droughts, frosts, and cyclones (Gould et al. 1999; Wright 1999), which frequently kill immature trees and inhibit fruiting, compounding the impact of an unpredictable climate (Dewar and Richard 2007) and resource base (Sauther 1998).

Of Madagascar's original habitat, 90% has been lost largely due to anthropogenic disturbance (Mittermeier et al. 2006), which decreases resource abundance, diversity, and seasonal predictability (Tecot 2008). Lemurs in heavily disturbed areas are most vulnerable to climatic change because forest fragmentation limits dispersal (Ganzhorn et al. 1997; Wright 1999), causing crowding, and intensifying the effects of resource scarcity. Maintaining diversity in disturbed areas requires an understanding of species' responses to habitat degradation. Researchers have begun to assess the impact of anthropogenic disturbance on lemurs, noting alterations in locomotion, behavior, diet, distribution, and density (Johnson and Overdorff 1999; Grassi 2006; Arrigo-Nelson 2006; Irwin 2008), although such measures alone may be insufficient to assess habitat quality (Hofer and East 1998).

Insights into the way lemurs cope with habitat disturbance can be gained from studying the proximate mechanisms that mediate their responses. Glucocorticoids like cortisol are indicators of stress (Hofer and East 1998); elevated cortisol levels imply the temporary, adaptive redirection of energy from long-term functions (growth, immunity, and reproduction) to ward an individual's more immediate needs. However, a prolonged response due to chronic stress becomes maladaptive (Selye 1956; Sapolsky 1987); long-term inhibition of these functions is particularly detrimental to reproductive success in slowly reproducing species like primates.

Stressors in the natural habitat can be estimated by measuring cortisol levels in feces and urine (Risler et al. 1987; Whitten et al. 1998; Ziegler and Wittwer 2005) and have been used to assess the effects of habitat degradation on primates (Chapman et al. 2006; Martínez-Mota et al. 2007). Populations with higher corticoid levels are assumed to be exposed to greater stress, suggesting that more degraded habitats should induce higher cortisol levels; but detailed ecological assessments quantifying habitat differences and seasonal changes are often lacking, impeding the accurate interpretation of cortisol profiles.

I investigated physiological responses of red-bellied lemurs (*Eulemur rubriventer*) to habitat disturbance by compiling cortisol excretion profiles, assessing the animals' response to food fluctuations, and comparing these responses among groups in disturbed and undisturbed rain forest sites in south-eastern Madagascar.

Methods

Sites

Data were collected in two adjacent rain forest sites, Talatakely (disturbed, i.e., DIST) and Vatoharanana (undisturbed, i.e., UND), within Ranomafana National Park, south-eastern Madagascar. As a result of selective logging from 1986 to 1989, DIST has lower productivity and less seasonally distributed fruiting events than UND and large stands of invasive Chinese guava (*Psidium* sp.) (Turk 1995; Balko 1998; Tecot 2008). UND was lightly logged from 1987 to 1989 (Hemingway 1995) and consists of continuous primary forest.

Phenological Sampling

Monthly phenological assessments were made on all lianas and trees ≥2.5 cm diameter at breast height ($n = 1{,}674$), in three botanical plots (100 m × 10 m, 5 m × 50 m, and 10 m × 25 m) per site (Tecot 2008). Seasonal food availability was determined by dividing the number of plants with ripe fruit (*E. rubriventer*'s main dietary component) by the number of plants assessed in each site monthly.

Subjects

Red-bellied lemurs are a highly frugivorous, monogamous species with allomaternal care, living in family groups of 2–5 individuals and typically gestating May–September (Overdorff 1996b; Durham 2003; Overdorff and Tecot 2006; Tecot 2008, 2010). Aggression is extremely rare (Overdorff and Tecot 2006), and there is no discernible hierarchy that might affect cortisol levels. One 3.5-year-old male

emigrated during the study (during his mother's early pregnancy), and was subsequently excluded from the study; no effect on cortisol levels was detected in group members (Tecot 2008). I present data from 11 adults in 5 habituated groups ($n_{DIST}=3$, $n_{UND}=2$) over 17 months (November 2003–March 2005).

Fecal Collection

One to two fresh, whole fecal samples, uncontaminated by water or urine, were collected per individual per week, between 07:00 and 12:00 to control for any daily rhythm in cortisol excretion. Samples were flattened in aluminum foil, dried within 4 h by a fire or in an oven at 70 °C for steroid preservation, and stored in Whirl-paks (Nasco, Fort Atkinson, WI) with desiccants. Both drying techniques resulted in high recovery and sample stability (Tecot 2008).

Hormone Extraction

Fecal samples were ground and sifted to remove debris, and 0.1 g was extracted per sample ($n=923$) into ethanol–water (50:50) (Strier and Ziegler 1997). Samples were mixed, centrifuged, and the 5 ml supernatant poured off. To free conjugated steroids, 1 ml was separated and 4 ml solvent was added. Samples were mixed and centrifuged and the solvent was aspirated into culture tubes, evaporated in a water bath, and resuspended in 1 ml 30% methanol. Samples were purified through solid-phase extraction columns (Strata X, Phenomenx, 8BS100TAK), conditioned with 1 ml 100% methanol and 1 ml distilled water. 1.0 ml of sample was added and washed with 5% methanol. Steroids were eluted off the column with 2 ml 100% methanol, evaporated, and reconstituted in 1 ml 30% methanol.

Assay Procedures

Cortisol values were determined by enzyme immunoassay (EIA). Samples from adults were assayed in duplicate. 100-µl samples were evaporated and diluted 1:2 in EIA buffer. 250-µl enzyme-labeled antigen (horseradish peroxidase cortisol) was added to the standards and samples, and 100-µl mixture was added to each well for binding during a 2-h incubation. Solid-phase washing separated bound and free cortisol. 100-µl substrate was added, and absorbance was calculated. All results are expressed in ng/g feces. The slope of serially diluted fecal extracts was parallel to the slope of the standard curve ($t_{[22]}=1.85$, ns, $P>0.05$). Accuracy was achieved by adding 100-µl fecal pool in duplicate to each of the standard curve points and was determined to 96.68 ± 1.79% SEM, $n=6$. Low pool ($n=30$) interassay coefficient of variation (CV) was 16% and intraassay CV was 3.6%. High pool ($n=31$) interassay CV was 11.9% and intraassay CV was 2.1%.

Analyses

For each individual, weekly mean cortisol levels were calculated, yielding equivalent numbers of weekly mean values from individuals in the disturbed site ($n=466$) and the undisturbed site ($n=457$). Because baseline levels approached zero, no adjustment (e.g., percent change from baseline) was used. Cortisol levels (expressed as fecal glucocorticoid metabolites, fGCs) were not normally distributed and were log transformed. A Linear Mixed-Effects Model was employed (Hruschka et al. 2005) using SPSS 15.0 (SAS Institute, Cary, NC). The REPEATED subcommand was used to model the possible correlation of the residual errors for each individual. MIXED was used to construct a least squares model to test all relationships with fGCs, using Type III sums of squares for evaluating effects and Akaike's information criterion for choosing models. Four models were constructed: one to test for an effect of sex ($n_{female}=413$ and $n_{male}=507$)[1]; one to test for site differences in overall fGC levels; one to test for monthly differences overall and by site with a month × site interaction; and one to test for seasonal differences overall and by site with a season × site interaction.

Results

Overall and Monthly Cortisol Levels

fGCs were predicted in the model based on weekly values with ID repeated to take into account repeated values from individuals with potentially different hormonal profiles. Male and female fGCs were not significantly different [$F(1,260.448)=0.590$, $P=0.443$], so data were combined. Table 21.1 reports descriptive statistics for fGCs for UND and DIST. Significant monthly differences were recorded [$F(16,318.710)=4.528$, $P<0.001$], with the lowest levels occurring in March–May 2004 and the highest levels from September to November 2004.

To compare sites, fGCs were predicted based on monthly values with group repeated to take into account potential group-level differences. UND had significantly higher fGCs overall [$F(1,14.384)=12.726$, $P<0.01$], and fluctuations were greater in magnitude, indicated by greater variance in individual, weekly, and monthly mean fGCs (Table 21.1) than recorded at DIST. Controlling for month, fGCs differed significantly across sites [$F(1,84.234)=7.733$, $P<0.01$]. A site × month interaction indicated significantly higher fGCs in UND for 5 months [$F(16,115.486)=3.053$, $P<0.001$]. fGCs varied significantly across months in UND [$F(16,109.752)=6.179$, $P<0.001$] but not in DIST [$F(16,120.311)=0.913$, $P=0.56$] (Fig. 21.1).

[1] Three samples were from adults whose sex and ID were undetermined.

Table 21.1 Descriptive statistics for individual fGCs by sample, weekly mean, monthly mean, overall and by site

	Samples	Minimum	Maximum	Variance	Standard deviation	Mean	N
All	DIST	1.5	137	358.96	18.95	24.71	466
	UND	0.85	323.10	1005.84	31.71	32.92	457
	Total	**0.85**	**323.10**	**695.73**	**26.38**	**28.78**	**923**
Weekly	DIST	3.05	137.00	301.19	17.35	24.33	346
	UND	1.32	161.98	722.81	26.89	32.10	318
	Total	**1.32**	**161.98**	**517.40**	**22.75**	**28.05**	**664**
Monthly	DIST	5.63	69.59	143.16	11.96	24.56	110
	UND	6.88	93.25	347.92	18.65	32.82	85
	Total	**5.63**	**93.25**	**247.96**	**15.75**	**28.16**	**195**

Totals in bold represent both sites combined

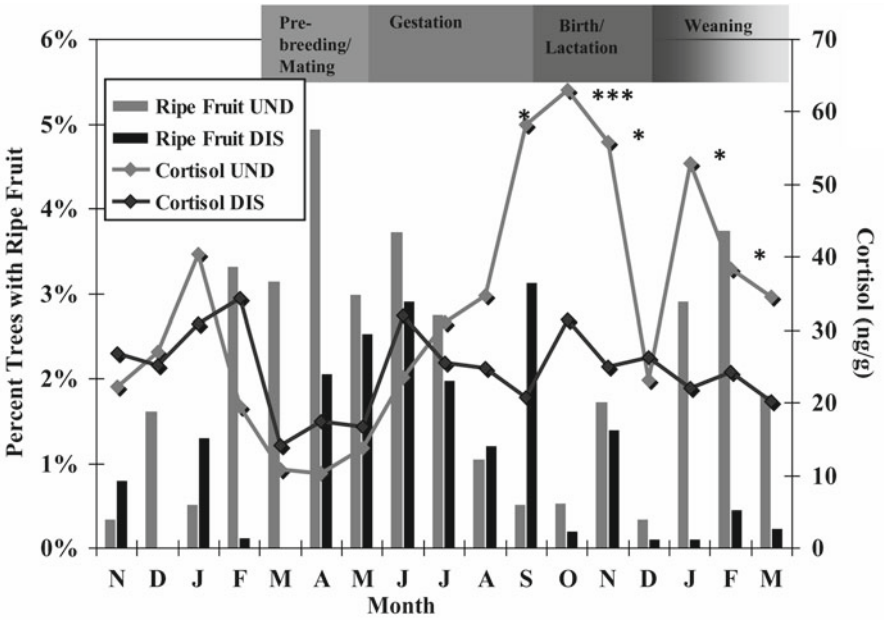


Fig. 21.1 Fruit availability and *Eulemur rubriventer* fGCs in disturbed and undisturbed forests, November 2003–March 2005, by month and reproductive stage

Seasonal Cortisol Levels

fGCs were predicted based on monthly values with individual ID repeated to take into account repeated values from individuals with potentially different hormonal profiles. fGCs were significantly higher during fruit scarcity [$F(1,175.64) = 10.482$, $P < 0.001$, Fig. 21.2]. A significant season × site interaction [$F(1,175.64) = 14.036$, $P < 0.001$] was indicated in UND [$F(1,136.489) = 20.421$, $P < 0.001$] but not in DIST

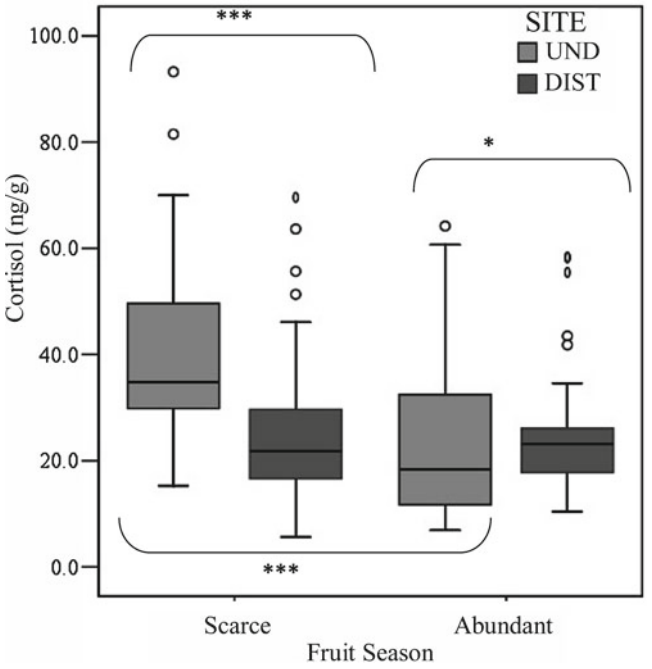


Fig. 21.2 Box plot of fGC site differences during fruiting seasons. *Lines* within *boxes* are medians based on weekly means, *boxes* enclose 25–75% of the data, *whiskers* enclose 5–95% of the data, and *open symbols* indicate outliers

[$F(1,187.370)=0.161$, $P=0.69$]. Sites did not differ when fruit was abundant [$F(1,86.279)=0.670$, $P=0.415$] but fGCs were significantly higher in UND than in DIST during fruit scarcity [$F(1,86.\ 996)=19.141$, $P<0.001$, Fig. 21.2].

Discussion

This study established fGC profiles for *E. rubriventer* and adds to the growing database of wild lemur corticoid profiles (Cavigelli 1999; Gould et al. 2005; Pride 2005a, b; Fichtel et al. 2007). Lowest levels occurred March–May, between weaning and mating. Cortisol levels often increase prior to breeding in species where male competition for females is high (Perret and Predine 1984; Fichtel et al. 2007), and low cortisol levels have been observed prior to breeding in species like *E. rubriventer*, where mate competition is low (Strier et al. 1999; Lynch et al. 2002; but see Gould et al. 2005). Low prebreeding levels may also be related to high food abundance at this time.

Highest fGCs were excreted from September to November, at the convergence of parturition and fruit scarcity, and were sustained for approximately 3 months until fruit became abundant and infants gained independence. Thus, cortisol profiles

reflect a combination of reproductive and ecological pressures. These results contrast with low birth season cortisol levels observed in male *Propithecus verreauxi* (Fichtel et al. 2007) and *P. edwardsi* (Tecot, unpublished data), possibly because those males do not participate in infant care. *E. rubriventer* may reduce birth season stress by their lack of aggression, by allomaternal care, and by high fruit abundance and extensive time spent feeding before breeding (Tecot 2008) which allows them to lay down energy reserves.

This is the first study to compare lemur fGCs in disturbed and undisturbed habitats. Contrary to expectations, fGCs in UND were higher and more variable overall. Sites converged during fruit abundance, as expected if finding food is not energetically challenging. Comparisons during fruit scarcity are more telling, as it responses to environmental challenge that are evolutionarily significant. Food scarcity elicited little response from DIST, and fGCs were higher in UND. Lower levels in DIST might imply that these animals experience less stress (possibly due to the opportune presence of *Psidium*), and that *E. rubriventer* is a flexible species; but seasonal and monthly results suggest that DIST did not launch a full physiological response. Feeding on *Psidium* may have buffered DIST animals during the first fruit scarcity period, resulting in comparable fGCs in both sites, but the animals did not use this food source during the second fruit scarcity/birth season in DIST despite its availability, and DIST fGCs remained low, while fGCs reached their maximum in UND (Tecot 2008).

Low and largely invariable fGCs may result from excessive stress or because more sensitive individuals have been selected out of the population (Romero 2004). Attenuation may reduce the chances of additional pathological stress due to chronic stress and increase chances of survival in difficult environments. However, prolonged attenuation may also indicate insufficient coping: infant mortality between September 2003 and March 2005 was higher in DIST (60%) than in UND (0%) (Tecot 2008, 2010).

My results underscore the importance of longitudinal studies: comparisons during optimal conditions are unlikely to reflect responses to environmental challenges and single season comparisons do not indicate individuals' abilities to respond to the environment. fGC fluctuations across challenging and unchallenging seasons within populations should be compared. This study suggests that populations with higher mean fGCs may not be more stressed, insofar as stress refers to any negative effect on an individual's chances of survival and reproduction (Hofer and East 1998). Severely muted hormonal and behavioral responses to known environmental challenges (Tecot 2008) coupled with high infant mortality (Tecot 2010) indicate that the DIST population may be at risk of declining.

Conclusions

This study determined that physiological adjustments occur in tandem with changes in food availability, and cortisol excretion is elevated and prolonged when food scarcity converges with reproduction; energy mobilization in *E. rubriventer* is essential at this time. While prolonged cortisol elevations may become pathological, animals

may forego reproduction, or display an attenuated response, in energetically poor environments. Thus, in altered habitats with unpredictable, lower quality, less abundant resources, selection may be exerted on conception or infant survival. Results from this study indicate that *E. rubriventer* cope in such environments with an attenuated response, resulting in relatively higher infant mortality during the first 3 months of life (Tecot 2010). Differences in habitat quality between DIST and UND have existed for at least 20 years (Balko 1998; Tecot 2008), and population densities, body weights, and group sizes of other lemur species (*Prolemur simus* and *Propithecus edwardsi*) have decreased over time (Wright and Andriamihaja, in preparation). *E. rubriventer* may sacrifice reproduction for survival in this selectively logged forest.

Acknowledgments My research was conducted with permission and support from the following: the Malagasy government, ANGAP, MICET, ICTE, and Centre ValBio; expert research technicians Telo Albert, Rasendrinirina Victor, Rakotonirina T. E., and Rakotoniaina J. F.; friend and researcher Rakotonirina Laingoniaina; research assistants T. Calhoon, A. Hall, and D. Waters; funding agencies the American Society of Primatologists, the National Science Foundation (#0424234), Primate Action Fund, Primate Conservation, Inc., and UT Austin; T. Ziegler and D. Wittwer from the WNPRC Assay Services Laboratory; and D. Overdorff, P. Wright, and my family, particularly Sleeper.

References

Arrigo-Nelson SJ (2006) The impact of habitat disturbance on the feeding ecology of the Milne-Edwards' sifaka (*Propithecus edwardsi*) in Ranomafana National Park. Unpublished PhD thesis, Stony Brook University, Stony Brook, NY

Balko EA (1998) A behaviorally plastic response to forest composition and logging disturbance by *Varecia variegata variegata* in Ranomafana National Park, Madagascar. Unpublished PhD thesis, SUNY-CESF, Syracuse, NY

Cavigelli SA (1999) Behavioural patterns associated with faecal cortisol levels in free-ranging female ring-tailed lemurs, *Lemur catta*. Anim Behav 57:935–944

Chapman CA, Wasserman MD, Gillespie TR, Speirs ML, Lawes MJ, Saj TL, Ziegler TE (2006) Do food availability, parasitism, and stress have synergistic effects on red colobus populations living in forest fragments? Am J Phys Anthropol 131:525–534

Dewar RE, Richard AF (2007) Evolution in the hypervariable environment of Madagascar. Proc Natl Acad Sci USA 104:13723–13727

Durham DL (2003) Variation in responses to forest disturbance and the risk of local extinction: a comparative study of wild Eulemurs at Ranomafana National Park, Madagascar. Unpublished PhD thesis, University of California, Davis, CA

Fichtel C, Kraus C, Ganswindt A, Heistermann M (2007) Influence of reproductive season and rank on fecal glucocorticoid levels in free-ranging male Verreaux's sifakas (*Propithecus verreauxi*). Horm Behav 51:640–648

Ganzhorn JU, Malcomber S, Andrianantoanina O, Goodman SM (1997) Habitat characteristics and lemur species richness in Madagascar. Biotropica 29:331–343

Gould L, Sussman RW (1999) Natural disasters and primate populations: the effects of a 2-year drought on a naturally occurring population of ring-tailed lemurs (*Lemur catta*) in southwestern Madagascar. Int J Primatol 20:69–84

Gould L, Ziegler TE, Wittwer DJ (2005) Effects of reproductive and social variables on fecal glucocorticoid levels in a sample of adult male ring-tailed lemurs (*Lemur catta*) at the Beza Mahafaly Reserve, Madagascar. Am J Primatol 67:5–23

Grassi C (2006) Variability in habitat, diet, and social structure of *Hapalemur griseus* in Ranomafana National Park Madagascar. Am J Phys Anthropol 131:50–63
Hemingway CA (1995) Feeding and reproductive strategies of the Milne-Edwards' sifaka, Propithecus diadema edwardsi. 9533037, Duke University, United States – North Carolina
Hofer H, East ML (1998) Biological conservation and stress. In: Moller AP, Milinski M, Slate PJB (eds) Advances in the study of behavior, vol 27. Academic, San Diego, pp 405–525
Hruschka DJ, Kohrt BA, Worthman CM (2005) Estimating between- and within-individual variation in cortisol levels using multilevel models. Psychoneuroendocrinology 30:698–714
Irwin MT (2008) Diademed sifaka (*Propithecus diadema*) ranging and habitat use in continuous and fragmented forest: higher density but lower viability in fragments? Biotropica 40:231–240
Johnson SE, Overdorff DJ (1999) Census of brown lemurs (*Eulemur fulvus* spp.) in southeastern Madagascar: methods-testing and conservation implications. Am J Primatol 47:51–60
Lynch JW, Ziegler TE, Strier KB (2002) Individual and seasonal variation in fecal testosterone and cortisol levels of wild male Tufted Capuchin monkeys, Cebus apella nigritus. Horm Behav 41:275–287
Martínez-Mota R, Valdespino C, Sánchez-Ramos MA, Serio-Silva JC (2007) Effects of forest fragmentation on the physiological stress response of black howler monkeys. Anim Conserv 10:374–379
Mittermeier RA, Konstant WR, Hawkins F, Louis EE, Langrand O, Ratsimbazafy J, Rasoloarison R, Ganzhorn JU, Rajaobelina S, Tattersal I, Meyers DM (2006) Lemurs of Madagascar, 2nd edn. Conservation International, Washington, DC
Overdorff DJ (1996a) Ecological correlates to activity and habitat use of two prosimian primates: *Eulemur rubriventer* and *Eulemur fulvus rufus* in Madagascar. Am J Primatol 40:327–342
Overdorff DJ (1996b) Ecological correlates to social structure in two lemur species in Madagascar. Am J Phys Anthropol 100:487–506
Overdorff DJ, Tecot SR (2006) Social pair-bonding and resource defense in wild red-bellied lemurs (*Eulemur rubriventer*). In: Gould L, Sauther ML (eds) Lemurs: ecology and adaptation. Springer Media, New York, pp 235–245
Perret M, Predine J (1984) Effects of long-term grouping on serum cortisol levels in *Microcebus murinus* (Prosimii). Horm Behav 18:346–358
Pride E (2005a) Optimal group size and seasonal stress in ring-tailed lemurs (*Lemur catta*). Behav Ecol 16:550–560
Pride E (2005b) High faecal glucocorticoid levels predict mortality in ring-tailed lemurs (*Lemur catta*). Biol Lett 1:60–63
Risler L, Wasser SK, Sackett GP (1987) Measurement of excreted steroids in *Macaca nemestrina*. Am J Primatol 12:91–100
Romero LM (2004) Physiological stress in ecology: lessons from biomedical research. Trends Ecol Evol 19:249–255
Sapolsky RM (1987) Stress, social status, and reproductive physiology in free-living baboons. In: Crews D (ed) Psychobiology of reproductive behavior: an evolutionary perspective. Prentice Hall, Englewood Cliffs, NJ, pp 291–322
Sauther ML (1998) The interplay of phenology and reproduction in ringtailed lemurs: implications for ringtailed lemur conservation. Folia Primatol 69:309–320
Selye H (1956) The stress of life. McGraw-Hill, New York
Strier KB, Ziegler TE (1997) Behavioral and endocrine characteristics of the reproductive cycle in wild muriqui monkeys, *Brachyteles arachnoides*. Am J Primatol 42:299–310
Strier KB, Ziegler TE, Wittwer DJ (1999) Seasonal and social correlates of fecal testosterone and cortisol levels in wild male muriquis (*Brachyteles arachnoides*). Horm Behav 35:125–134
Tecot S (2008) Seasonality and predictability: the hormonal and behavioral responses of the red-bellied lemur, *Eulemur rubriventer*, in Southeastern Madagascar. Unpublished PhD thesis, University of Texas, Austin
Tecot S (2010) It's all in the timing: out of season births and infant survival in *Eulemur rubriventer*. Int J Primatol 31:715–735

Turk D (1995) A guide to trees of Ranomafana National Park and central eastern Madagascar. USAID, Washington, DC

Whitten PL, Brockman DK, Stavisky RC (1998) Recent advances in noninvasive techniques to monitor hormone-behavior interactions. Yearb Phys Anthropol 41:1–23

Wright PC (1999) Lemur traits and Madagascar ecology: coping with an island environment. Yearb Phys Anthropol 42:31–72

Ziegler TE, Wittwer DJ (2005) Fecal steroid research in the field and laboratory: improved methods for storage, transport, processing, and analysis. Am J Primatol 67:159–174

Chapter 22
Photoperiod-Related Changes in Thermoregulatory Capacity in Gray Mouse Lemurs *(Microcebus murinus)*

Jérémy Terrien and Fabienne Aujard

Abstract Seasonal endocrinal changes, such as modulation of insulin-like growth factor 1 (IGF-1) levels, may allow animals to cope with temperature variations. To test this hypothesis, we evaluated the effects of season on thermoregulatory capacities in a photoperiod-responsive species, the gray mouse lemur (*Microcebus murinus*). Adult male mouse lemurs were exposed to ambient temperatures (Tas) of 12, 25, and 34 °C, and we monitored changes in daily rhythms of body temperature (Tb) and IGF-1 blood levels. Additionally, we observed the exploration and choice of Ta in a thermal gradient over 24 h after animals had been acclimated to 25 °C. Under winter-like short photoperiod (SP) exposure, mouse lemurs in the thermal gradient showed marked behavioral adjustments and Tb fluctuations, in response to Ta fluctuations similar to those occurring in the Malagasy winter. In contrast, under summer-like long photoperiod (LP), behavioral responses and Tb changes were only moderate, corresponding to the lower Ta fluctuations observed in summer. Overall, IGF-1 levels remained higher under LP than under SP, whatever the Ta. Thermal challenges evoked different modulations of IGF-1 according to season, e.g., a slight increase under SP and a transient decrease under LP after heat challenge. Altogether, our results indicate that photoperiod exerts a major influence on thermoregulatory capacities, with IGF-1 playing an important role in mechanisms of thermogenesis/thermolysis.

Résumé Les changements endocriniens saisonniers, telles que les modulations des niveaux d'IGF-1 (Insulin-like Growth Factor 1), pourraient permettre aux animaux de faire face aux variations de température. Pour tester cette hypothèse, nous avons évalué les effets de la saison sur les capacités thermorégulatrices chez une espèce sensible à la photopériode, le Microcèbe gris (*Microcebus murinus*). Des microcèbes

J. Terrien (✉) • F. Aujard
Mécanismes Adaptatifs et Evolution, UMR CNRS/MNHN,
7179, 4 avenue du Petit Château, 91800 Brunoy, France
e-mail: jeremy.terrien@hotmail.fr

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_22,

mâles adultes ont été exposés à des températures ambiantes (Tas) de 12, 25 et 34°C. Nous avons suivi les changements de rythmes journaliers de la température corporelle (Tb) et des niveaux sanguins d'IGF-1. De plus, nous avons observé l'exploration et le choix de Ta dans un gradient thermique sur 24 h, après avoir acclimaté les animaux à 25°C. En photopériode courte (SP), les microcèbes placés dans un gradient thermique ont montré des ajustements comportementaux et des fluctuations de Tb marqués, suivant des fluctuations de Ta semblables à celles observées pendant l'hiver malgache. En photopériode longue, en revanche, les variations de Tb et la réponse comportementale sont plus modérées, correspondant à de plus petites fluctuations de Ta observées en été. Globalement, les niveaux d'IGF-1 sont plus élevés en LP qu'en SP, quelle que soit la Ta. Les challenges thermiques ont montré des modulations de l'IGF-1 différentes selon la saison, comme par exemple une légère augmentation en SP et une diminution progressive en LP lors de l'exposition à 34°C. Ensemble, ces résultats indiquent que la photopériode exerce un effet majeur sur les capacités thermorégulatrices, l'IGF-1 jouant un rôle important dans les mécanismes de thermogenèse et thermolyse.

Introduction

Gray mouse lemurs (*Microcebus murinus*) show strong seasonality in many of their biological functions, which can be reproduced in captivity by photo-entrainment using artificial lighting. Under short photoperiod (SP) exposure, mouse lemurs enter a state of sexual rest and exhibit a significant gain in body mass, while during the long photoperiod (LP) season animals become sexually active and lose weight (Génin and Perret 2000; Perret and Aujard 2001). To save energy, mouse lemurs have developed both behavioral (gregariousness, passive warming-up, and nesting in buffered holes) and autonomic (hypometabolism) responses (Seguy and Perret 2005). The modulation of hypothermia occurs daily under normothermic conditions to compensate for low energy storage capacity (Aujard and Vasseur 2001). Many heterotherms reduce their metabolism to compensate for the high cost of maintaining normothermia by minimizing the cost of heat production (Geiser and Ruf 1995), and this mechanism may be enhanced by exposure to cold ambient temperatures (Ta). Animals exposed to high Tas avoid hyperthermia by resting in buffered nests and lose excess body heat by sudation and panting (Kenney and Munce 2003). In captive gray mouse lemurs, modulation of the hypothermic phase varies according to photoperiod and Ta (Seguy and Perret 2005; Aujard et al. 1998). Importantly, nonshivering thermogenesis (NST) taking place in the brown adipose tissue (BAT) occurs during the active diurnal warming phase and is used particularly during cold challenges (Génin et al. 2003). Insulin-like growth factor type 1 (IGF-1), a growth factor enhancing cellular proliferation and maturation, may activate cold-induced BAT development in rats (Duchamp et al. 1997) increasing plasma IGF-1 levels. Under warm exposure, mouse lemur responses are chiefly behavioral, associated with enhanced thermolytic processes such as panting, sweating, and intense salivation (Génin et al. 2003). The aim of this study was to investigate whether acclimation

to a given photoperiod confers specific capacities to cope with thermal challenges in gray mouse lemurs. We monitored seasonal changes in the spontaneous choice of Ta for daily resting periods and compared the responses of mouse lemurs acclimated to either winter-like or summer-like photoperiodic conditions after exposure to cold or warm Tas. We measured daily rhythms of body temperature (Tb) and IGF-1 plasma levels at various Tas.

Methods

All subjects were adult *M. murinus* males (mean age ± SEM: 2.3 ± 0.3 years), born in the laboratory breeding colony at Brunoy (Agreement 2007-DDSV-079). Temperature selection was monitored in 40 animals exposed to a thermal gradient (Aujard et al. 2006), 20 of which had been acclimated to long photoperiod (LP) and 20 to short photoperiod (SP). In a second experiment, 12 mouse lemurs acclimated to each photoperiod were kept for 9 days at the control Ta of 25 °C. Subsequently, six animals from each photoperiod regime were exposed for 9 days to cold (12 °C) and six to warm (34 °C) Ta. Tb was measured by telemetry every 10 min. We analyzed the following parameters: mean Tb (in °C) during the active nocturnal phase (Tb_{night}); mean Tb during the resting diurnal phase (Tb_{day}); minimal Tb value (Tb_{min}); time of occurrence of Tb_{min} (H_{min}); and time of occurrence of the beginning of daily Tb decrease (H_{decr}). The last two parameters were expressed in minutes relative to light onset. Times of occurrence preceding light onset (phase advances) were expressed by positive values, while phase delays were expressed by negative values.

To measure plasma IGF-1 levels, blood was taken at the control Ta of 25 °C and after 2 days (short-term response) and 9 days (long-term response) of cold or warm exposure. IGF-1 plasma levels were related to the body mass of the animal and expressed in ng/ml × 100 g BM. Values are means ± SEM. We used *t*-tests to assess thermal gradient data. All other data were analyzed with Linear Mixed Effect models in software R version 2.6.0 (The R Foundation for Statistical Computing 2007). We treated photoperiod and Ta as fixed effects, and animal identities as random effects.

Results

Photoperiod-Dependent Thermal Choice in the Thermal Gradient

We tracked the animals' positions and time spent at each Ta in the thermal gradient over 24 h. Overall, mouse lemurs explored the different nests available, i.e., the different Tas available, during the nocturnal phase until selecting a specific one for the diurnal sleeping period. In mouse lemurs acclimated to summer-like LP, the average Tas (integrating the time spent at each given Ta) visited in the dark phase (23.3 ± 0.9 °C) was not significantly different from the Ta chosen in the light phase

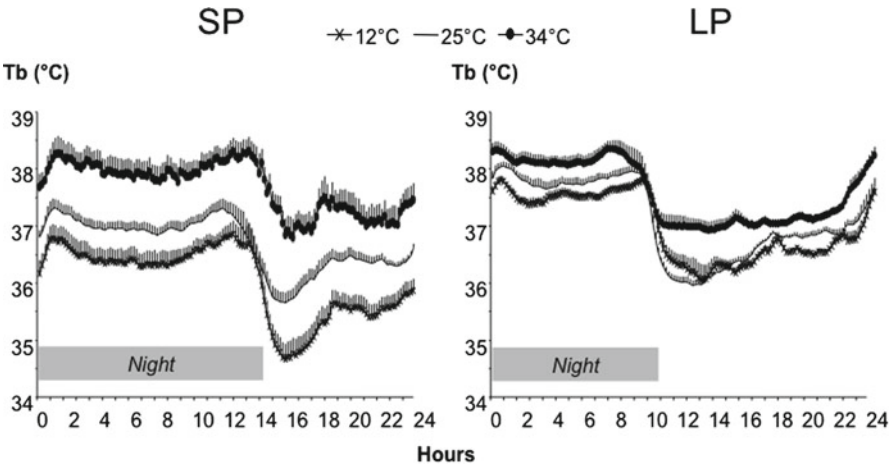


Fig. 22.1 Daily rhythms of body temperature (Tb in °C) observed in adult mouse lemurs acclimated to short (SP, *left*) and long (LP, *right*) photoperiods after exposure to 12, 25, and 34 °C. Data are given as mean ± SEM. $N = 6$ animals per group

(21.1 ± 1.8 °C − t_{19} = 1.25, NS). In contrast, animals acclimated to winter-like SP exhibited a significant day/night difference in explored/selected Tas (t_{19} = 3.06, $P < 0.01$); animals chose warmer Tas during the day (26.0 ± 1.6 °C) than during the night (21.7 ± 1.5 °C). Average Tas explored during the night did not differ significantly between animals acclimated to either SP or LP (t_{38} = 0.94, NS), but Tas chosen for the resting period were significantly higher in animals acclimated to SP than those acclimated to LP (t_{38} = 2.12, $P < 0.05$).

Effect of Photoperiod on Tb Rhythms

At 25 °C, animals under both LP and SP acclimation exhibited very robust daily rhythms of Tb with high values during the nocturnal active phases and lower values during the diurnal resting phases. The effects of Ta challenges on Tb levels were significant, independent of season (Tb_{night}: $F_{2,23}$ = 21.0, $P < 0.001$; Tb_{day}: $F_{2,23}$ = 20.3, $P < 0.001$; and Tb_{min}: $F_{2,23}$ = 19.7, $P < 0.001$), with deepening of daily hypothermia during cold exposure and general Tb rise during warm exposure. However, acclimation under SP revealed greater effects of thermal challenges on Tb than under LP (Fig. 22.1). For example, Tb_{min} averaged 34.6 ± 0.3 °C at 12 °C under SP exposure and 35.9 ± 0.2 °C under LP exposure. At 34 °C, Tb_{min} of animals averaged 36.7 ± 0.3 °C under SP exposure and 36.6 ± 0.1 °C under LP exposure.

Both H_{decr} and H_{min} were affected by the different thermal exposures ($F_{2,23}$ = 4.7, $P < 0.05$ and $F_{2,23}$ = 3.1, $P < 0.06$, respectively). The occurrence of Tb_{min} was delayed after cold exposure in animals under LP (−156 ± 36 min vs. −209 ± 30 min, respectively), but not under SP (−83 ± 13 min vs. −84 ± 14 min, for 12 °C and 25 °C, respectively). At 34 °C, H_{min} was delayed, whatever the season. The effects of

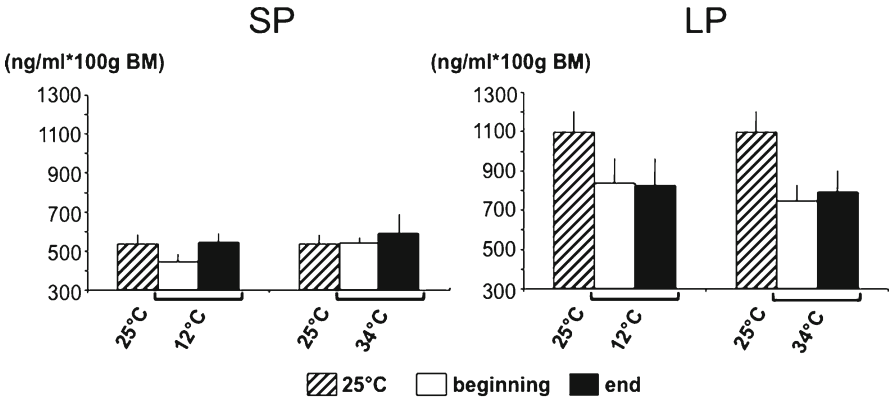


Fig. 22.2 IGF-1 plasma levels (mean + SEM, ng/ml × 100 g BM) observed in adult mouse lemurs acclimated to short (SP, *left*) and long (LP, *right*) photoperiods and after 2 days (short-term) and 9 days (long-term) exposure to 12 and 34 °C

thermal treatments on H_{decr} were photoperiod dependent ($F_{1,23} = 7.8$, $P < 0.05$). The timing of Tb decrease was advanced under both cold (146 ± 21 min vs. 67 ± 15 min) and warm (146 ± 21 min vs. 60 ± 23 min) exposures in SP acclimated animals, whereas no effect of Ta was observed under LP (cold: 51 ± 14 min vs. 47 ± 14 min; warm: 51 ± 14 min vs. 74 ± 22 min). Finally, H_{decr} occurred earlier in animals under SP than LP exposure, especially at 25 and 12 °C.

Effect of Photoperiod on IGF-1 Levels

IGF-1 levels were affected by thermal treatments ($F_{4,40} = 6.1$, $P < 0.001$), photoperiod ($F_{1,10} = 8.1$, $P < 0.05$), and by the interaction between these two factors ($F_{4,40} = 3.1$, $P < 0.05$), as attested by Fig. 22.2. Compared with control levels at Ta = 25 °C (537 ± 48 ng/ml × 100 g BM), cold exposure induced a short-term decrease of IGF-1 levels in animals under SP (444 ± 42 ng/ml × 100 g BM) and a return to reference values after 9 days of cold exposure (543 ± 48 ng/ml × 100 g BM). Exposure to 34 °C induced a slight increase in IGF-1 levels (short term: 541 ± 30 ng/ml × 100 g BM; long term: 592 ± 92 ng/ml × 100 g BM). Under LP exposure, control IGF-1 levels (1,098 ± 109 ng/ml × 100 g BM) were higher than those measured under SP. Whatever the thermal exposure, IGF-1 levels decreased relative to control levels but always remained higher than those observed under SP (Fig. 22.2).

Discussion

The thermal gradient study provided insights into the influence of photoperiod on thermoregulation in gray mouse lemurs. SP acclimation enhanced behavioral adjustments, as mouse lemurs clearly exhibited a daily rhythm between Tas explored

during the night and Tas selected for diurnal rest. In particular, mouse lemurs acclimated to SP chose warm Tas for the whole resting period, in accordance with the low minimal Tas observed in the Malagasy winter. Moreover, the Tas chosen for the resting phase (26.0 ± 1.6 °C) are in a range ensuring minimal energy expenditure and evaporation (Aujard et al. 1998). During the night, Tas selected were lower than during the day, allowing the animals to avoid hyperthermia during the active phase. These choices were not made by mouse lemurs acclimated to LP, suggesting that these animals were physiologically prepared for a narrower Ta range, similar to that observed in the Malagasy summer. The physiological state and, particularly, sex steroid hormone levels may explain these differences in thermoregulatory capacities. Mouse lemurs exhibit strong seasonal variations in sex hormone levels (Perret 1992) which are known to enhance the production of body heat (Hampl et al. 2006). Under SP, behavioral thermoregulation may be necessary to maintain normothermia in order to compensate for endocrine depression of thermogenesis effectors.

During cold exposure, thermoregulatory mechanisms, which both produce and retain body heat, are strongly enhanced. Under both SP and LP conditions, animals had lower Tbs after cold exposure. However, the differences in Tb observed between animals exposed to 25 and 12 °C were more pronounced under SP. Moreover, the temporal organization of daily hypothermia was affected differently by photoperiod. Under SP there was a less marked effect on the timing of hypothermia than under LP. Thus cold exposure may evoke different thermogenic processes depending on the photoperiod. Under SP exposure, corresponding to the winter season during which food resources are scarce, the best energy compromise is to avoid the high cost of normothermia maintenance by undergoing daily torpor (Geiser and Ruf 1995). We propose that SP-acclimated mouse lemurs are physiologically prepared to respond efficiently to the cold. The short-term decrease and long-term increase in IGF-1 levels may be the consequence of the peripheral recruitment of endocrine parameters for BAT activation, as indicated by studies of rodents (Florez-Duquet et al. 1998), followed by an increase in the peripheral synthesis of growth factors for BAT (Duchamp et al. 1997). Animals exposed to LP would benefit from a physiological state providing multiple thermogenic processes, such as high sex steroid endocrine levels (Perret 1992), as observed for IGF-1 in this study. This seasonal response may allow LP-acclimated animals to respond efficiently to cold, even when they are not physiologically prepared for it. However, the temporal organization of hypothermia seems more affected by LP than by SP, which may reflect disturbances induced by unpredictable thermal exposure. Our results from the warm exposure study support this conclusion. Under SP, when high temperatures were not expected, the rise in Tb was greater between 25 and 34 °C than in animals acclimated to LP. Since LP mimics summer, LP-acclimated animals are probably better prepared to face heat stress by promoting thermolysis, i.e., losing body heat and reducing sources of thermogenesis. This is reflected in decreased IGF-1 levels in LP animals exposed to warmth. Under SP, these endocrine levels increased very slowly, but there was no evidence for an inappropriate endocrine response induced by stress such as observed in pigs (Carroll et al. 1999).

Conclusion

Our results indicate that acclimation to a given photoperiod, either winter-like SP or summer-like LP, confers different physiological characteristics that condition the animals' behavioral and physiological responses to thermal challenges. With respect to observed variation in IGF-1 levels between SP and LP exposed animals, we propose that IGF-1 plays a major role in cold-associated responses (enhanced nonshivering thermogenesis) as well as during heat challenge (decreased thermogenesis).

References

Aujard F, Vasseur F (2001) Effect of ambient temperature on the body temperature rhythm of male gray mouse lemurs (*Microcebus murinus*). Int J Primatol 22:43–56

Aujard F, Perret M, Vannier G (1998) Thermoregulatory responses to variations of photoperiod and ambient temperature in the male lesser mouse lemur: a primitive or an advanced adaptive character? J Comp Physiol B 168:540–548

Aujard F, Seguy M, Terrien J, Botalla R, Blanc S, Perret M (2006) Behavioral thermoregulation in a non human primate: effects of age and photoperiod on temperature selection. Exp Gerontol 41:784–792

Carroll JA, Buonomo FC, Becker BA, Matteri RL (1999) Interactions between environmental temperature and porcine growth hormone (pGH) treatment in neonatal pigs. Domest Anim Endocrinol 16:103–113

Duchamp C, Burton KA, Geloen A, Dauncey MJ (1997) Transient upregulation of IGF-I gene expression in brown adipose tissue of cold-exposed rats. Am J Physiol 272:E453–E460

Florez-Duquet M, Horwitz BA, McDonald RB (1998) Cellular proliferation and UCP content in brown adipose tissue of cold-exposed aging Fischer 344 rats. Am J Physiol 274:R196–R203

Geiser F, Ruf T (1995) Hibernation versus daily torpor in mammals and birds: physiological variables and classification of torpor patterns. Physiol Zool 68:935–966

Génin F & Perret M (2000) Photoperiod-induced changes in energy balance in gray mouse lemurs. Physiol Behav 71(3–4):315–321

Génin F, Nibbelink M, Galand M, Perret M, Ambid L (2003) Brown fat and nonshivering thermogenesis in the gray mouse lemur (*Microcebus murinus*). Am J Physiol 284:R811–R818

Hampl R, Starka L, Jansky L (2006) Steroids and thermogenesis. Physiol Res 55:123–131

Kenney WL, Munce TA (2003) Aging and human temperature regulation. J Appl Physiol 95:2598–2603

Perret M (1992) Environmental and social determinants of sexual function in the male lesser mouse lemur (*Microcebus murinus*). Folia Primatol 59:1–25

Perret M, Aujard F (2001) Regulation by photoperiod of seasonal changes in body mass and reproductive function in gray mouse lemurs (*Microcebus murinus*): differential responses by sex. Int J Primatol 22:5–24

Seguy M, Perret M (2005) Factors affecting the daily rhythm of body temperature of captive mouse lemurs (*Microcebus murinus*). J Comp Physiol B 175:107–115

R Development Core T (2007) R: a language and environment for statistical computing. (R Foundation for Statistical Computing, Vienna, Austria)

Chapter 23
Spoilt for Choice: Selection of Hibernacula by *Cheirogaleus medius*

Kathrin H. Dausmann

Abstract Animals maximize fitness by choosing their surroundings, including shelters for resting phases. *Cheirogaleus medius* is a small, nocturnal Malagasy lemur that hibernates in tree holes for up to 7 months a year. I compared certain characteristics of tree holes used during the active season with those used during the hibernation season to assess their relative effectiveness in reducing energy expenditure and predation risk. The tree holes chosen as hibernacula only differed from those used for diurnal rest in their tendency to be located in larger trees. Large, well-insulated trees would allow a better controlled pattern of energy expenditure in hibernating animals rather than decreasing total amounts of energy expended.

Resume Les animaux maximisent leur fitness en choisissant des micro-environnements tels que les gites de repos. *Cheirogaleus medius* est un petit lémurien qui hiberne dans des trous d'arbre pendant des périodes qui peuvent atteindre sept mois par an. J'ai comparé certaines caractéristiques des trous d'arbres utilisés pendant la saison d'activité à ceux utilisés pendant la saison d'hibernation afin d'évaluer leur efficacité à réduire la dépense d'énergétique et éviter les prédateurs. Les trous d'arbre choisis pour hiberner ne diffèrent de ceux utilisés comme site de repos diurne que par le fait qu'ils sont généralement trouvés dans de plus grands arbres. Les grands arbres bien isolés thermiquement permettraient une organisation mieux contrôlée de la dépense énergétique, plutôt qu'une diminution de celle-ci.

K.H. Dausmann (✉)
Department of Ecology and Conservation, University of Hamburg, Hamburg, Germany
e-mail: kathrin.dausmann@uni-hamburg.de

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_23,

Introduction

Selecting a suitable shelter for resting is crucial for the survival of most animals and may involve burrows in the ground, nests, tree holes, or other structures. Shelters may afford protection from predators (Christian and Tracy 1984; Day and Elwood 1999; Singhal et al. 2007; Biebouw et al. 2009), climatic extremes (Aquino and Encarnación 1986; Anderson 1998) and/or other adversities, or facilitate access to foraging sites (Chapman 1989; Day and Elwood 1999; Hankerson et al. 2007). However, the animals' requirements are likely to vary with the seasons (Christian and Tracy 1984). If potential sites are abundant, animals should choose those that best secure survival, e.g., minimize energy expenditure and predation risk.

Fat-tailed dwarf lemurs (*Cheirogaleus medius*) are small (130–280 g), nocturnal primates of western Madagascar. They live in monogamous family groups (Fietz 1999) and are unique among primates in that they hibernate for up to 7 months during the cold dry austral winter, when food and water are scarce (Petter 1978; Dausmann et al. 2004; Fietz and Dausmann 2006). Daily rest and hibernation take place in tree holes, either alone or with members of the family group (Dausmann et al. 2005). These shelters differ from the hibernacula used by temperate and arctic hibernators (i.e., deep burrows or caves) in having more variable physical properties such as insulation and height above ground. Since the choice of hibernaculum may be crucial to survival, I aimed to clarify whether *C. medius* use different kinds of tree holes to rest during the diurnal phase of the active period and during hibernation, and what factors are decisive in their choice of hibernacula. I tested two hypotheses:

Energy conservation. Energy is limited for a hibernator. During hibernation, metabolic regulation is considerably reduced, and body temperature is determined exogenously. Depending on the insulation capacities of a tree hole, which damp ambient temperature (T_a) fluctuations to a greater or lesser extent, body temperature (T_b) patterns may range from very stable to highly fluctuating (>20 °C per day) (Dausmann et al. 2004, 2005, 2009). Well-insulated tree holes confer relatively stable T_as, but force animals to warm up actively during arousal, increasing metabolic costs. In contrast, badly insulated tree holes force animals to increase their metabolic rates by remaining normothermic but allow cheap, passive warming-up.

Predator avoidance. A drawback of hibernation is the loss of defensive capacity through immobility, and tree holes used as hibernacula should afford effective antipredator protection. Predators of *C. medius* include raptors (Madagascar harrier hawk, *Polyboroides radiatus*; Madagascar buzzard, *Buteo brachypterus*; Madagascar long-eared owl, *Asio madagascariensis*), mammals (fossa, *Cryptoprocta ferox*; narrow-striped mongoose, *Mungodictis decemlineata*), and snakes (Madagascar ground boa, *Acrantophis madagascariensis*; Madagascar tree boa, *Sanzinia madagascariensis*; Malagasy cat-eyed snake, *Madagascarophis colubrinus*).

Materials and Methods

I conducted the study in the Kirindy/CFPF forest, a dry deciduous forest near the west coast of Madagascar. Animals were caught with Sherman live traps, injected with subcutaneous identification transponders (Trovan, EURO I.D. Usling GmbH, Weilerswist, Germany), and released in the late afternoon of the capture day at the capture site. Selected animals were equipped with radio-collars (4 g TW-4 button cell tags, Biotrack Ltd., Wareham, UK). Sleeping sites and sleeping group compositions of the radio-collared individuals were checked almost daily during the animals' diurnal resting phase. I located sleeping sites, identified the tree species, and recorded pertinent data from the trees used. Whenever the sleeping site was accessible from the ground or from a ladder, identities and exact locations of the animals were additionally checked with the transponder reading system.

Forty-four adult animals (26 males and 18 females) were followed over 3 years (some over several research seasons). In total, 1,859 sleeping site usages were observed during the rainy season (December–March), 3,032 during the dry season (May–August), and, 602 during the April transition period. Only holes that had been used more than five times during the respective seasons were included in the analyses, to exclude those sites that were occupied occasionally and may have proved inadequate.

To test the energy conservation hypothesis, I measured the height and diameter at breast height (DBH) of the tree, both indices of age and general size, and scored the degree of ambient shading by surrounding vegetation (little, medium, and complete). Wherever frequently used holes were accessible, I used temperature loggers (thermochron i-buttons, Dallas Semiconductor, USA) to measure T_a and tree hole temperature (T_{tree}). T_a loggers were installed on the southern side of the tree at the height of the hole and covered from direct sun with a white roof. T_{tree} loggers were placed inside the holes about 10 cm from the animals. Temperatures were recorded continuously every 20 or 30 min during the coldest months (May–August). To assess insulation capacities, I calculated an insulation index for each tree hole (mean $|T_a - T_{tree}|$).

I estimated the capacity of a hole to afford protection against predator attacks from physical parameters of the trees and resting holes pertaining to predator access. These included (1) condition of the tree or branch housing the hole (dead or alive), (2) number of entrances to the hole, (3) size of the largest entrance to the hole, (4) height of the lowest entrance above ground, and (5) height of the animal above ground within the hole.

Results

Tree Species Used as Sleeping Sites

I identified 148 different holes used as sleeping sites by 44 *C. medius* individuals. Across all seasons, of the 120 tree species found in the Kirindy/CFPF forest large enough to house dwarf lemurs (DBH > 10 cm), resting sites were found only in 31

species, reflecting nonrandom selection of tree species ($\chi^2 = 488.7$; df = 5, $P < 0.001$). Further, 69.3 % of all sleeping sites were distributed among only seven tree species (Fig. 23.1). Comparing between seasons, tree species used also differed significantly ($\chi^2 = 17.45$; df = 6; $n_{act} = 88$, $n_{hib} = 21$; $P < 0.01$; Fig. 23.2). Fewer species (15 spp.) were used during hibernation than during the active period (31 spp.), with some species used only during the active period but none used exclusively for hibernation.

Characteristics of Hibernacula

Each *C. medius* family used 9.6 ± 2.4 ($n = 11$) different tree holes within their territories during the active period but only 2.9 ± 1.1 ($n = 10$) as hibernacula. Of the latter, 36.4 % were not used during the active period and were used exclusively as hibernacula. The same hibernacula were often used in several hibernation periods. Only 14.4 % of holes were used during both periods and were excluded from the analyses to clarify potential differences, as were tree holes used during the transition period of April.

The tree species used predominantly during the hibernation period, *Commiphora arofy*, had a DBH of 48.3 ± 13.1 cm ($n = 25$) and is one of the largest trees in the forest. The species used most often for resting during the active period had lower DBHs of 27.7 ± 11.5 cm (*Brachylaena microphylla*; $n = 23$), 18.6 ± 3.4 cm (*Securinega seyrigii*; $n = 20$), and 25.0 ± 5.6 cm (*Strychnos madagascariensis*; $n = 12$). On average, trees used as sleeping sites during hibernation had a DBH of 41.4 ± 19.7 cm and a height of 15.0 ± 4.7 m. They were both significantly larger in diameter and taller than trees used during the active period (DBH = 26.5 ± 5.6 cm; *U*-test: $n_{act} = 88$, $n_{hib} = 21$; $Z = -3.4$; $P < 0.01$; height = 11.2 ± 4.7 m; *U*-test: $n_{act} = 88$, $n_{hib} = 21$; $Z = -3.3$; $P < 0.01$).

Energy Conservation Hypothesis

I could not determine T_{tree} of *C. arofy* directly, as the heights of the tree holes and thickness of the walls made it impossible to insert temperature loggers. Instead, I analyzed the general relationship between DBH and insulation indices; the larger the tree, the better their holes were insulated (Spearman rank correlation: $n = 38$, $r_s = 0.78$, $P < 0.01$; Fig. 23.3). Average insulation indices per tree ranged from 0.27 °C to 5.93 °C, with maximal $T_a - T_{tree}$ reaching 19.7 °C. There was no significant difference between tree holes used during the active and hibernation periods with regard to shading (χ^2-test: $n_{act} = 75$, $n_{hib} = 17$; $\chi^2 = 2.2$; $P > 0.05$).

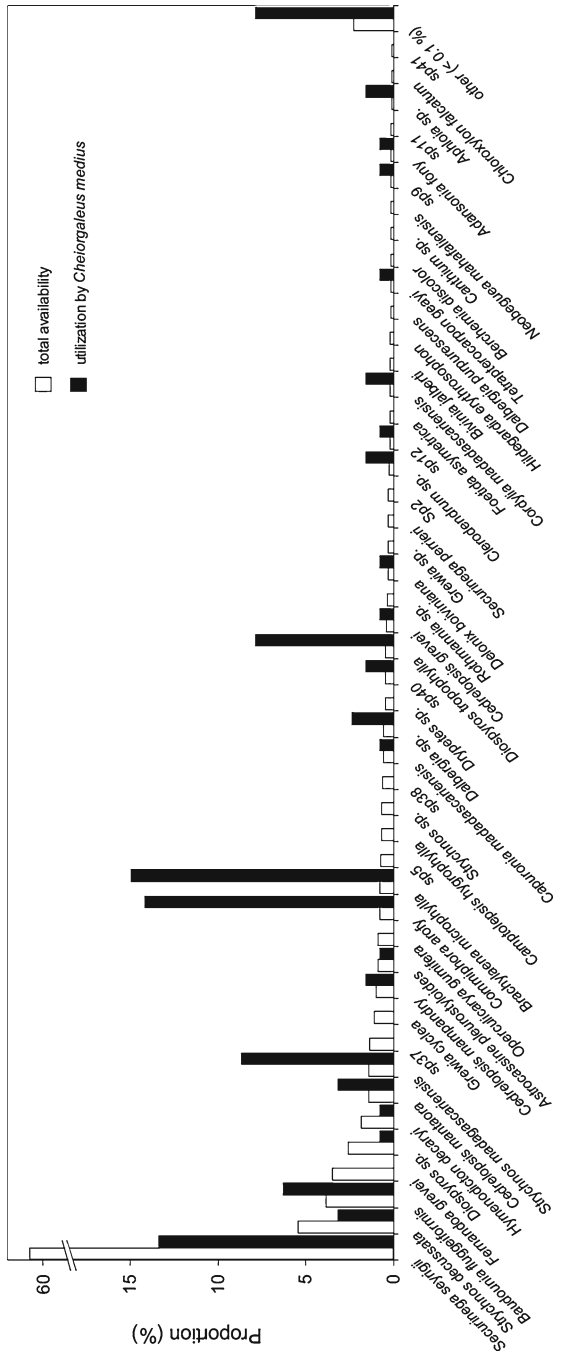


Fig. 23.1 Comparison of the proportions of tree species in the Kirindy/CFPF forest with a DBH > 10 cm and those with tree holes used by *Cheirogaleus medius* as resting sites (active and hibernation period)

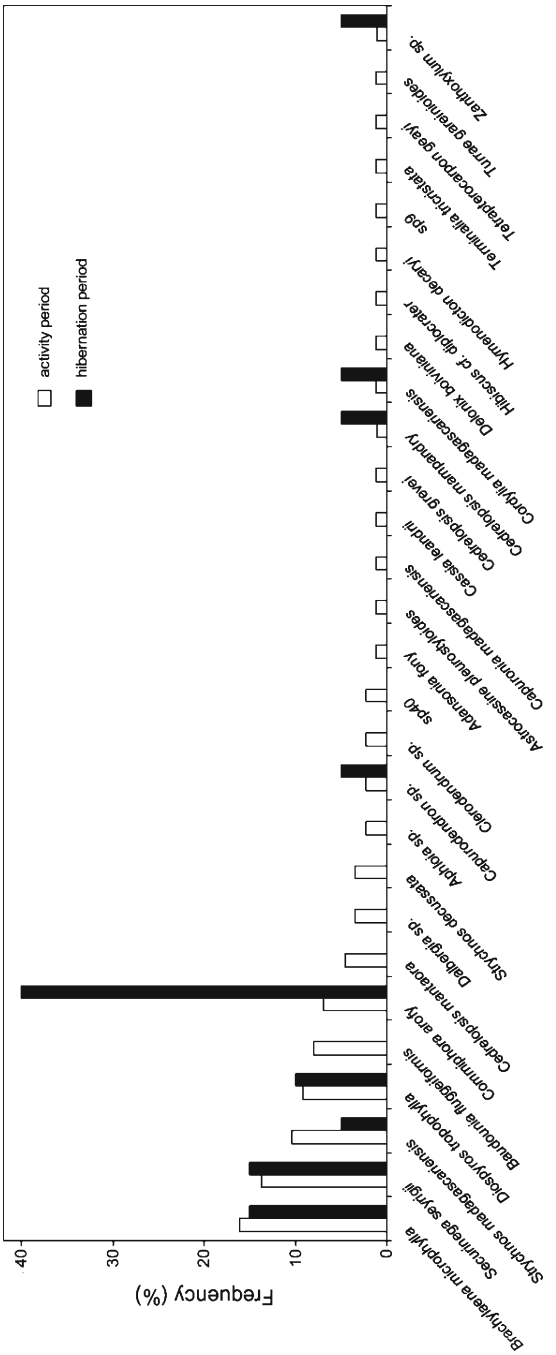


Fig. 23.2 Frequencies of tree species with tree holes used by *Cheirogaleus medius* as resting sites either exclusively during the active period or during the hibernation period

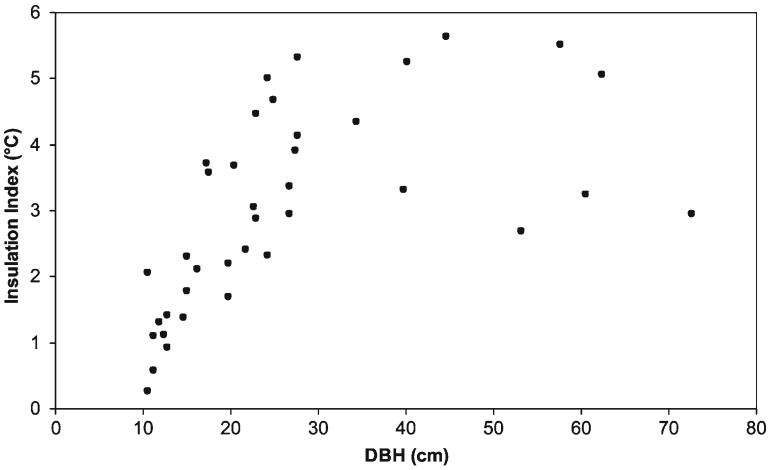


Fig. 23.3 Relationship between diameter at breast height (DBH) of the trees and average insulation index of tree holes (mean $|T_a - T_{tree}|$) used by *Cheirogaleus medius* as resting sites ($R^2 = 0.56$)

Table 23.1 Parameters of tree holes related to protection from predators for resting animals

Variables tested	Active period	*N*	Hibernation period	*n*
Tree/branch dead	47%	73	40%	15
Number of entrances	1.5 ± 1.1	48	1.1 ± 0.3	12
Minimal entrance size	6.3 ± 3.6 cm	40	5.9 ± 2.4 cm	10
Height of entrance	4.7 ± 2.5 m	57	5.8 ± 2.6 m	14
Height of animal	4.5 ± 2.7 m	78	4.8 ± 2.5 m	19

Only holes used exclusively during either the active or the hibernation period are included. *N* varies because of differences in accessibility of the tree holes, but this limitation is consistent across seasons. There are no significant differences

Predation Avoidance Hypothesis

There were no significant differences between holes used in the active and hibernation periods (χ^2- and *U*-tests: $P > 0.05$; Table 23.1) in any of the parameters measured, although all values point in the direction that would have been expected if protection from predators were important in hibernaculum choice.

Discussion

Despite the availability of numerous tree species large enough to afford shelter in tree holes, *C. medius* chose nesting sites in only ~25 % of them throughout the year. The number of different sleeping sites used by fat-tailed dwarf lemurs (148 sites

used by 44 individuals) is similar to that observed in other cheirogaleids living in the same or similar habitats [*Microcebus murinus*: 51 sites used by 12 individuals (Schmid 1998), 50 sites used by 10 individuals (Radespiel et al. 1998); *M. griseorufus*: 151 sites used by 26 individuals (Génin 2010)], as well as some other lemurs in the Kirindy/CFPF forest that rest in tree holes [*Lepilemur ruficaudatus*: 97 sites used by 19 individuals (Zinner et al. 2003)]. This begs the question why usage rate is so different in sympatric *Phaner pallescens* (300 sites used by 19 individuals; Schülke and Kappeler 2005).

When the hibernation period approaches, most *C. medius* retreat into tree holes not used previously during the active period. Almost 40 % of the tree holes used as hibernacula is used exclusively for this purpose. Every family group occupies fewer hibernacula than diurnal resting sites, and the same hibernacula are used over several years, indicating that good quality hibernacula are limited. This is supported by the observation that individuals that have only recently become territory holders may not hibernate within their new territories but may use tree holes at several territories' distance (unpublished data). *C. medius* do not usually leave their defended territories (Fietz 1999), and these individuals may return to their natal territories for hibernation despite potential territorial conflicts along the way (which become less intense as the hibernation season approaches), because this is safer than remaining in their new territories where they are not yet familiar with suitable hibernacula.

What differentiates a good hibernaculum from a regular tree hole used during the active period? Neither the energy expenditure hypothesis nor the predator avoidance hypothesis provides a complete explanation. Well-insulated tree holes allow animals to maintain relatively constant body temperature but force individuals to use expensive, active warming-up for arousal. By contrast, in poorly insulated tree holes, increased metabolic rates caused by higher daytime temperatures (passive warming-up) are counterbalanced by lower metabolic rates during the cool hours of the night. These strategies are energetically equivalent, at around 30 kJ energy expenditure per day (~70 % energy savings compared with normothermia; Dausmann et al. 2009). Larger trees with better insulation capacities are preferred by *C. medius* during hibernation, implying that the animals prefer relatively constant temperatures during this time. If it is not the total amount of energy saved, it may be the pattern of energy expenditure that is decisive for hibernacula choice. Cooling down and heating up rapidly is always a challenge for an organism due to problems in tissue perfusion and provisioning of organelles (Carey et al. 2003). This factor could render the maintenance of constant body temperature over longer periods advantageous for hibernators.

None of the parameters relating to predator access was significantly different between the trees chosen during the active and hibernation periods. However, this does not mean that predation pressure was negligible; rather, predator avoidance is probably equally important in both seasons, as confirmed by the species' high mortality rates (about 20 % per year; Fietz and Dausmann 2003).

Interpretation is complicated by the fact that the data collected to distinguish the two hypotheses are not independent. While larger DBH measurements may describe trunks that afford better insulation to hibernators, they also describe certain

preferred tree species like *Commiphora arofy*, the bark of which has a particularly smooth surface which may prove difficult for predators like snakes and mammals to climb. Many Malagasy trees, including *C. arofy*, are known for their strong scent which may conceal the presence of hibernators from predators or deter parasites.

Clearly, the criteria for hibernacula selection by *C. medius* are complex and quite flexible, as dwarf lemurs survive hibernation in many types of tree holes. Even though the characteristics of the tree hole used for hibernation dramatically influence the patterns of body temperature, metabolic rate, and thus energy expenditure, dwarf lemurs can switch from one mode to the other not only between seasons but also within a hibernation season from one day to the next when they change sleeping sites. This flexibility may help the animals to escape the fact that *C. arofy* is not only *their* preferred tree during hibernation but also the preferred tree of wood cutters.

Acknowledgments I thank the Commission Tripartite of the Malagasy Government, the Laboratoire de Primatologie et des Vertébrés de l'Université d'Antananarivo, the Parc Botanique et Zoologique de Tsimbazaza, the Ministère pour la Production Animale, and the Département des Eaux et Forêts for permits to work in Madagascar, and the Centre de Formation Professionnelle Forestière de Morondava for their hospitality and permission to work on their concession. I thank the German Primate Centre and P. Kappeler for the opportunity to work at the field station, and the Deutscher Akademischer Austauschdienst and Deutsche Forschungsgemeinschaft for financial aid. Thanks to B. Lewis for holding the other end of the measuring tape. All experiments comply with Malagasy and German legislation.

References

Anderson JR (1998) Sleep, sleeping sites, and sleep-related activities: awakening to their significance. Am J Primatol 46:63–75

Aquino R, Encarnación F (1986) Characteristics and use of sleeping sites in *Aotus* (Cebidae, Primates) in the Amazon lowlands of Peru. Am J Primatol 11:319–331

Biebouw K, Bearder S, Nekaris A (2009) Tree hole utilisation by the hairy-eared dwarf lemur (*Allocebus trichotis*) in Analamazaotra Special Reserve. Folia Primatol 80:89–103

Carey HV, Andrews MT, Martin SL (2003) Mammalian hibernation: cellular and molecular responses to depressed metabolism and low temperature. Physiol Rev 83:1153–1181

Chapman CA (1989) Spider monkey sleeping sites – use and availability. Am J Primatol 18:53–60

Christian KA, Tracy CR (1984) Physiological and ecological consequences of sleeping-site selection by the Galapagos land iguana (*Conolophus pallidus*). Ecology 65:752–758

Dausmann KH, Glos J, Ganzhorn JU, Heldmaier G (2004) Hibernation in a tropical primate. Nature 429:825–826

Dausmann KH, Glos J, Ganzhorn JU, Heldmaier G (2005) Hibernation in the tropics: lessons from a primate. J Comp Physiol B 175:147–155

Dausmann KH, Glos J, Heldmaier G (2009) Energetics of tropical hibernation. J Comp Physiol B 179:345–357

Day RT, Elwood RW (1999) Sleeping site selection by the golden-handed tamarin *Saguinus midas midas*: the role of predation risk, proximity to feeding sites, and territorial defence. Ethology 105:1035–1051

Fietz J (1999) Monogamy as a rule rather than exception in nocturnal lemurs: the case of the fat-tailed dwarf lemur, *Cheirogaleus medius*. Ethology 105:259–272

Fietz J, Dausmann KH (2003) Costs and potential benefits of parental care in the nocturnal fat-tailed dwarf lemur (*Cheirogaleus medius*). Folia Primatol 74:246–258

Fietz J, Dausmann KH (2006) Big is beautiful: fat storage and hibernation as a strategy to cope with marked seasonality in the fat-tailed dwarf lemur (*Cheirogaleus medius*). In: Gould L, Sauther ML (eds) Lemurs: ecology and adaptation. Springer, New York, pp 97–110

Génin F (2010) Who sleeps with whom? Sleeping site selection in *Microcebus griseorufus*. J Mammal 91:942–951

Hankerson SJ, Franklin SP, Dietz JM (2007) Tree and forest characteristics influence sleeping site choice by golden lion tamarins. Am J Primatol 69:976–988

Petter J-J (1978) Ecological and physiological adaptations of five sympatric nocturnal lemurs to seasonal variations in food production. In: Chivers DJ, Herbert J (eds) Recent advances in primatology. Academic, New York, pp 211–223

Radespiel U, Cepok S, Zietemann V, Zimmermann E (1998) Sex-specific usage of sleeping sites in grey mouse lemurs (*Microcebus murinus*) in northwestern Madagascar. Am J Primatol 46:77–84

Schmid J (1998) Tree holes used for resting by gray mouse lemurs (*Microcebus murinus*) in Madagascar: insulation capacities and energetic consequences. Int J Primatol 19:797–808

Schülke O, Kappeler PM (2005) So near and yet so far: territorial pairs but low cohesion between pair partners in a nocturnal lemur, *Phaner furcifer*. Anim Behav 65:331–343

Singhal S, Johnson MA, Ladner JT (2007) The behavioral ecology of sleep: natural sleeping site choice in three *Anolis* lizard species. Behaviour 144:1033–1052

Zinner D, Hilgartner RD, Kappeler PM, Pietsch T, Ganzhorn JU (2003) Social organization of *Lepilemur ruficaudatus*. Int J Primatol 24:869–888

Chapter 24
Seasonality and Behavioral Energy Strategies in *Microcebus berthae* and *M. murinus*

Melanie Dammhahn and Peter M. Kappeler

Abstract To survive and reproduce successfully in highly seasonal regions, animals must balance their energy budgets during lean seasons. We conducted a comparative study of two sympatric mouse lemur species to identify species-specific energy saving strategies for coping with seasonality and evaluated their consequences for female fitness. Since August 2002 we captured, marked and recaptured individuals of coexisting populations of *Microcebus berthae* and *M. murinus* in Kirindy Forest and recorded activity by direct observations of radio-collared females. The species differed in their seasonal activity patterns: female *M. berthae* maintained high activity levels throughout the year, whereas female *M. murinus* largely ceased activity during the cold dry season. In *M. berthae*, low survival restricted female reproductive potential. Consequently, females maximized the condition in which they entered the reproductive season. In contrast, *M. murinus* females maximized survival but entered the reproductive season in poor condition. Thus, mouse lemur species subjected to the same environmental conditions show different species-specific behavioral energy strategies to cope with pronounced seasonality.

Resume Pour survivre et se reproduire avec succès and des régions très saisonnières, les animaux devraient équilibrer leur budget énergétique pendant la saison difficile. Nous avons conduit une étude comparative portant sur deux espèces sym-

M. Dammhahn (✉)
Abteilung Verhaltensökologie & Soziobiologie, Deutsches Primatenzentrum,
Kellnerweg 4, 37077 Göttingen, Germany
e-mail: mdammha@gwdg.de

P.M. Kappeler
Abteilung Verhaltensökologie & Soziobiologie, Deutsches Primatenzentrum,
Kellnerweg 4, 37077 Göttingen, Germany

Abteilung Soziobiologie/Anthropologie, Universität Göttingen,
Kellnerweg 6, 37077 Göttingen, Germany
e-mail: pkappel@gwdg.de

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_24,

patriques de microcèbes afin d'identifier deux stratégies spécifiques d'économie d'énergie utilisées pour faire face à la saisonnalité, et évaluer leurs conséquences sur le fitness des femelles. Depuis août 2002, nous avons capturé, marqué et recapturé des individus dans deux populations syntopiques de *Microcebus berthae* and *M. murinus*, dans la forêt de Kirindy, et observé directement des femelles suivies par radio-pistage. Les deux espèces ont des rythmes d'activité saisonnière différents : les femelles *M. berthae* maintiennent un niveau d'activité élevé tout le long de l'année, alors que les femelles *M. murinus* cessent pratiquement toute activité pendant la fraiche saison sèche. In *M. berthae*, la faible survie réduit la durée de la carrière reproductive des femelles. En conséquence, les femelles maximisent leur condition physique pendant la période du début de la saison de reproduction. Par contre, les femelles *M. murinus* maximisent leur survie, mais commencent la reproduction en moins bonnes conditions. Donc, ces deux espèces de microcèbes, qui font face aux mêmes conditions environnementales, utilisent des stratégies énergétiques saisonnières différentes.

Introduction

Small endothermic animals face high energetic costs in seasonally cold or unproductive environments and have evolved behavioral and physiological adaptations to overcome these energetic constraints. Small mammals with restricted mobility typically reduce energy expenditure during climatically or energetically unfavorable times (Lovegrove 2005), which may involve reducing body temperature and metabolism for short or extended periods (daily torpor and hibernation, respectively); the latter is usually preceded by a period of accumulating fat reserves (Geiser 2004). Under highly seasonal conditions, reproduction may be traded off against maintenance requirements during the lean part of the year (Schmid and Kappeler 2005; Brown and Sibly 2006), but maximizing reproductive success requires energy balancing strategies that allow both survival and successful reproduction. Because female mammals typically invest more energy directly in each offspring than males, the factors determining female fitness [birth rate, length of reproductive life, and survival rate of offspring (van Schaik 1989)] are strongly influenced by a female's energetic constitution (Speakman 2008).

The smallest primate species live in highly seasonal environments and show variable energy strategies (Schülke and Ostner 2007). While physiological and behavioral strategies have been intensively studied in primates (reviewed in Schmid and Kappeler 2005; Schülke and Ostner 2007), their implications for reproductive performance remain largely unknown. In this study, we aimed (1) to describe behavioral strategies for coping with pronounced seasonality in two strepsirhine species and (2) to evaluate the consequences of potential species-specific strategies for female fitness. Specifically, we compared adaptations to cope with seasonality in 33 g *Microcebus berthae* and 60 g *M. murinus* (Cheirogaleidae) living sympatrically in Kirindy Forest/CNFEREF, one of the larger remaining fragments of the dry

deciduous forests of central western Madagascar. Mouse lemurs there must cope with three main types of environmental stress (1) wide daily temperature fluctuations with nocturnal temperatures as low as 5 °C; (2) a 7-month long dry season and (3) seasonal food scarcity, particularly of fruit and arthropods (Sorg and Rohner 1996; Schmid and Kappeler 2005; Dammhahn and Kappeler 2008b).

In Kirindy both mouse lemur species show only one reproductive cycle per year. The reproductive year of a *M. murinus* female starts with a short mating season in October followed by 2 months gestation, with 1–3 young being born in December/January and nursed for 2 months (Eberle and Kappeler 2002). By March the young are independent, leaving the mothers 4–6 weeks to acquire sufficient body fat to survive the major part of the dry season using daily torpor (Schmid and Kappeler 1998). Although less is known about the life history of *M. berthae*, they apparently follow a similar pattern, with mating starting in November (Dammhahn and Kappeler 2005). Pregnant females have been caught in December [with the exception of one pregnant female caught in April (Schwab 2000)], and juveniles have been trapped in March and April (Dammhahn, unpublished data).

The two species thus face the same environmental constraints and follow similar reproductive schedules. Furthermore, they have similar diets (Dammhahn and Kappeler 2008b, 2010) and are physiologically capable of entering spontaneous daily torpor to reduce energy expenditure when ambient temperatures are low (Schmid et al. 2000; Schmid and Speakman 2000). We investigated whether they exhibit similar behavioral strategies to cope with seasonal energy shortages without compromising their reproductive output.

Methods

Between August 2002 and December 2007, we captured, marked and regularly recaptured individuals of coexisting populations of *M. berthae* and *M. murinus* in a 25-ha study area in Kirindy forest (details in Dammhahn and Kappeler 2008a). The populations consisted of 50–70 *M. murinus* and 30–55 *M. berthae* individuals, for which we obtained monthly body mass and a set of measurements including body size, head width and head length. We equipped 13 *M. berthae* and 17 *M. murinus* females with radio collars (*M. berthae*: 1.8 g, BD-2, Holohil, Canada; *M. murinus*: 2 g, TW4, Biotrack, UK) to enable radio-tracking and focal animal observations. Radio transmitters weighed 5.3 ± 0.04% of the mass of *M. berthae* and 3.4 ± 0.04% of the mass of *M. murinus* individuals, and seasonal body mass changes of radio-collared and non-collared individuals did not differ (Dammhahn, unpublished data). We followed focal animals during their nocturnal activity for 2–4 h before switching to another animal and chose observation times opportunistically but evenly spread between 18:00 and 01:00 for each animal. We observed *M. berthae* for 288 h and *M. murinus* for 340 h, with 10–22 h per focal animal. To analyze seasonal patterns, we defined three periods based on differences in rainfall and food availability (Table 24.1). We categorized 1-min observation intervals as "inactive" [i.e., the focal

Table 24.1 Definitions of seasons used in the analyses

	Wet–dry	Dry	Dry–wet
Description	Transition between wet and dry season	Dry season	Transition between dry and wet season
Time period	March–May	June–September	October–December
Precipitation	Medium (100–450 mm) 20% of annual precipitation	Low (0–30 mm) 2% of annual precipitation	Medium (100–200 mm) 20% of annual precipitation
Resource availability	Fruit high Arthropods high	Fruit low Arthropods low	Fruit low Arthropods high

animal rested with eyes closed or was in a sleeping site (tree hole, leaf nest, between lianas, or branches)] or "active" (i.e., all other activities). We tested for seasonal variation using Kruskal–Wallis tests and differences between species using Mann–Whitney *U*-tests of arcsine transformed % data. We calculated average distances covered per hour, excluding time the individual was inactive, as the sum of all distances between subsequent locations of the subject at successive 1-min intervals, and tested for differences between seasons using the Wilcoxon signed-rank test.

Finally, we explored whether species-specific behavioral energy strategies affected two variables related to female fitness (1) body condition during the reproductive season and (2) survival until the reproductive season. To assess body condition, we fitted linear regression models over all seasons to log-transformed body mass as the dependent variable and log-transformed head width as the independent variable to remove allometric effects. We used head width as a proxy for body size because it can be measured more reliably in anesthetized mouse lemurs than head–body length, and these variables are highly correlated. We then compared female body condition between species for each season using *t*-tests on the residuals from the species-specific regressions. Based on capture–mark–recapture data of 92 *M. murinus* and 59 *M. berthae* females, we calculated the probabilities of apparent survival from before (March–May) to after (September–November) the dry season and compared this probability between species using a Chi-square test.

Results

Species-Specific Behavioral Energy Strategies

M. murinus activity varied seasonally, with almost complete inactivity during the dry season [Kruskal–Wallis, $H(2, n=30)=9.55$, $P<0.01$] (Fig. 24.1). In contrast, *M. berthae* remained active in all seasons [Kruskal–Wallis, $H(2, n=22)=3.30$, n.s.]. The species' activity periods differed both in the dry (Mann–Whitney *U*-test, $n_{Mbe}=12$, $n_{Mmu}=9$, $U=2.0$, $P<0.01$) and in the dry–wet season ($n_{Mbe}=8$, $n_{Mmu}=7$, $U=3.0$, $P<0.05$). *M. berthae* increased locomotor activity and travelled longer path

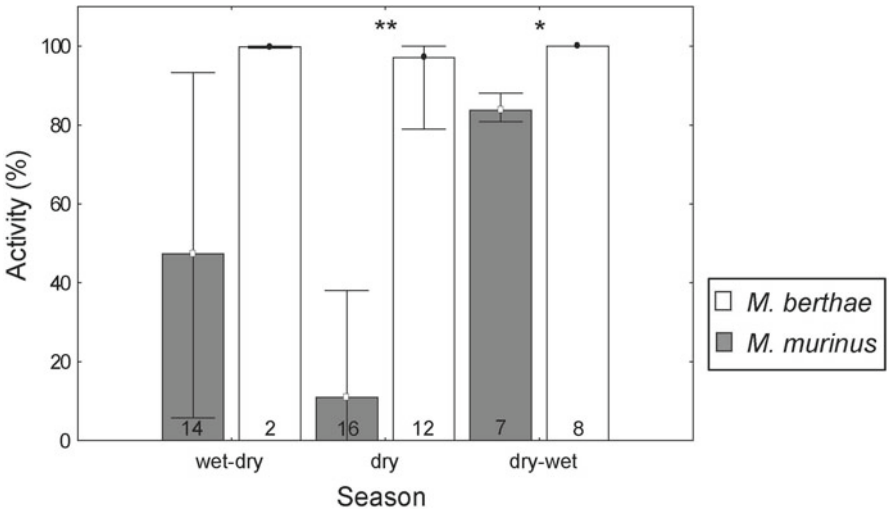


Fig. 24.1 Seasonal variation in activity patterns in *M. berthae* and *M. murinus*. Activity is represented as median (25–75% quartiles) percentages of active 1 min observation intervals during focal observations that were evenly spread between 18:00 and 01:00. Numbers represent sample size of focal individuals. $^{**}P<0.01$, $^{*}P<0.05$ (Mann–Whitney *U*-test with arcsine transformed % data)

lengths during the resource-poor dry season than at the onset of the subsequent wet season (Wilcoxon signed-rank test, $n=8$, $z=2.38$, $P<0.05$). The inactivity of *M. murinus* females precluded the analysis of path lengths for this species. At the end of the wet season, *M. murinus* females spent most time feeding (51%) and lived on their energy reserves in the dry season, indicated by a decrease in body mass related to individual activity level (Spearman rank correlation, $n=14$, $R=0.79$, $P<0.001$). In contrast, *M. berthae* females increased feeding time during the resource-poor dry season to 43% compared with 28% outside this season.

Effects of Species-Specific Behavioral Energy Strategies on Female Reproduction

Seasonal changes in body mass were similar in the two species (Fig. 24.2): females lost weight during the dry season, showed no weight change in the transition from dry to wet season and gained weight during the wet season. At the end of the wet season, *M. murinus* females were in better condition than *M. berthae* females (*t*-test, $n_{Mbe}=7$, $n_{Mmu}=33$, $t=-2.15$, $P=0.038$), whereas they were in similar condition during the dry season (*t*-test, $n_{Mbe}=69$, $n_{Mmu}=45$, $t=-0.45$, $P=0.651$) (Fig. 24.3). At the beginning of the wet season (i.e., the mating season), however, the pattern was reversed and *M. berthae* were in better condition than *M. murinus* (*t*-test, $n_{Mbe}=36$, $n_{Mmu}=70$, $t=4.61$, $P<0.001$). Apparent survival of the dry season was higher for *M. murinus* than *M. berthae* females (*M. murinus*: $P_s=0.77$, $n=92$; *M. berthae*, $P_s=0.52$, $n=59$; $\chi^2=9.95$, $P<0.05$).

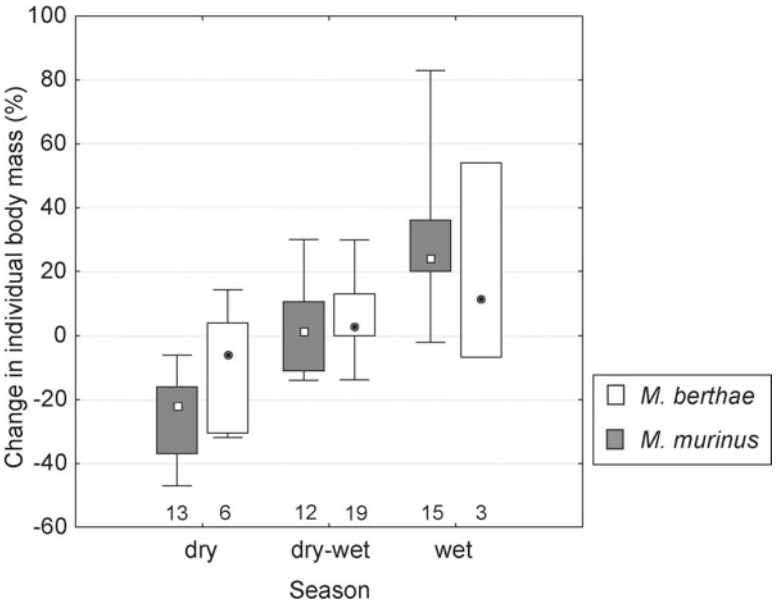


Fig. 24.2 Seasonal changes in individual body mass of female *M. berthae* and *M. murinus*. The *graph* shows medians (25–75% quartiles, min–max) of proportional differences over successive seasons. Numbers at the *bottom* represent sample sizes

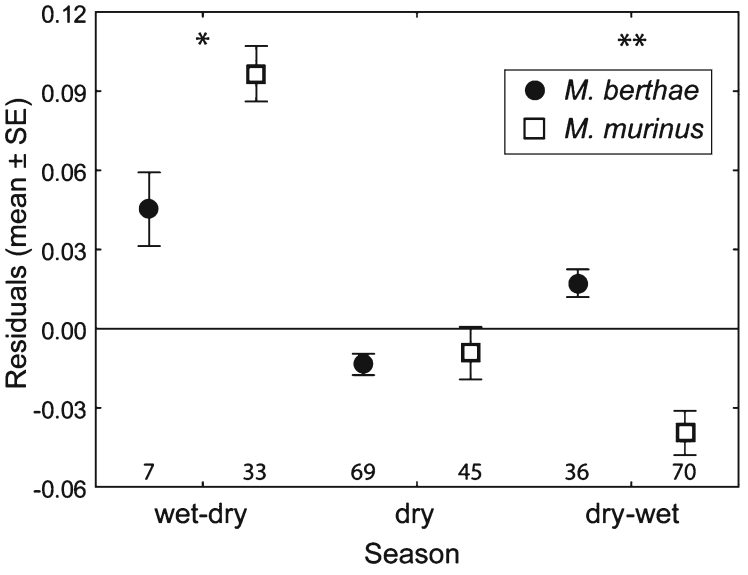


Fig. 24.3 Seasonal mean (±SE) residuals of linear regression models over all seasons by species with log body mass as the dependent variable and log head width as the independent variable. Numbers at the *bottom* represent sample sizes.*$P<0.05$, **$P<0.001$ (*t*-tests)

Discussion

We describe species-specific behavioral strategies for coping with pronounced seasonality in coexisting mouse lemur taxa, which include differences in seasonal activity patterns. *M. murinus* females underwent seasonal fattening and remained largely inactive during the cold, dry season in a state of torpor (Schmid and Kappeler 1998; Schmid 1999; Schmid and Speakman 2000; Rasoazanabary 2006). In contrast, female *M. berthae* remained active throughout the dry season and even increased feeding and ranging activity, a strategy also used by other primates (Hemingway and Bynum 2005). Although *M. berthae* entered spontaneous daily torpor under seminatural conditions (Schmid et al. 2000), they did so only during the day and in the colder half of the night. Female *M. berthae* may not be able to accumulate sufficient fat reserves during the wet season, as indicated by their poor body condition compared with *M. murinus* females. Thus, they managed their energy much like *M. murinus* males, which also combine activity with the use of daily torpor (Schmid and Kappeler 1998; Schmid 1999) but may undergo seasonal fattening (Génin et al. 2005).

M. berthae females had low survival probabilities from one annual reproductive season to the next, limiting their reproductive potential. Females apparently maximized the condition in which they entered the reproductive period, thereby increasing birth and survival rates of offspring. A shift of the mating season from the end of the lean season towards the productive wet season (Dammhahn and Kappeler 2005) might further enhance female condition during pregnancy. The energy strategy used by *M. murinus* females maximized their survival, increasing the females' probabilities of reproducing more than once in their lifetimes. Lahann et al. (2006) demonstrated higher life expectancies for *M. murinus* in seasonal dry forests compared with a less seasonal littoral forest. Although body condition decreased with length of inactivity, female *M. murinus* remained inactive until the onset of the mating season (October) in Kirindy and thus entered pregnancy in a less favorable body condition than *M. berthae* females. In less seasonal habitats females enter the reproductive season with higher body mass and produce 2–3 litters/year (Lahann et al. 2006). Breeding communally (Eberle and Kappeler 2006) might provide *M. murinus* females with an alternative mechanism of enhancing offspring survival (and birth rate) when body condition is less optimal.

Our study highlights the pronounced variability in energy strategies used by members of the Cheirogaleidae (Schülke and Ostner 2007), which exceeds that of other families of small primates (Lorisidae: Müller et al. 1985; Galagidae: Mzilikazi et al. 2006). *M. murinus* females resembled *Cheirogaleus medius*, a true hibernator (Dausmann et al. 2004), behaviorally and physiologically, whereas *M. berthae* resembled mouse lemur species inhabiting more favorable habitats (e.g., *M. ravelobensis* and *M. murinus* in north-western Madagascar, Radespiel 2006) and coexisting *M. murinus* males. Both activity patterns serve to balance energy and ensure survival and reproduction in highly seasonal environments. Comparisons of reproductive success await genetic analyses. Further comparative investigations of the

speciose Cheirogaleidae, combining behavioral and physiological data with long-term monitoring of individual reproductive success in wild populations, will ultimately provide a basis for understanding the impact of energy strategies on fitness.

Acknowledgments We acknowledge the authorization and support of this study by Profs O. Ramilijaona and D. Rakotondravony (Université d'Antananarivo), the Commission Tripartite and the CAFF of the Direction des Eaux et Forêts, the CNFEREF Morondava. We thank Rodin Rasoloarison, Léonard Razafimanantsoa, Tiana Andrianjanahary, Jean-Claude de Beroboka, Bruno Tsiverimana and the Equipe Kirindy for assistance in the field. Financial support was generously provided by DFG (Ka 1082/10-1and2), the Margot Marsh Biodiversity Foundation, DPZ Göttingen and Christian-Vogel-Fond (GfP).

References

Brown JH, Sibly RM (2006) Life-history evolution under a production constraint. Proc Natl Acad Sci USA 103:17595–17599

Dammhahn M, Kappeler PM (2005) Social system of *Microcebus berthae*, the world's smallest primate. Int J Primatol 26:407–435

Dammhahn M, Kappeler PM (2008a) Small-scale coexistence of two mouse lemur species (*Microcebus berthae* and *M. murinus*) within a homogeneous competitive environment. Oecologia 157:473–483

Dammhahn M, Kappeler PM (2008b) Comparative feeding ecology of sympatric *Microcebus berthae* and *M. murinus*. Int J Primatol 29:1567–1589

Dammhahn M, Kappeler PM (2010) Scramble or contest competition over food in solitarily foraging mouse lemurs (*Microcebus* spp.): new insights from stable isotopes. Am J Phys Anthropol 141:181–189

Dausmann KH, Glos J, Ganzhorn JU, Heldmaier G (2004) Hibernation in a tropical primate. Nature 429:825–826

Eberle M, Kappeler PM (2002) Mouse lemurs in space and time: a test of the socioecological model. Behav Ecol Sociobiol 51:131–139

Eberle M, Kappeler PM (2006) Family insurance: kin selection and cooperative breeding in a solitary primate (*Microcebus murinus*). Behav Ecol Sociobiol 60:582–588

Geiser F (2004) Metabolic rate and body temperature reduction during hibernation and daily torpor. Annu Rev Physiol 66:239–274

Génin F, Schilling A, Perret M (2005) Social inhibition of seasonal fattening in wild and captive gray mouse lemurs. Physiol Behav 86:185–194

Hemingway CA, Bynum N (2005) The influence of seasonality on primate diet and ranging. In: Brockman DK, van Schaik CP (eds) Seasonality in primates. Cambridge University Press, Cambridge, pp 57–104

Lahann P, Schmid J, Ganzhorn JU (2006) Geographic variation in populations of *Microcebus murinus* in Madagascar: resource seasonality or Bergmann's rule? Int J Primatol 27:983–999

Lovegrove BG (2005) Seasonal thermoregulation responses in mammals. J Comp Physiol B 175:231–247

Müller EF, Nieschalk U, Meier B (1985) Thermoregulation in the slender loris (*Loris tardigradus*). Folia Primatol 44:216–226

Mzilikazi N, Masters J, Lovegrove BG (2006) Lack of torpor in free-ranging southern lesser galagos *Galago moholi*: ecological and physiological considerations. Folia Primatol 77:465–476

Radespiel U (2006) Ecological diversity and seasonal adaptations of mouse lemurs (*Microcebus* spp.). In: Gould L, Sauther ML (eds) Lemurs: ecology and adaptation. Springer, New York, pp 211–233

Rasoazanabary E (2006) Male and female activity patterns in *Microcebus murinus* during the dry season at Kirindy forest, western Madagascar. Int J Primatol 27:437–463

Schmid J (1999) Sex-specific differences in activity patterns and fattening in the gray mouse lemur (*Microcebus murinus*) in Madagascar. J Mammal 80:749–757

Schmid J, Kappeler PM (1998) Fluctuating sexual dimorphism and differential hibernation by sex in a primate, the gray mouse lemur (*Microcebus murinus*). Behav Ecol Sociobiol 43:125–132

Schmid J, Kappeler PM (2005) Physiological adaptations to seasonality in nocturnal primates. In: Brockman DK, van Schaik CP (eds) Seasonality in primates. Cambridge University Press, Cambridge, pp 129–155

Schmid J, Ruf T, Heldmaier G (2000) Metabolism and temperature regulation during daily torpor in the smallest primate, the pygmy mouse lemur (*Microcebus myoxinus*) in Madagascar. J Comp Physiol B 170:59–68

Schmid J, Speakman JR (2000) Daily energy expenditure of the gray mouse lemur (*Microcebus murinus)*: a small primate that uses torpor. J Comp Physiol B 170:633–641

Schülke O, Ostner J (2007) Physiological ecology of cheirogaleid primates: variation in hibernation and torpor. Acta Ethol 10:13–21

Schwab D (2000) A preliminary study of spatial distribution and mating system of the pygmy mouse lemur (*Microcebus cf myoxinus*). Am J Primatol 51:41–60

Sorg JP, Rohner U (1996) Climate and tree phenology of the dry deciduous forest of the Kirindy Forest. In: Ganzhorn JU, Sorg JP (eds) Ecology and economy of a tropical dry forest in Madagascar. Erich Goltze GmbH and Co., Göttingen, pp 57–80

Speakman JR (2008) The physiological costs of reproduction in small mammals. Philos Trans R Soc Lond B Boil Sci 363:375–398

Van Schaik CP (1989) The ecology of social relationships amongst female primates. In: Standen V, Foley RA (eds) Comparative socioecology. Blackwell, Oxford, pp 195–218

Part VI
Sensory Ecology, Communication and Cognition

Chapter 25
The Ecology of Touch: Are Prosimians Special?

Magdalena N. Muchlinski

Abstract The size of the infraorbital foramen (IOF), through which the infraorbital nerve (ION) passes, has been used to infer the number of vibrissae (whiskers) an animal has, which in turn has informed phylogenetic and ecological interpretations of extinct primates. The functional significance of IOF area, however, has not been tested. I present a comparison of relative IOF area among extant mammals. My results show that (1) relative IOF area is a good indicator of ION size and thus of touch sensitivity of the rostrum; (2) primates and other euarchontans have low IOF areas relative to most other mammals; (3) IOF area and vibrissal count correlate, but not strongly; and (4) among primates IOF area covaries with diet, such that frugivores have relatively larger IOFs than do folivores or insectivores. This dietary signal holds for prosimians and anthropoids, and prosimians do not have enlarged IOFs compared with anthropoids.

Resume La taille du Foramen Infra-Orbital (FIO), au travers duquel passe le nerf infraorbital (NIO), est utilisée comme caractère indicateur du nombre de vibrisses (moustaches) qui peut aider à interpréter les espèces éteintes de Primates, en termes de phylogénie et d'écologie. Cependant, la signification fonctionnelle du FIO n'a jamais été testée. Je présente une comparaison de la taille relative du FIO chez les Mammifères actuels. L'analyse montre que (1) la surface relative du FIO est un bon indicateur de la taille du NIO, et donc de la sensibilité tactile du museau; (2) les Primates et les autres Euarchontes ont un relativement petit FIO comparés à la plupart des autres Mammifères; (3) la surface du FIO est faiblement mais significativement corrélée au nombre de vibrisses; (4) chez les Primates, la surface du FIO co-varie avec le régime alimentaire, les frugivores ayant de plus grands FIO

M.N. Muchlinski (✉)
Department of Anatomy and Neurobiology, College of Medicine, Chandler Medical Center MN210, University of Kentucky, 800 Rose Street, Lexington, KY 40536, USA
e-mail: magdalena.muchlinski@uky.edu

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_25,

que les folivores et les insectivores. Cet effet du régime s'applique aussi bien aux Prosimiens qu'aux Anthropoïdes, et les Prosimiens n'ont pas de plus grands FIO que les Anthropoïdes.

Introduction

The infraorbital foramen (IOF) lies below the inferior margin of the orbit, and transmits the infraorbital nerve (ION) to specialized mechanoreceptors (Pacinian corpuscles, Merkel's discs, and Ruffini corpuscles) associated with the rhinarium, vibrissae (whiskers), and upper lip (Ebara et al. 2002). Kay and Cartmill (1977) proposed a functional explanation for relative IOF size which could be extended to infer ecological and phylogenetic information from fossils. They quantified IOF area from multiple species across four mammalian groups ("insectivores," carnivores, primates, and marsupials) and regressed those values against the species' cranial lengths. The groups showed distinctly different relationships: terrestrial "insectivores" and carnivores had relatively large IOFs, followed by marsupials, prosimians, and anthropoids. The authors attributed the observed grade shifts in relative IOF area between primate and nonprimate mammals, and between anthropoids and prosimians, to differences in the number of vibrissae. Since then, paleontologists have implicitly or explicitly assumed that IOF size relates to vibrissal count, which is explicable in terms of ecology and phylogeny (e.g., Ni et al. 2004). However, assumptions linking IOF area to ION size and vibrissal numbers are untested and have led to confusing and/or conflicting interpretations of the primate fossil record (Gingerich 1981; Simons 1987; Ni et al. 2004). I tested systematically several assumptions concerning the relationship of IOF area to other anatomical structures and to ecology (Muchlinski 2008a, 2010a, b) and found IOF area to be a good proxy for maxillary mechanoreceptivity (touch sensitivity of the face), which has implications for phylogenetic and ecological interpretations of fossils. I provide a summary of these results, paying special attention to the prosimians.

IOF Area and Fossil Interpretation: Past and Present Research

I explored variation in relative IOF area using a more extensive mammalian sample than that used in 1977 by Kay and Cartmill (Muchlinski 2010a). The results of the two studies agreed in several respects. Both found that (1) primates have smaller IOFs than most nonprimate mammals; (2) dermopterans display a primate-like reduction in IOF area relative to cranial length; and (3) scandentian IOFs are relatively smaller than those of most nonprimate mammals, but larger than those of

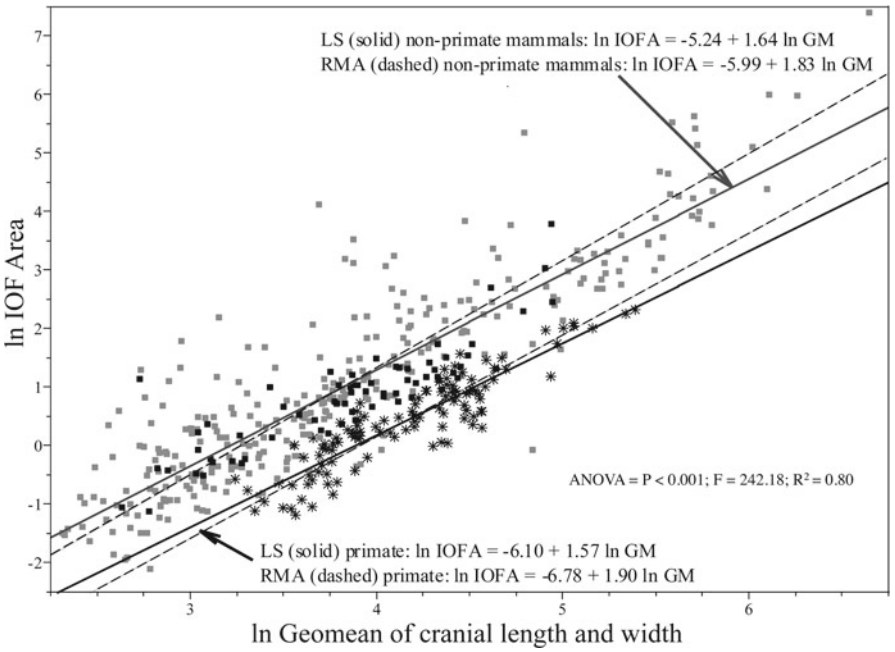


Fig. 25.1 A scatter plot of the relationship between ln infraorbital foramen area and ln geometric mean of cranial length and width among mammals [metatherian mammals (*black filled square*); eutherian mammals (*gray filled square*); primates (*black star*)]. Cranial length (mm) is the linear distance between prosthion and opisthocranion. Cranial width (mm, bizygomatic width) is the linear distance between the most lateral points of the zygomatic arches. I multiplied bizygomatic width and cranial length by one another, and took the square root of that value to calculate a geometric mean for cranial shape (GM). Each *symbol* represents a species mean. Data were taken from Muchlinski (2010a). A least squares (*solid lines*) and reduced major axis (*dashed line*) regression is fitted to all primates and to all nonprimate mammals. An ANCOVA found significant differences between primates and nonprimate mammals in relative IOF area

most primates (Fig. 25.1). The studies diverged, however, with respect to the two primate suborders. Kay and Cartmill (1977) found prosimians to have larger IOFs than anthropoids, while I (Muchlinski 2010a) found no significant difference in relative IOF area between the two (Fig. 25.2). This result is noteworthy because relative IOF area has been used by paleontologists to assign primate fossils to one or other suborder, or to support proposed subordinal affiliations suggested by other character states (Beard and Wang 2004; Ni et al. 2004). My findings indicate that IOF area has limited phylogenetic implications. While relative IOF area can indicate whether or not a fossil is euarchontan (i.e., with negative values for IOF residuals from the overall mammalian regression), it cannot be used to distinguish primates from other euarchontans or anthropoids from prosimians.

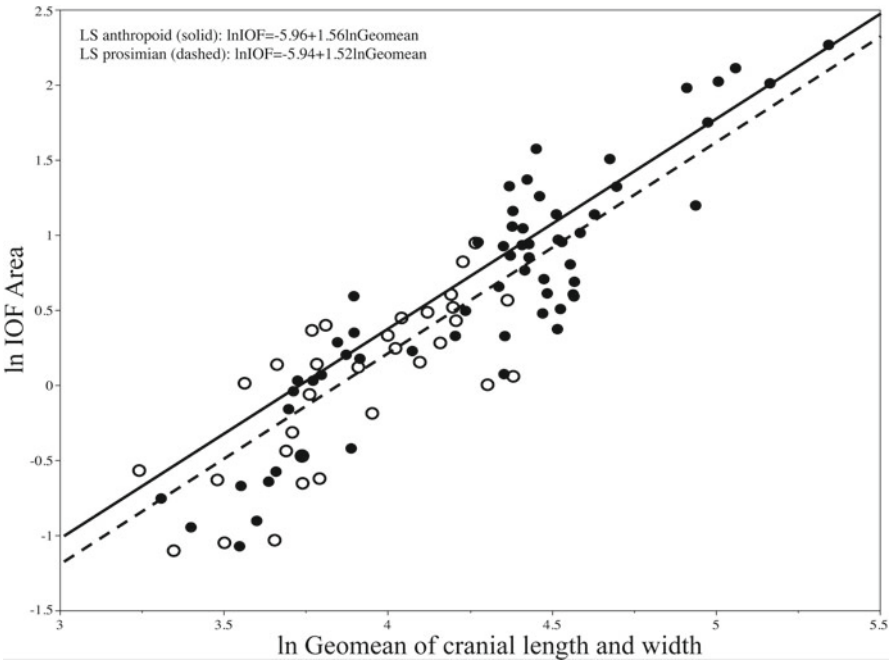


Fig. 25.2 A scatter plot of the relationship between ln infraorbital foramen area and ln geometric mean of cranial length and width among primates (see Fig. 25.1 legend for calculation of the geometric mean). *White circles* represent prosimians and *black circles* anthropoids. The *solid line* is the least-squares regression for anthropoids and the *dashed line* is for prosimians. There is complete overlap in relative IOF areas between the suborders. An ANCOVA found no significant differences in either the slope or *y*-intercept between the suborders. Data for this analysis was taken from Muchlinski (2010a)

Vibrissae and the Infraorbital Foramen

Like Kay and Cartmill (1977), I found a significant positive correlation ($r=0.57$, $P<0.001$) between vibrissal count[1] and IOF area among mammals (Muchlinski 2010a). Primates showed an average reduction of 37% in relative IOF area compared with nonprimate mammals, but did not differ from them in total numbers of

[1] There are two types of mystacial vibrissae: macro- and microvibrissae. Macrovibrissae are long, laterally oriented hairs usually arranged in distinct rows on the muzzle. Microvibrissae are shorter, less organized, and confined to the area just above the upper lip. Most studies have focused on macrovibrissae, since they are considered to be of greater importance to mammalian environmental navigation. Brecht et al. (1997) have called this assumption into question by suggesting that the macrovibrissae appear to be critical for spatial tasks, while microvibrissae are involved in object recognition. I counted both macro- and microvibrissae to derive total vibrissal count.

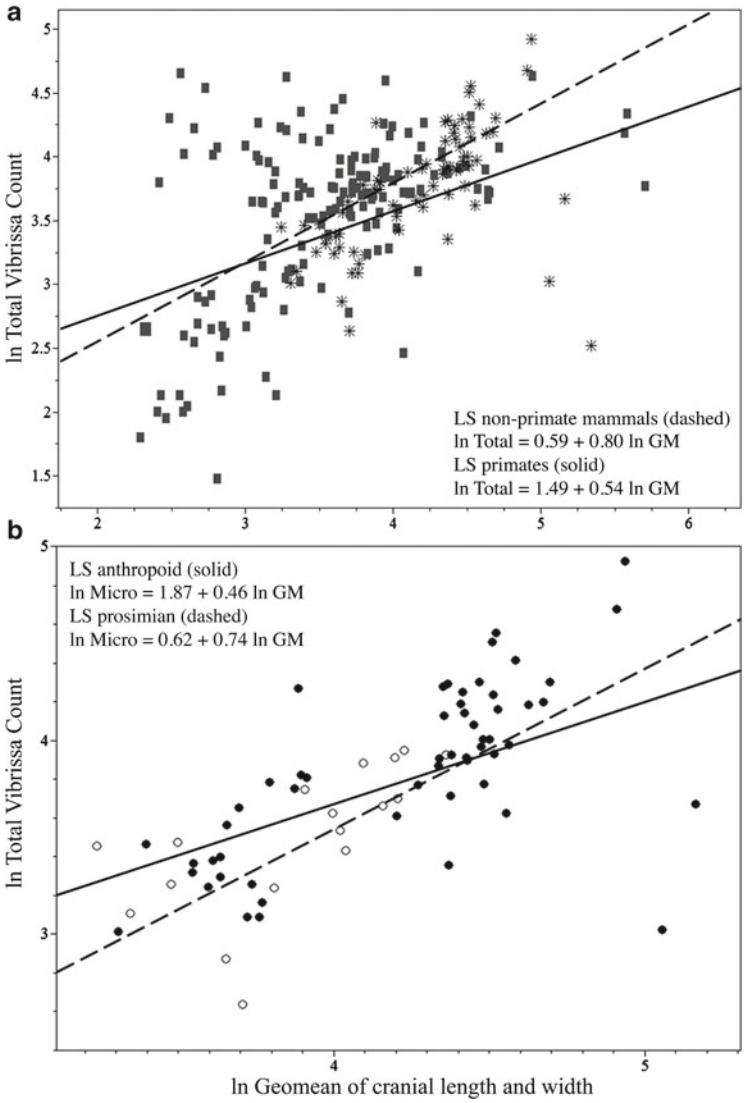


Fig. 25.3 Scatter plot illustrating the relationship between ln total vibrissal count and ln geometric mean of cranial length and width (calculated as before) among (**a**) primates and nonprimate mammals and (**b**) anthropoids and prosimians. An ANCOVA indicated no significant differences between primates and nonprimate mammals or between anthropoids and prosimians. Vibrissae and IOF area data were taken from Muchlinski (2010a)

vibrissae (Muchlinski 2010a; Fig. 25.3a), rendering the link between IOF area and total vibrissal count tenuous. These findings contradict earlier reports that vibrissal count is low among primates (Huber 1930; le Clark 1959). An equally surprising finding is that prosimians and anthropoids do not differ significantly in total

vibrissae (Muchlinski 2010a; Fig. 25.3b). Because there is considerable variation in the total number of vibrissae among mammals, IOF area cannot be used to estimate the absolute vibrissal number for any given mammal.

What Is the Functional Significance of the IOF Area?

If IOF area cannot be used to predict vibrissal numbers, then what (if anything) is its functional significance? The IOF transmits the sensory infraorbital nerve to specialized mechanoreceptors that respond to mechanical stimuli such as tension, pressure, vibration, and displacement (Brecht et al. 1997). Some of these receptors can be found around the vibrissal shaft (Ebara et al. 2002), but others can be found in the upper lip and surrounding maxillary region. The sensory acuity of an anatomical region (e.g., finger tips, palms of hands, and lips) correlates with the number of receptors located there (Kandel et al. 2000). Generally, as the number of receptors increases, a thicker nerve is required to transmit the sensory information from the receptors to the brain (Cull et al. 2003). Thus, the size of the infraorbital nerve may be a good indicator of the sensory acuity of the maxillary region. The cross-sectional area of the ION accounts for ~85% of IOF cross-sectional area (Muchlinski 2008b). The strong relationship between the areas of the IOF and the ION indicates that, in the absence of nerve tissue, the size of the IOF can be used as a proxy for maxillary mechanoreception.

Previous ecological interpretations based on the IOF have been vague and inconclusive. This uncertainty is due in part to an assumption that the functional significance of IOF area is constant across orders, but an animal's reliance on maxillary mechanoreception can be affected by its activity pattern (e.g., nocturnality or low light conditions, Klages et al. 2002) or by its preferred substrate (arboreal: Ahl 1987; aquatic/subterranean: Baron et al. 1990; Crish et al. 2003). Each mammalian order appears to have unique ecological correlates with maxillary mechanoreception, which may be less important for primates in environmental navigation than it is for nonprimate mammals (e.g., rodents: Brecht et al. 1997) as indicated by IOF area. However, maxillary mechanoreception appears to be important for primates in feeding (Muchlinski 2008a, b). Primate frugivores have relatively larger IOFs compared with insectivores and folivores, while IOF area does not differ significantly between insectivores and folivores (Fig. 25.4). This pattern holds for prosimians considered separately and for primates in general (Table 25.1).

The pattern may be related to the anterior rostrum's role in fruit evaluation and processing. Fruit selection is distinct from insect and leaf assessment in that fruit testing depends more heavily on premaxillary and rostral sensory cues (Lucas 1994; Ungar 1998; Dominy et al. 2001). Dominy (2004) found no correlation between fruit color and sugar content, indicating that color is not a signal of fruit edibility. Rather, tactile cues and taste (ethanol content) are better for fruit evaluation (Dominy et al. 2001; Dominy 2004). Hands play an important role in evaluating fruit texture,

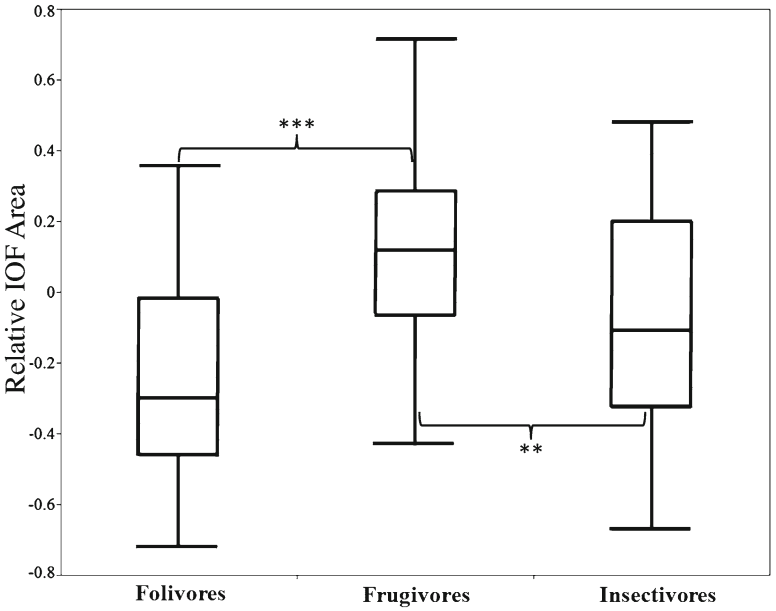


Fig. 25.4 *Box* and *whisker plot* of the results of a Wilcoxon rank-sum test illustrating the relationship between relative IOF area (cranial size-independent residuals) and dietary categories. Frugivores have significantly larger IOFs than both folivores ($P<0.0001$) and insectivores ($P<0.01$). Dietary data and IOF area were taken from Muchlinski (2010b)

Table 25.1 Pairwise comparisons of relative IOF area between dietary groups

	Frugivore/folivore		Frugivore/insectivore		Folivore/insectivore	
	Z	*P*	*Z*	*P*	*Z*	*P*
All primates	−3.27	<0.001	−3.22	<0.001	0.81	0.42
Anthropoids	−3.22	<0.001	−2.52	<0.01	0.52	0.6
Prosimians	−1.16	<0.01	−2.57	<0.01	−1.16	0.24

but the premaxillary region is also critical (Dominy 2004). When a primate grasps a fruit, it inspects it haptically with the digits, lips, and incisors, which are all mechanically sensitive (Dominy 2004). For example, *Eulemur rubriventer* use their hands to pull terminal branches with fruit clusters to their faces, followed by mouth and lip evaluation prior to selection and ingestion (Tecot personal communication). Spider monkeys bite and taste fruits to determine their maturity, because color is an unreliable guide (van Roosmalen 1985). Hylander (1975) and Anthony and Kay (1993) found frugivores to have broader and more spatulate incisors than insectivores or folivores; husking fruit requires more incisal preparation than either leaf or insect consumption (Hylander 1975). Like broad incisors, increased maxillary mechanoreception (and consequently larger IOFs) may be adaptations for fruit selection.

Are Prosimians Special?

Figures 25.1 and 25.3 show that prosimians and anthropoids do not differ in either relative IOF area or vibrissal count. If the IOF is an accurate measure of touch acuity of the rostrum, then anthropoids and prosimians show no discernable differences in this sense. Rather, primates in general may have reduced maxillary mechanoreception in comparison with noneuarchontan mammals. Differences in feeding ecology may account for the observed variation in IOF area within the order primates. Although diet and IOF area covary, many questions regarding touch acuity of the rostrum remain unanswered. We understand little about why prosimians do not differ from anthropoids with regard to relative IOF area (maxillary mechanoreception) and vibrissal count. Future research into the reduction of maxillary mechanoreception among primates should focus on how and why primates use their muzzles and hands. In a sense, the fact that prosimians are not "special" relative to anthropoids makes them "special" compared with other mammals that use maxillary mechanoreception sensory cues very differently: prosimians and anthropoids apparently approach their sensory worlds in a similar, primate fashion.

Acknowledgments I thank L. J. Shapiro, E. C. Kirk, N. J. Dominy, R. W. Sussman, O. Y. Martin, R. D. Martin, S. R. Tecot, L. J. Alport, and R. Lewis, the National Science Foundation grant 0622422, the Field Museum of Natural History, the University of Texas at Austin, and PEO.

References

Ahl AS (1987) Relationship of vibrissal length and habits in the Sciuridae. J Mammal 68:848–853

Anthony MRL, Kay RF (1993) Tooth form and diet in ateline and alouattine primates: reflections on the comparative method. Am J Sci 293A:356–382

Baron G, Stephan H, Frahm HD (1990) Comparison of brain structure volumes in Insectivora and primates IX. Trigeminal complex. J Hirnforsch 31:193–200

Beard CK, Wang J (2004) The eosimiid primates (Anthropoidea) of the Heti Formation, Yuanqu Basin, Shanxi and Henan provinces, People's Republic of China. J Hum Evol 46:401–432

Brecht M, Preilowski B, Merzenich MM (1997) Functional architecture of the mystacial vibrissae. Behav Brain Res 84:81–97

Crish SD, Rice FL, Park TJ, Comer CM (2003) Somatosensory organization and behavior in naked mole-rats I: vibrissae-like body hairs comprise a sensory array that mediates orientation to tactile stimuli. Brain Behav Evol 62:141–151

Cull G, Cioffi GA, Dong J, Homer L, Wang L (2003) Estimating normal optic nerve axon numbers in non-human primate eyes. J Glaucoma 12:301–306

Dominy NJ (2004) Fruits, fingers, and fermentation: the sensory cues available to foraging primates. Integr Comp Biol 44:295–303

Dominy NJ, Lucas PW, Osorio D, Yamashita N (2001) The sensory ecology of primate food perception. Evol Anthropol 10:171–186

Ebara S, Kumamoto K, Matsuura T, Mazurkiewicz JE, Rice FL (2002) Similarities and difference in the innervation of mystacial vibrissal follicle-sinus complexes in the rat and cat: a confocal microscopic study. J Comp Neurol 449:103–119

Gingerich PD (1981) Early Cenozoic Omomyidae and the evolutionary history of tarsiiform primates. J Hum Evol 10:345–348
Huber E (1930) Evolution of facial musculature and the cutaneous field of trigeminus. Part II. Q Rev Biol 5:389–437
Hylander WL (1975) Incisor size and diet in anthropoids with special reference to *Cercopithecidae*. Sci 189:1095–1098
Kandel ER, Schwartz JH, Jessell TM (2000) Principles of neural science, 4th edn. McGraw-Hill, New York
Kay RF, Cartmill M (1977) Cranial morphology and adaptations of *Palaechthon nacimienti* and other Paromomyidae (Plesiadapoidea, ?Primates), with a description of a new genus and species. J Hum Evol 6:19–32
Klages M, Muyakshin S, Soltwedel T, Arntz WE (2002) Mechanoreception, a possible mechanism for food fall detection in deep-sea scavengers. Deep Sea Res I 49:143–155
le Clark WEG (1959) The antecedents of man. Harpers, New York
Lucas PW (1994) Categorization of food items relevant to oral processing. In: Chivers DJ, Langer P (eds) The digestive system in mammals: food, form and function. Cambridge University Press, Cambridge, pp 197–219
Muchlinski MN (2008a) Ecological and morphological correlates of infraorbital foramen size and its implications for interpreting the fossil record. Unpublished PhD thesis, University of Texas at Austin
Muchlinski MN (2008b) The relationship between the infraorbital foramen, infraorbital nerve, and maxillary mechanoreception: implications for interpreting the paleoecology of fossil mammals based on infraorbital foramen size. Anat Rec 291:1221–1226
Muchlinski MN (2010a) A comparative analysis of vibrissae count and infraorbital foramen area in primates and other mammals. J Hum Evol 58:447–473
Muchlinski MN (2010b) Ecological correlates of infraorbital foramen area in primates. Am J Phys Anthropol 141:131–141
Ni X, Wang Y, Hu Y, Li C (2004) A euprimate skull from the early Eocene of China. Nature 427:65–68
Simons EL (1987) New faces of *Aegyptopithecus* from the Oligocene of Egypt. J Hum Evol 16:273–289
Ungar P (1998) Dental allometry, morphology, and wear as evidence for diet in fossil primates. Evol Anthropol 6:205–217
Van Roosmalen M (1985) Subcategorizing foods in primates. In: Chivers DJ, Wood BA (eds) Food acquisition and processing in primates. Plenum, New York, pp 167–176

Chapter 26
The Importance of Olfaction for Predator Detection in Spectral Tarsiers

Sharon L. Gursky

Abstract A limitation of many experimental studies in predation is that they assume primates only use visual and auditory cues to discern the presence of predators and ignore the importance of olfactory cues. This is an obvious gap in predation research, given the importance of chemical information, particularly for nocturnal species. I conducted a study of the role of olfactory signals in predator detection by spectral tarsiers, *Tarsius spectrum*, at Tangkoko Nature Reserve in Sulawesi, Indonesia. For 80 nights, 20 adult tarsiers were exposed to a wooden civet model covered in civet urine, a wooden civet without urine, a stick covered in civet urine, and a stick without urine. Antipredator responses were overwhelmingly more frequent and more intense in the presence of civet urine, indicating that olfactory cues play an important role for spectral tarsiers in detecting terrestrial predators.

Resume Une limite de nombreuses études expérimentales portant sur la prédation est qu'elles se fondent sur l'idée que seules la vision et l'audition sont utilisées pour détecter un prédateurs, et ignorent l'importance de l'olfaction. C'est une faille évidente de la recherche sur la prédation, dans la mesure où l'olfaction est particulièrement importante pour la détection des prédateurs, surtout pour les animaux nocturnes. J'ai mené cette étude dans la Réserve Naturelle de Tangkoko, à Sulawesi, en Indonésie. Au cours de 80 nuits, 20 tarsiers adultes ont été exposés à un modèle de civette en bois, et à un bâton de bois tous deux imbibés ou non d'odeur de civette. Les réponses anti-prédatrices ont été considérablement plus fréquentes et plus intenses en présence d'urine de civette, ce qui indique que les indices olfactifs jouent un rôle important dans la détection des prédateurs par les tarsiers spectraux.

S.L. Gursky (✉)
Department of Anthropology, Texas A&M University, MS 4352, College Station, TX 77843, USA
e-mail: gursky@tamu.edu

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_26,

Introduction

Predation is an important selective pressure structuring the behavior of nonhuman primates (Cheney and Wrangham 1986; Isbell 1994; Hill and Dunbar 1998; Janson 1998; Stanford 1998; Wright 1998; Bearder et al. 2002; Chap. 12). Primates have evolved a variety of adaptations to thwart predators, including concealment, vigilance, flight, alarm calls, mobbing, group living, and polyspecific associations (Caine 1984; Cheney and Wrangham 1986; Cords 1990; Ferrari and Ferrari 1990; Baldellou and Henzi 1992; Cowlishaw 1994; Lima 1995; Gould 1996; Iwamoto et al. 1996; Bshary and Noe 1997; Bearder et al. 2002). Despite numerous studies of primate antipredator strategies (Gursky and Nekaris 2006), observations of actual predation events on wild primates are surprisingly limited (Cheney and Wrangham 1986; Isbell 1994; Chap. 12).

To overcome this limitation, primatologists generally rely on indirect indicators of predation pressure. Predator models and vocalizations have been presented to various bird and mammal species to mimic the presence of predators (Cheney and Seyfarth 1981; Macedonia and Evans 1993; Chapman and Chapman 1996; Gursky 2005), and have shed much light on how animals modify their behavior to avoid being preyed upon. The best known study involves vervet monkeys (*Chlorocebus aethiops*): Cheney and Seyfarth (1981) observed that the monkeys produced acoustically distinct alarm calls in response to different predator classes (large cats, raptors, and snakes), and responded with different, appropriate escape responses. More recently, Fichtel and van Schaik (2006) conducted experiments on captive sifakas (*Propithecus verreauxi*) using vocal playbacks and models of predators. The sifakas emitted functionally referential alarm calls for aerial predators, and general alarm calls for terrestrial predators and other situations associated with high arousal, such as group encounters.

An obvious limitation of most of these experimental studies is that they assume that primates are only using visual and auditory cues to detect predators, and ignore the importance of olfactory cues for the prey species (e.g., Gursky 2005). Olfactory cues are particularly important for nocturnal prey species in predator detection. For example, upon smelling cat urine, rats experience long-term decreases in their locomotor activity, grooming, and reproductive behavior. In addition, the odor of cats causes rats to retreat to a strategic location whence the predator can be safely monitored (Apfelbach et al. 2005). Mice (*Mus musculus*) reduced scent marking in the presence of ferret urine (*Mustela putorius*) (Roberts et al. 2001). Similar behavioral changes are seen in rabbits, voles, beavers, and a variety of other mammals (Apfelbach et al. 2005).

The importance of olfactory cues for locating predators should be obvious, since predators regularly use olfactory or chemical signals to locate prey. For example, small mustelids find voles using odor cues like urine and fecal scent marks (Koivula and Korpimäki 2001) and female voles in estrus are more likely to be preyed upon than nonestrus females (Cushing 1985). Timber rattlesnakes locate prey using chemical signals (Clark 2004).

Olfaction is clearly an important sense for tarsiers (MacKinnon and MacKinnon 1980; Niemitz 1984; Wright et al. 2003). Not only do they regularly scent mark their territories with urine and scent glands, but they also have a larger number of nasal turbinates than monkeys and apes (Hill 1955; Fleagle 1999; Gursky 2003). They also have a wet rhinarium, as is characteristic of mammals that rely on their olfactory sense (Hill 1955; Fleagle 1999).

In contrast, tarsier visual abilities are not well developed relative to other nocturnal primates. Tarsiers are probably secondarily nocturnal (Martin 1990; Müller and Thalmann 2000), as indicated by the presence of a *fovea centralis*, a feature of the retina associated with diurnal primates. They also lack a reflective *tapetum lucidum* behind the retina to absorb and magnify light, found in nearly all nocturnal mammals (Fleagle 1999). To compensate, tarsiers have developed extraordinarily large eyes, and their eyeballs protrude largely from their sockets; the volume of a tarsier eye is greater than that of its brain (Niemitz 1984). Given their well-developed olfactory senses and relatively poor night vision, tarsiers are likely to rely more heavily on olfaction and less on vision, particularly for detecting predators.

My goal was to ascertain the importance of olfactory cues for spectral tarsiers in discerning the presence of civets. Civets not only prey on spectral tarsiers (Gursky 1997) but also produce a very musky smell from urine marking throughout their territories (Rozhnov and Rozhnov 2003). I predicted that spectral tarsiers would respond consistently to the presence of a civet model covered in urine, as well as to a stick covered in civet urine, but would ignore sticks free of civet urine. By distinguishing between visual and olfactory cues, I aimed to develop a better understanding of the sensory detection of predators by spectral tarsiers.

Methods

Study Site

Sulawesi, the eleventh largest island in the world, lies east of Borneo and north-west of Australia—New Guinea (1°34′N, 125°14′E). It is the largest and most central island of the Wallacea biogeographical region, where the Australian and Asian regions meet. The fauna and flora of Sulawesi is a blend of Asian and Australian elements, as well as high numbers of endemic taxa (Whitten et al. 1987).

The study was conducted at Tangkoko Nature Reserve on the eastern tip of the northern arm of the island, an area of ~3,000 ha with a full range of forest types: beach formation forest, lowland, submontane, and mossy cloud forest on the summit of Mt. Tangkoko (MacKinnon and MacKinnon 1980; Whitten et al. 1987; Gursky 1997). The reserve is far from pristine due to heavy, selective logging and encroaching gardens. The forest canopy is discontinuous and comprised largely of *Ficus* trees. Annual rainfall averages 2,300 mm. Details of the habitats at Tangkoko Nature Reserve can be found in Gursky (1997).

Data Collection

The study was conducted from June to August 2007. Ten tarsier groups were located by means of the early morning vocalizations tarsiers emit on returning to their sleeping sites. Vocalizations were given for 3–5 min and could be heard for 300–400 m. Mist nets were set up at the sleeping sites approximately an hour before dusk and monitored. On capture, all adults were marked with color- and pattern-specific bird bands and radiocollared.

Over 20 nights, each of the adult individuals in the ten groups was exposed to a wooden model civet covered in civet urine (Wildlife Control Supplies, Simsbury, CT). During these experiments, I remained behind a blind of large *Livistonia* leaves, 5 m from the focal tarsier. The model was attached to a bamboo stick and exposed to the subject for 20 min, after which it was retracted behind the blind. I recorded the subject's behavior, including its height prior to exposure, all alarm and contact calls emitted, direction of movement, whether other group members moved toward the model, and the focal individual's distance from the model.

On an additional 20 nights, each adult individual was again exposed to a wooden model civet, but no civet urine was applied. For the third and fourth experimental variations, sticks either covered with civet urine or lacking any additive were placed near each of the 20 tarsiers, and the responses of the focal animal recorded.

Results

The responses of the spectral tarsiers varied in accordance with the sensory information they received. When presented with a wooden model civet covered in civet urine, all individuals emitted alarm calls (Figs. 26.1, 26.2, 26.3). The urine-coated civet model was never ignored. In 77% of these trials, spectral tarsiers mobbed the predator model for 8–33 min (mean = 21 min, SD = 6.3). The number of individuals mobbing the civet ranged from 2 to 6 (mean = 3.2, SD = 0.97). In contrast, when exposed to the same model without urine, the spectral tarsiers only alarm called in 40% of trials, significantly less than in the presence of urine ($\chi^2 = 233.49$, df = 18; $P = 0$). Indeed, they ignored the clean model in 46% of trials, a highly significant difference from the trials with urine ($\chi^2 = 154.02$, df = 18; $P = 0$). Although the tarsiers mobbed the urine-free model in 15% of the trials, this was significantly less than in the presence of urine ($\chi^2 = 180.42$, df = 18; $P = 0$). Mobbing lasted from 7 to 28 min (mean = 17 min, SD = 3.9). The number of individuals mobbing the civet ranged from 2 to 5 and averaged 3.1 (SD = 0.67).

In the presence of a stick covered with civet urine, the spectral tarsiers almost always alarm called (93% of trials) and rarely (7%) ignored the stick. The frequency of this response was not statistically different from that elicited by the urine-coated wooden model ($\chi^2 = 0.4900$ df = 18; $P = 0.4839$). Spectral tarsiers approached the urine-coated stick in 93% of the trials. When first exposed to the urine-coated stick,

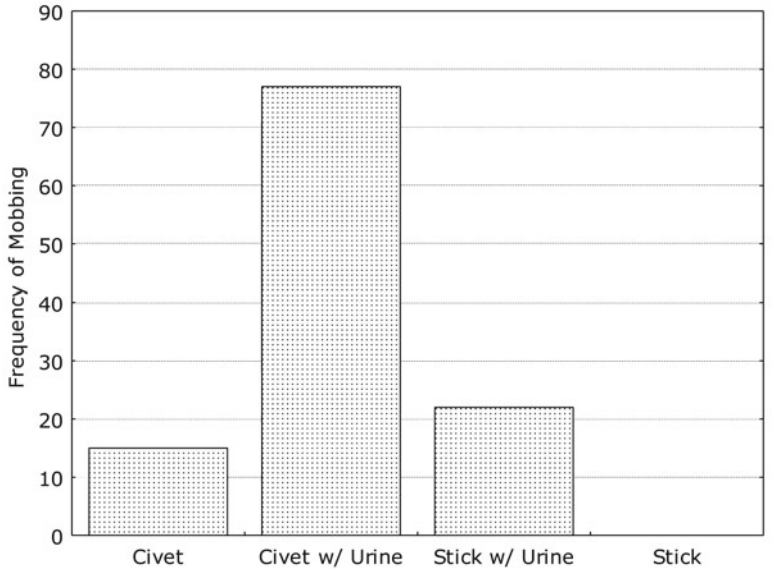


Fig. 26.1 Variation in the mobbing behavior of spectral tarsiers to visual and olfactory cues of predators

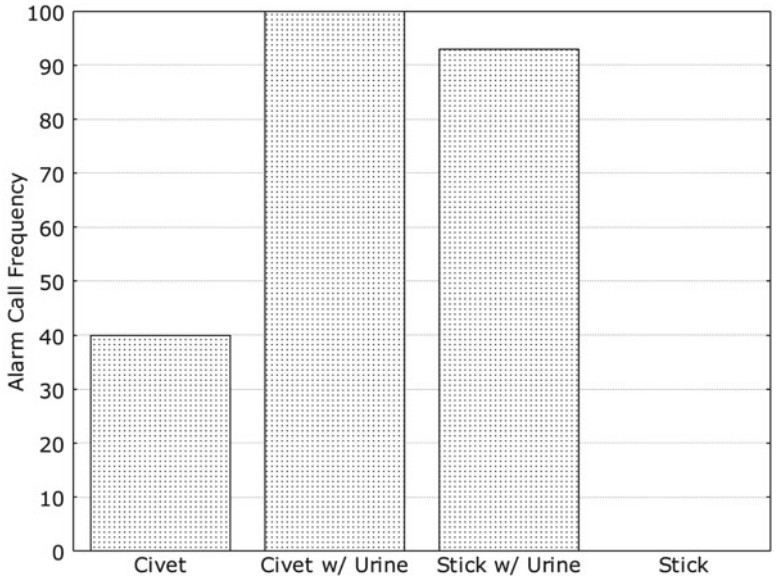


Fig. 26.2 Variation in the alarm calling frequency of spectral tarsiers to visual and olfactory cues of predators

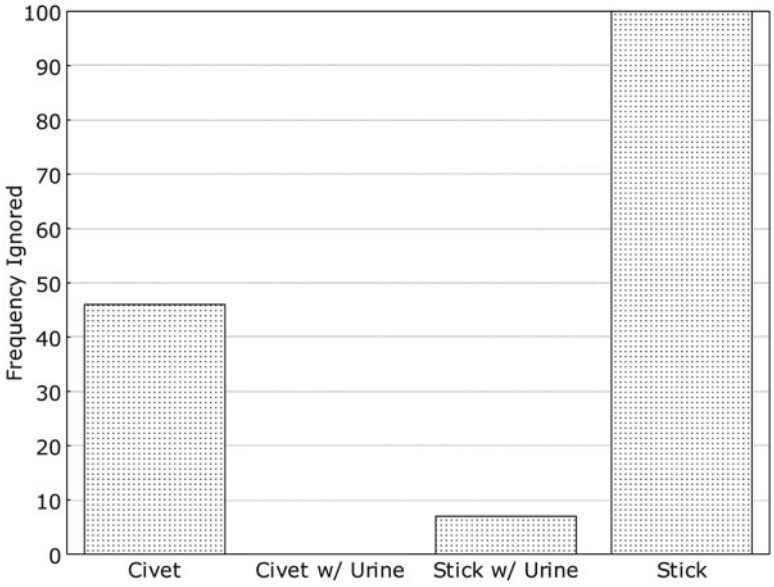


Fig. 26.3 Variation in the frequency with which spectral tarsiers ignored visual and olfactory cues of predators

the focal animal's distance from it was 5 m. In 72% of trials, tarsiers approached the stick to <30 cm, frequently sniffing the stick and countermarking it with their own urine. Most surprisingly, in 25% of trials, tarsiers mobbed the stick! Spectral tarsiers never mobbed or alarm called in response to a stick without urine. In 100% of trials using clean sticks, the spectral tarsiers ignored the stick completely.

Discussion

Olfactory cues are clearly important to spectral tarsiers for identifying terrestrial predators. They rarely (≤7% of trials) ignored olfactory predator cues regardless of whether they were confirmed by visual cues, responding with alarm calls. When the olfactory signal was augmented by visual information in the form of a wooden civet model, the tarsiers mobbed the model in 77% of trials. When the olfactory signals were presented on a stick, the tarsiers mobbed significantly less (25%) but still significantly more than the frequency with which they mobbed the odor-free civet model (15%). Olfactory signals consistently elicited higher levels of antipredator response than did visual cues with no odor, but the strongest reaction occurred when olfactory signals were augmented by visual cues.

These results are illuminating but not surprising in light of the chemistry of urine and feces of predators, which contain sulfurous metabolites (Nolte et al. 1994). For animals at risk of contributing to a predator's diet, it would be advantageous to be able to recognize these metabolites and react accordingly. Such an early warning system is likely to be more effective than relying on a reaction to the predator's presence.

Small, nocturnal mammals, being particularly vulnerable to ambush attacks by cryptic predators, would benefit greatly from being able to assess predation risk from chemical gradients around those predators. Most studies on small mammals indicate their awareness of chemical signals from predators, which triggers risk avoidance behavior (Dickman 1992; Kats and Dill 1998; Jones and Dayan 2000).

Further research on the responses of tarsiers to olfactory cues from other predators is clearly needed. In particular, it would be interesting to explore how spectral tarsiers respond to olfactory cues in feces of civets, raptors, and pythons. Studies of the responses of other prosimian primates, nocturnal and diurnal, to olfactory cues of potential predators are also required.

Acknowledgments Funding for this research was provided by Primate Conservation, Inc., the Margot Marsh Biodiversity Fund, and Texas A&M University. I thank the Indonesian Institute of Sciences (LIPI), the Directorate General for Nature Preservation and Forest Protection (PHPA) in Manado, Bitung, Tangkoko, and Jakarta, SOSPOL, POLRI, the University of Indonesia, Jatna Supriatna and Noviar Andayani for their sponsorship while in Indonesia. Special thanks to my field assistants (Ben and Felik) for their help with data collection. The protocol for this research was reviewed and approved by the Texas A&M University IACUC committee.

References

Apfelbach F, Brinkerhoff R, Haddad N, Orrock J (2005) Corridors and olfactory predator cues affect small mammal behavior. J Mammal 86:662–669

Baldellou M, Henzi S (1992) Vigilance, predator detection and the presence of supernumerary males in vervet monkey troops. Anim Behav 43:451–461

Bearder SK, Nekaris KAI, Buzzell CA (2002) Dangers in the dark: are some nocturnal primates afraid of the dark? In: Miller LE (ed) Eat or be eaten: predator sensitive foraging among primates. Cambridge University Press, Cambridge, pp 21–40

Bshary R, Noe R (1997) Anti-predation behavior of red colobus monkeys in the presence of chimpanzees. Behav Ecol Sociobiol 41:321–333

Caine N (1984) Visual scanning by tamarins. Folia Primatol 43:59–67

Chapman CA, Chapman LJ (1996) Interdemic variation in mixed-species association patterns: common diurnal primates of Kibale National Park, Uganda. Behav Ecol Sociobiol 47:129–139

Cheney DL, Seyfarth RM (1981) Selective forces affecting the predator alarm calls of vervet monkeys. Behaviour 76:25–61

Cheney DL, Wrangham RW (1986) Predation. In: Smuts B, Cheney D, Seyfarth R, Wrangham RW, Struhsaker T (eds) Primate societies. Chicago University Press, Chicago, pp 227–239

Clark R (2004) Timber rattlesnakes (*Crotalus horridus*) use chemical cues to select ambush sites. J Chem Ecol 30:607–617

Cords M (1990) Vigilance and mixed-species association of some East African forest monkeys. Behav Ecol Sociobiol 26:297–300

Cowlishaw G (1994) Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. Anim Behav 53:667–686
Cushing B (1985) Estrous mice and vulnerability to weasel predation. Ecology 66:1976–1978
Dickman CR (1992) Predation and habitat shift in the house mouse, *Mus domesticus*. Ecology 73:313–322
Ferrari S, Ferrari M (1990) Predator avoidance behavior in the buffy headed marmoset *Callithrix falviceps*. Primates 31:323–338
Fichtel C, van Schaik CP (2006) Semantic differences in sifaka (*Propithecus verreauxi*) alarm calls: a reflection of genetic or cultural variants? Ethology 112:839–849
Fleagle JG (1999) Primate adaptation and evolution. Academic, New York
Gould L (1996) Vigilance behavior during the birth and lactation season in naturally occurring ring-tailed lemurs (*Lemur catta*) at the Beza-Mahafaly Reserve, Madagascar. Int J Primatol 17:331–347
Gursky S (1997) Modeling maternal time budgets: the impact of lactation and gestation on the behavior of the spectral tarsier, *Tarsius spectrum*. Unpublished PhD thesis, SUNY-Stony Brook
Gursky S (2003) Predation experiments on infant spectral tarsiers, *Tarsius spectrum*. Folia Primatol 74:272–284
Gursky S (2005) Predator mobbing in spectral tarsiers. Int J Primatol 26:207–221
Gursky S, Nekaris KAI (2006) Primate anti-predator strategies. Springer, New York
Hill WCO (1955) Primates: comparative anatomy and taxonomy. II. Haplorrhini: Tarsiodea. Edinburgh University Press, Edinburgh
Hill R, Dunbar RIM (1998) An evaluation of the roles of predation rate and predation risk as selective pressures on primate grouping behaviour. Behaviour 135:411–430
Isbell LA (1994) Predation on primates: ecological patterns and evolutionary consequences. Evol Anthropol 3:61–71
Iwamoto T, Mori A, Kawai M, Bekele A (1996) Anti-predator behavior of gelada baboons. Primates 37:389–397
Janson C (1998) Testing the predation hypothesis for vertebrate sociality: prospects and pitfalls. Behaviour 135:389–410
Jones M, Dayan T (2000) Foraging behavior and microhabitat use by spiny mice, *Acomys cahirinus* and *A. russatus*, in the presence of Blanford's fox (*Vulpes cana*) odor. J Chem Ecol 26:455–469
Kats LB, Dill LM (1998) The scent of death: chemosensory assessment of predation risk by prey animals. Ecoscience 5:361–394
Koivula M, Korpimäki E (2001) Do scent marks increase predation risk of microtine rodents? Oikos 95:275–281
Lima SL (1995) Back to the basics of anti-predatory vigilance: the group size effect. Anim Behav 49:11–20
Macedonia J, Evans C (1993) Variation among mammalian alarm call systems and the problem of meaning in animal signals. Ethology 93:177–197
MacKinnon J, MacKinnon K (1980) The behavior of wild spectral tarsiers. Int J Primatol 1:361–379
Martin RD (1990) Primate origins and evolution. Princeton University Press, Princeton
Müller AE, Thalmann U (2000) Origin and evolution of primate social organisation: a reconstruction. Biol Rev 75:405–435
Niemitz C (1984) Biology of tarsiers. Gustav Fischer, Stuttgart
Nolte DL, Mason JR, Epple G, Aronov E, Campbell DL (1994) Why are predator urines aversive to prey? J Chem Ecol 20:1505–1516
Roberts SC, Gosling LM, Thornton EA, McClung J (2001) Scent-marking by male mice under the risk of predation. Behav Ecol 12:698–705
Rozhnov V, Rozhnov Y (2003) Roles of different types of excretions in mediated communication by scent marks of the common palm civet, *Paradoxurus hermaphroditus* Pallas, 1777 (Mammalia, Carnivora). Biol Bull 30:584–590

Stanford CB (1998) Predation and male bonds in primate societies. Behaviour 135:513–533
Whitten AJ, Mustafa M, Henderson GS (1987) The ecology of SULAWESI. Gadjah Mada University Press, Yogyakarta
Wright PC (1998) Impact of predation risk on the behavior of *Propithecus diadema edwardsi* in the rain forest of Madagascar. Behaviour 135:483–512
Wright PC, Simons EL, Gursky S (2003) Tarsiers: past, present and future. Rutgers University Press, Piscataway, NJ

Chapter 27
Size of Olfactory Structures in Strepsirhines: Ontogenetic and Ecological Factors

Timothy D. Smith, Laura J. Alport, and Anne M. Burrows

Abstract The importance of olfaction in social and dietary contexts for strepsirhine primates has been established by numerous field studies. Such work supports inferences drawn from data on olfactory structures in the primate brain. Surprisingly few detailed studies exist on development and variations in the peripheral olfactory organs. This chapter provides an update on ontogeny and distribution of the olfactory and vomeronasal neuroepithelia in the nasal fossa of strepsirhines.

Resume De nombreuses observations de terrain ont démontré le rôle majeur que joue l'olfaction dans les comportements sociaux et alimentaires des primates strepsirhiniens. Ce type d'étude corrobore les généralisations tirées des recherches sur les structures olfactives des primates au niveau cérébral. Il est cependant étonnant que peu de travaux concernent le développement et les variations des structures olfactives au niveau périphérique. Ce chapitre est une mise au point de l'ontogénie et de la distribution des neuroépithéliums olfactifs et voméronasaux dans les fosses nasales des Strepsirhiniens.

T.D. Smith (✉)
School of Physical Therapy, Slippery Rock University, Slippery Rock, PA 16057, USA

Department of Anthropology, University of Pittsburgh, 3302 WWPH, Pittsburgh, PA 15260, USA
e-mail: timothy.smith@sru.edu

L.J. Alport
Department of Anthropology, University of Texas at Austin, Austin, TX 78712, USA
e-mail: laura.alport@gmail.com

A.M. Burrows
Department of Anthropology, University of Pittsburgh, 3302 WWPH, Pittsburgh, PA 15260, USA

Department of Physical Therapy, Duquesne University, 600 Forbes Avenue,
Pittsburgh, PA 15282, USA
e-mail: burrows@duq.edu

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_27,

Introduction

Mammalian olfactory anatomy comprises two neural parts, the main and accessory olfactory systems (MOS and AOS). Strepsirhine primates possess this "dual" olfactory arrangement (Fig. 27.1), a derived feature of tetrapods, or possibly their immediate predecessors (Halpern and Martínez-Marcos 2003; González et al. 2010).

Strepsirhines possess well-developed olfactory systems (Maier 1980; Stephan et al. 1982), and field studies indicate that olfaction is an ecologically and socially important sensory modality for them (Mertl-Millhollen 2006; Siemers et al. 2007; Colquhoun 2011). Studies on primate olfactory systems have considered the relative sizes of the main olfactory bulb (MOB) and accessory olfactory bulb (AOB) (Barton et al. 1995; Alport 2004; Barton 2006) acquired from a large database of brain structure volumes (Stephan et al. 1982). To control for allometric effects, regression residuals of olfactory bulb volume against overall brain volume were analyzed. While the relative size of both olfactory bulbs is larger in nocturnal than in diurnal species, only relative MOB size correlates strongly with diet. Frugivorous strepsirhines appear to have the relatively largest MOB size compared with folivores. On the other hand, AOB size correlates more strongly with social variables and activity patterns in strepsirhines (Barton et al. 1995; Barton 2006). For instance, species with dispersed social networks have relatively larger AOBs than group-living species.

In addition to these correlations, the accessory olfactory systems (AOS) and main olfactory systems (MOS) of mammals have long been known to have either synergistic or overlapping functions (Halpern and Martínez-Marcos 2003). Thus, it is possible that strepsirhines vary in the degree to which they rely ecologically or socially on each system. Indeed, relative MOB size correlates with social variables

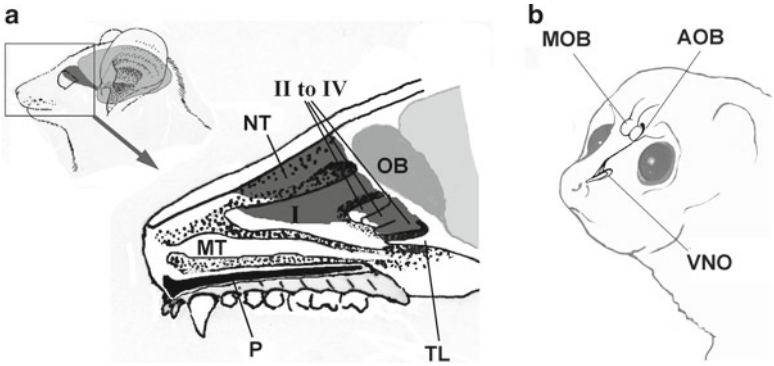


Fig. 27.1 Main and accessory olfactory systems of strepsirhines, based on *Microcebus murinus* (**a**) and *Otolemur garnettii* (**b**). The olfactory bulb (OB) mostly comprises the "main olfactory bulb," and it receives axons from the olfactory neuroepithelium, which covers the dorsocaudal surfaces of the nasoturbinal (NT), the ethmoturbinals (I–IV), and adjacent parts of the nasal septum (not pictured). Olfactory surface area is indicated by *dark gray* (1B). The accessory olfactory bulb (AOB, 1B) comprises a small dorsolateral patch of the entire OB mass. The AOB receives axons from the vomeronasal organ (VNO). Drawings by T.D.S. (**a**) and L.J.A. (**b**). Figure (**b**) is © 2008, Laura J. Alport

(Alport 2004), and the possibility that the AOS can detect food odorants reveals more potential for functional overlap (Halpern et al. 2005). The increasingly complex picture of olfactory chemoreception in mammals demands closer scrutiny of physiological and anatomical variations in these sensory systems. Here, we discuss variation and ontogeny of the peripheral sensory organs of the MOS and AOS: the olfactory neuroepithelium, which transmits its axons to the MOB, and the vomeronasal neuroepithelium, which transmits its axons to the AOB.

Olfactory Neuroepithelium

The works of Kollmann and Papin (1925) and Cave (1973) provide a comprehensive description of the internal anatomy of the strepsirhine nose and demonstrate a fundamental distinction between strepsirhine and haplorhine nasal configurations. In all strepsirhines, the posterior-most ethmoturbinal(s) are sequestered within an enclosed space termed the olfactory recess (ethmoturbinal recess and cupular recess), separated from the nasopharyngeal meatus by a bony plate called the transverse lamina (Fig. 27.1a; Smith et al. 2007a, b). This appears to be a primitive arrangement for mammals. In many nonprimate mammals, the olfactory recess is predominantly lined with olfactory neuroepithelium (Clancy et al. 1994; Craven et al. 2007).

The few detailed studies of the histology of strepsirhine nasal fossae suggest they resemble the general mammalian pattern (Loo 1974; Smith et al. 2007a, b), although a dichotomy exists among taxa. In cheirogaleids and lorisoids, only the last ethmoturbinal is fully enclosed in the olfactory recess (Fig. 27.1a); the first ethmoturbinal is proportionally long and elaborated and overlaps the maxilloturbinal substantially. In lemurids, the majority of ethmoturbinals II–IV are fully sequestered (Smith and Rossie 2008; Smith et al. 2011; Smith, unpublished observations), and the first ethmoturbinal shows less maxilloturbinal overlap (Smith et al. 2007a, b).

The distribution of olfactory epithelium across ethmoturbinals in strepsirhines is generally similar to other mammals (Loo 1974). However, Smith et al. (2007a, b) noted that olfactory and nonolfactory epithelia scale differently relative to head or snout size. In galagids and cheirogaleids, nonolfactory surface area is nearly isometric with cranial or palatal length, whereas olfactory surface area is negatively allometric. Ontogenetic data indicate that the most rostral ethmoturbinal grows in tandem with palatal (and thus snout) length. However, disproportionately more of the surface area is nonolfactory (Smith et al. 2007a, b), suggesting the term "olfactory snout" may be a misnomer for strepsirhines.

Vomeronasal Neuroepithelium

The strepsirhine vomeronasal organ is organized similarly to that of most other mammals and an accessory olfactory bulb is present (Fig. 27.1b). The vomeronasal organ is an elongated tube composed of a discrete, ventromedial neuroepithelium and a dorsolateral nonsensory epithelium (Schilling 1970; Smith et al. 2007a, b).

Table 27.1 Measurements of the vomeronasal neuroepithelium in strepsirhine primates

Species	Neonatal VNNEL (*n*)	Adult VNNEL (*n*)
Microcebus murinus	2.9 (1)	5.5–6.1 (2)
Cheirogaleus medius	2.7–2.9 (2)	4.3–4.6 (2)
Galago moholi	1.9 (1)	3.8–4.3 (2)
Otolemur garnettii	3.0 (2)	6.3 (9)
Otolemur crassicaudatus	3.3 (2)	7.0 (6)
Eulemer macaco	3.1 (1)	8.4 (1)

Few departures from this organization have been observed. Evans (2006) described a relatively reduced (immature) neuroepithelium in a newborn *Nycticebus coucang* and an unusual vomeronasal organ in adult *Lemur catta*, in which the entire epithelial tube was neuroepithelium (Evans 1984). However, Smith et al. (2007a, b, unpublished observations) observed a typical vomeronasal organ morphology in newborn and adult *Lemur catta*. The descriptions by Evans (1984, 2006) should be confirmed with other samples to exclude the possibility that they are not from aberrant specimens or observations based on inappropriate cross-sectional levels.

Few studies have provided quantitative details on the vomeronasal neuroepithelium (VNNE) of strepsirhines (Schilling 1970; Hedewig 1980a, b; Evans and Schilling 1995). Our study of *Otolemur* (Smith et al. 2005) includes the largest sample to date. In this genus, the thickness and volume of the VNNE are sexually dimorphic (males > females) and also vary with age. Growth is likely on a par with that observed in rats. Unpublished data on VNNE length in neonatal and adult specimens from six species suggest this may be true of most or all strepsirhines (Table 27.1). Although length is a crude proxy for receptor numbers, VNNE lengths are approximately twice as long in adults as in newborns in all species except *Cheirogaleus medius*. VNNE volumetric increase in strepsirhines appears to be exponential (Smith et al. 2005). In terms of growth, the VNNE of strepsirhines may resemble that of certain rodents (e.g., rats; Segovia and Guillamon 1982; Weiler et al. 1999).

Ontogeny of the Peripheral Olfactory Structure in Strepsirhines

We examined the olfactory neuroepithelium (OE) and VNNE of neonatal strepsirhines (Smith et al. 2007a, b). At birth, strepsirhines vary in rostrocaudal length of the VNNE and OE, with the latter scaling closely with cranial length (Fig. 27.2a). In contrast, VNNE length is more variable (Fig. 27.2b); certain taxa have long VNNE relative to cranial length (cheirogaleids), and some, relatively short VNNE (*Lemur catta* and *Hapalemur griseus*). Each of these plots suggests some phylogenetic and/or ecological effects. OE length could be interpreted to distribute in two linear grades, with nocturnal groups scaling higher than diurnal groups, as in adult olfactory bulbs (Barton et al. 1995). Although VNNE length shows a similar

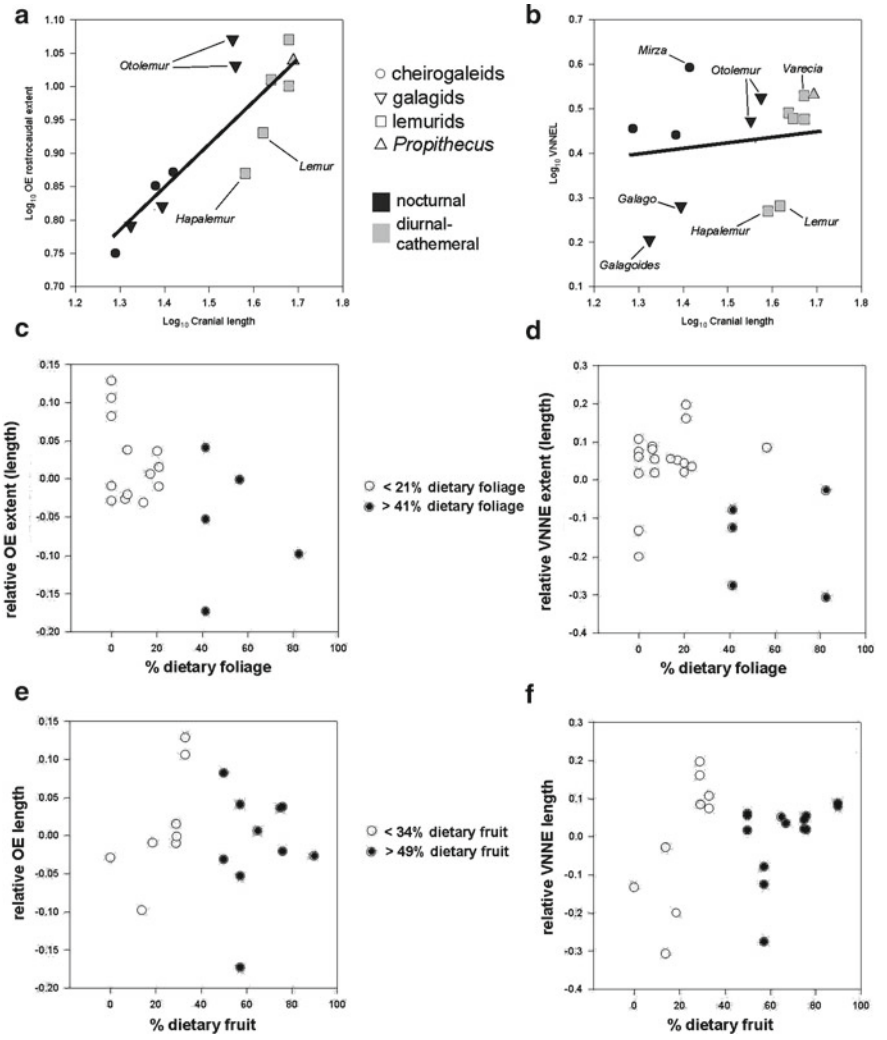


Fig. 27.2 (**a**) Olfactory neuroepithelium (OE) and (**b**) vomeronasal neuroepithelium (VNNE) rostrocaudal length plotted against cranial length in strepsirhines at birth. All data were log transformed. Lines are from linear regression equations. Some data points represent means of more than one specimen. (**c**–**f**) Scatter plots of relative OE length (*left*), and relative VNNE extent (*right*) against % dietary foliage (**c**, **d**) and % dietary fruit (**e**, **f**)

pattern, certain species or families are outliers. Smith et al. (2007a, b) analyzed these measurements with respect to life history characteristics and found that more altricial species (those with shorter relative gestational lengths and smaller relative neonatal masses) have a relatively longer VNNE at birth. These findings suggest that ecological trends relating to activity pattern may be established at birth in strepsirhines.

Table 27.2 Pearson correlation coefficients of the $\log_{10}$ and relative VNNE and relative OE length measurements with dietary variables

		% Dietary fruit	% Dietary foliage
Relative VNNE length	Pearson correlation	0.284	–0.422[a]
	Sig. (2-tailed)	0.189	0.045
	N	23	23
Relative OE length	Pearson correlation	0.009	–0.551[a]
	Sig. (2-tailed)	0.973	0.018
	N	18	18

[a]Correlation is significant at $P<0.05$

Table 27.3 Mann–Whitney *U*-test of relationship between olfactory structure length and activity pattern (nocturnal vs. cathemeral-diurnal)

	Relative VNNE length	Relative OE length
Mann–Whitney *U*	46.000	15.000
Z	–1.231	–1.747
Asymp. Sig. (2-tailed)	0.218	0.081
Exact Sig. [2×(1-tailed)]	0.235(a)	0.091(a)

We reanalyzed the above sample, including additional specimens for a total of 23 specimens representing 14 species, with respect to dietary variables. Since the MOS and AOS covary in strepsirhines (Barton 2006), we analyzed both olfactory systems. Measurements were taken using a light microscope, including the length of the VNNE and OE on one side of the nasal cavity [see Smith et al. (2007a, b) for further details]. Data were corrected for body size using cranial length and analyzed in relation to diet and activity pattern. "Relative length" of the epithelia was equivalent to the residuals from linear regression equations of log-transformed VNNE or OE lengths relative to cranial lengths.

Figure 27.2c–f illustrates the distribution of relative OE and VNNE lengths plotted against % dietary fruit or foliage. As suggested by the plots, statistical analyses reveal no significant correlation between percent frugivory and relative VNNE or OE length. In contrast, percent folivory was negatively correlated with relative OE length (Pearson $r=-0.55$; $P=0.01$; Table 27.2). Relative VNNE length was also negatively correlated with percent Folivory (Pearson $r=-0.422$; $P=0.045$). The negative correlation between folivory and olfactory structures could be explained by relaxed selection pressure on olfaction in folivores compared with other dietary specialists. Given the small sample, it is not clear how phylogeny or other factors (e.g., body size) may have influenced these results.

In contrast to the pattern observed in adult strepsirhines, Mann–Whitney *U*-tests showed no significant differences in relative VNNE or OE length between nocturnal and diurnal/cathemeral species (Table 27.3). Further analysis with larger samples

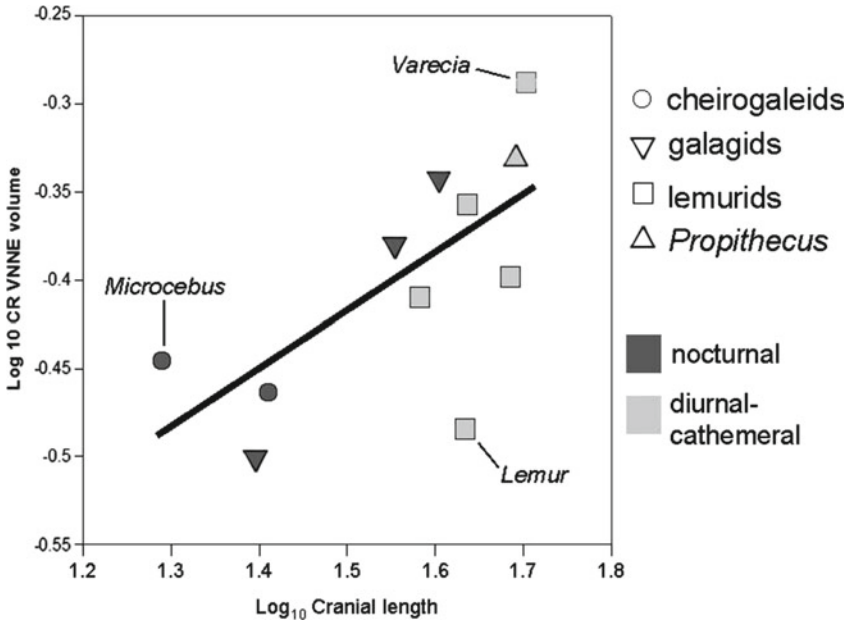


Fig. 27.3 Cube root (CR) of vomeronasal neuroepithelium (VNNE) rostrocaudal length plotted against cranial length in strepsirhines at birth. All data were log transformed. Lines are from a linear regression equation. Some data points represent means of more than one specimen

may yield different results, or they may simply reflect certain phylogenetic trends. For example, an apparent dichotomy between nocturnal and diurnal species is also a separation between cheirogaleids and galagids versus lemurids and *Propithecus*. The difficulty of excluding phylogenetic constraints was previously noted by Smith et al. (2007a, b), and sample sizes remain too small to resolve the issue at present.

Another unresolved issue is the extent to which these linear data correspond to measurements like surface area or volume, which may relate more closely to olfactory sensitivity in that they correlate with cell numbers in two- or three-dimensional space. Data on olfactory surface area are few for adult samples due to the rarity of well-preserved histological material. To date, only a few of the neonates examined by Smith et al. (2007a, b) have been measured for olfactory surface area. However, data on VNNE volume are shown in Fig. 27.3 (see Smith et al. 2005 for methods of measurement). This plot suggests a more linear relationship compared to the VNNE length plot (Fig. 27.2b), but they show similarities. In both plots, galagids show the most linear relationship between VNNE size and cranial length, and *Lemur* falls well below the regression line. Two litter-bearing species, *Microcebus* and *Varecia*, fall farthest above the regression line, offering support for the idea that altricial primates possess a relatively large VNNE at birth (Smith et al. 2007a, b).

Future Considerations

Quantitative data on peripheral olfactory structures are few. We have discussed the extent to which ecological correlates of vomeronasal and main olfactory structure size are reflected early in strepsirhine ontogeny. Although phylogenetic effects cannot be excluded at present, peripheral olfactory structures deviate from a clear linear relation to head size at birth. Our data suggest trends: size of peripheral olfactory structures may vary according to activity pattern or folivory.

Unfortunately, information on the ontogeny and cellular biology of mammalian olfactory organs, particularly the vomeronasal organ, is heavily biased toward rodents (Halpern and Martínez-Marcos 2003). Maturational characteristics of the VNNE and the VNO ducts vary among rodent species; some authors (e.g., Coppola et al. 1993) have suggested that the capacity for perinatal chemoreception also differs. Intriguingly, immunohistochemical markers of terminally differentiated vomeronasal and olfactory receptor neurons are expressed in some neonatal primates more than others (Smith et al. 2007a, b). Thus, growth and maturational studies of strepsirhine olfactory systems may yield important information for the evolution of primate sociosexual biology.

The sample described in this chapter comprises the largest data set of primate peripheral olfactory organs studied to date but has limited implications on its own. Data from adult samples are currently scarce, so postnatal ontogeny remains largely unknown. Further comparative studies of primate olfactory structures are essential. Given that the fossil record is largely silent on the evolution of soft tissue structures (Smith et al. 2007a, b), extant strepsirhines remain our primary window into understanding the chemosensory systems of primate ancestors.

Acknowledgments We thank the N.J. Dominy and B.M. Siemers for inviting us to participate in this timely discussion. Thanks also to two reviewers and J. Masters for helping to improve our manuscript.

References

Alport LJ (2004) Comparative analysis of the role of olfaction and the neocortex in primate intrasexual competition. Anat Rec 281A:1182–1189

Barton RA (2006) Olfactory evolution and behavioral ecology in primates. Am J Primatol 68:545–558

Barton RA, Purvis A, Harvey PH (1995) Evolutionary radiation of visual and olfactory brain systems in primates, bats and insectivores. Philos Trans R Soc Lond B 348:381–392

Cave AJE (1973) The primate nasal fossa. Biol J Linn Soc 5:377–387

Clancy AN, Schoenfeld TA, Forbes WB, Macrides F (1994) The spatial organization of the peripheral olfactory system of the hamster II: receptor surfaces and odorant passageways within the nasal cavity. Brain Res Bull 34:211–241

Coppola DM, Budde J, Millar L (1993) The vomeronasal duct has a protracted postnatal development in the mouse. J Morphol 218:59–64

Colquhoun IC (2011) A review and interspecific comparison of nocturnal and cathemeral strepsirhine primate olfactory behavioural ecology. Int J Zool, Article ID362976, 11 p. 10.1155/2011/362976

Craven BA, Neuberger T, Paterson EG, Webb AG, Josephson EM, Morrison EE, Settles GS (2007) Reconstruction and morphometric analysis of the nasal airway of the dog (*Canis familiaris*) and implications regarding olfactory airflow. Anat Rec 290:1325–1340

Evans CS (1984) On the structure and function of accessory chemoreceptive organs. Acta Zool Fenn 171:57–62

Evans CS (2006) Accessory chemosignaling mechanisms in primates. Am J Primatol 68:525–544

Evans CS, Schilling A (1995) The accessory (vomeronasal) chemoreceptor system in some prosimians. In: Alterman L, Doyle GA, Izard MK (eds) Creatures of the dark: the nocturnal prosimians. Plenum, New York, pp 393–411

González A, Morona R, López JM, Moreno N, Northcutt RG (2010) Lungfishes, like tetrapods, possess a vomeronasal system. Front Neuroanat 4:130

Halpern M, Martínez-Marcos A (2003) Structure and function of the vomeronasal system: an update. Prog Neurobiol 70:245–318

Halpern M, Daniels Y, Zuri I (2005) The role of the vomeronasal system in food preferences of the gray short-tailed opossum, *Monodelphis domestica*. Nutr Metab 2:6

Hedewig R (1980a) Vergleichende anatomische untersuchungen an den Jacobsonschen organen von *Nycticebus coucang* Boddaert, 1785 (Prosimiae, Lorisidae) und *Galago crassicaudatus.* E. Geoffroy, 1812 (Prosimiae, Lorisidae). I. *Nycticebus coucang*. Gegenb Morphol Jahrb 126:543–593

Hedewig R (1980b) Vergleichende anatomische untersuchungen an den Jacobsonschen organen von *Nycticebus coucang* Boddaert, 1785 (Prosimiae, Lorisidae) und *Galago crassicaudatus* E. Geoffroy, 1912 (Prosimiae, Lorisidae). II. *Galago crassicaudatus*. Gegenb Morphol Jahrb 126:676–722

Kollmann M, Papin L (1925) Etudes sur lémuriens Anatomie comparée des fosses nasales et de leurs annexes. Arch Morph Gén Exp 22:1–60

Loo SK (1974) Comparative study of the histology of the nasal fossa in four primates. Folia Primatol 21:290–303

Maier W (1980) Nasal structures in old and new world primates. In: Ciochon RL, Chiarelli B (eds) Evolutionary biology of the new world monkeys and continental drift. Plenum, New York, pp 219–241

Mertl-Millhollen AS (2006) Scent marking as resource defense by female *Lemur catta*. Am J Primatol 68:605–621

Schilling A (1970) L'organe de Jacobson du lemurien malgache *Microcebus. murinus*. Mem Mus d'Hist Nat A 61:203–280

Segovia S, Guillamon A (1982) Effects of sex steroids on the development of the vomeronasal organ in the rat. Dev Brain Res 5:209–212

Siemers BM, Goerlitz HR, Robsomanitrandrasana E, Piep M, Ramanamanjato JB, Rakotondravony D, Ramilijaona O, Ganzhorn JU (2007) Sensory basis of food detection in wild *Microcebus murinus*. Int J Primatol 28:291–304

Smith TD, Bhatnagar KP, Burrows AM, Shimp KL, Dennis JC, Smith MA, Maico-Tan L, Morrison EE (2005) The vomeronasal organ of greater bushbabies (*Otolemur* spp.): species, sex, and age differences. J Neurocytol 34:135–147

Smith TD, Rossie JB, Bhatnagar KP (2007a) Evolution of the nose and nasal skeleton in primates. Evol Anthropol 16:132–146

Smith TD, Alport LJ, Burrows AM, Bhatnagar KP, Dennis JC, Tuladhar P, Morrison EE (2007b) Perinatal size and maturation of the olfactory and vomeronasal neuroepithelia in lorisoids and lemuroids. Am J Primatol 69:74–85

Smith TD, Rossie JB (2008) The nasal fossa of mouse and dwarf lemurs (Primates, Cheirogaleidae). Anat Rec 291:895–915

Smith TD, Eiting TP, Rossie JB (2011) Distribution of olfactory and nonolfactory surface area in the nasal fossa of *Microcebus murinus*: implications for microcomputed tomography and airflow studies. Anat Rec 294:1217–1225

Stephan H, Baron G, Frahm HD (1982) Comparison of brain structure volumes in Insectivora and Primates, II. Accessory olfactory bulb (AOB). J Hirnforsch 23:575–591

Weiler E, McCulloch MA, Farbman AI (1999) Proliferation in the vomeronasal organ of the rat during postnatal development. Eur J Neurosci 11:700–711

Chapter 28
The Sensory Ecology of Foraging for Animal Prey

Björn M. Siemers

Abstract Many prosimians eat animal food, including arthropods and small vertebrates. This chapter explores the clues prosimians rely on to detect and identify animal prey, and their sensory adaptations for predation. Available observational and experimental datasets suggest that acoustic and visual (especially motion) cues, as well as olfactory and tactile ones, to a lesser degree, play a role. Different sensory channels are likely to operate in prey perception over different distances. It appears that acoustic cues first draw the animal's attention to prey at a distance, while visual cues are used for precise localization at closer range, and olfactory cues operate at very close range to allow the animal to abandon attacks on unpalatable arthropods. Future work should address the role of sensory ecology in shaping prey selection and resource partitioning in prosimians.

Resume De nombreux prosimiens se nourrissent de nourriture animale et en particulier d'insectes et de petits vertébrés. Ce chapitre explore les informations utilisées par les prosimiens pour détecter et identifier leurs proies, ainsi que les adaptations sensorielles à la prédation observées chez ces animaux. Les données expérimentales et les observations suggèrent que les informations acoustiques et visuelles (particulièrement le mouvement), et dans une moindre mesure, les informations olfactives et tactiles jouent un rôle dans la prédation. Différents sens sont probablement utilisées à plus ou moins grande distance des proies. Il apparait que les informations acoustiques sont les premières à alerter les animaux quand les proies sont éloignées, alors que les informations visuelles sont utilisées pour détecter les proies plus proches,

B.M. Siemers (✉)
Sensory Ecology Group, Max-Planck Institute for Ornithology,
Eberhard-Gwinner-Strasse, 82319 Seewiesen, Germany
e-mail: siemers@orn.mpg.de

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_28,

et qu'enfin, les informations olfactives permettent aux animaux d'abandonner les insectes non comestibles, à très courte distance. De futurs travaux devraient s'intéresser aux relations entre l'écologie sensorielle, la sélection des proies et le partitionnement des ressources chez les prosimiens.

Introduction

Many prosimians eat animal food (e.g., Charles-Dominique 1977; Hladik 1979). Arthropods and small vertebrates form an important part of the diet of Asian tarsiers (*Tarsius*) and lorises (*Loris* and *Nycticebus*), African bushbabies (*Galago*, *Galagoides*, and *Otolemur*) and pottos (*Arctocebus* and *Perodicticus*), and many Malagasy lemurs (*Daubentonia*, *Microcebus*, *Cheirogaleus*, *Mirza*, and *Phaner*). Plants have an evolutionary advantage when their flowers or fruit are conspicuous to the specific sensory systems of potential pollinators or seed dispersers (Howe and Smallwood 1982), but the opposite is true of animal prey, which are selected to avoid detection by foraging predators. This chapter explores the kinds of cues prosimians rely on to detect and identify animal prey and the adaptations of their sensory modalities for successful predation.

Auditory Cues

Prey animals inadvertently reveal their whereabouts by communication signals and locomotor sounds. Walking arthropods produce a series of broadband clicks when their feet and body touch the substrate; the amplitude of these sounds depends on arthropod size and type, as well as the nature of the substrate (Siemers and Güttinger 2006; Goerlitz and Siemers 2007; Goerlitz et al. 2008). Observational reports of hunting behavior in tarsiers (*Tarsius* spp., Niemitz 1979; MacKinnon and MacKinnon 1980), galagos (Charles-Dominique and Martin 1972; Doyle 1974), and mouse lemurs (Martin 1972) suggest that listening for prey-generated sounds plays a major role in prey perception by nocturnal, insectivorous prosimians. Their large, mobile pinnae (Coleman and Ross 2004) increase sound detection and localization (Obrist et al. 1993). Behavioral experiments have shown that mouse lemurs use arthropod rustling sounds to detect and potentially to identify their prey (Goerlitz and Siemers 2007; Siemers et al. 2007; Piep et al. 2008). When given the choice, they preferred the louder of two simultaneously presented rustling sounds, which would generally indicate larger and more profitable prey items (Goerlitz and Siemers 2007). The aye-aye (*Daubentonia madagascariensis*) listens with its enormous ears for sounds produced by wood-boring insects and reverberations from its own finger-tapping (Erickson 1991, 1994; Erickson et al. 1998). Prey sounds transmit through vegetation independently of illumination levels, and prosimians foraging in dense vegetation at night will generally be able to hear noisy prey over larger distances than they will be able to see it. With respect to what they actually hear, the auditory brainstem response (ABR) method now offers a time-efficient tool to measure at least some

aspects of prosimian auditory sensitivity under field conditions and using a comparative approach (Ramsier and Dominy 2010; Chap. 29).

Visual Cues

All nocturnal prosimians have large sensitive eyes, many with a light reflecting *tapetum lucidum* behind the retina that increases photon-harvesting ability (Ross 2000; Dkhissi-Benyahya et al. 2001; Kirk 2004). They can thus potentially use visual cues to detect and track prey. Cartmill's (1972, 1974, 1992) "visual predation hypothesis" suggests that enhanced visual prey detection was a major driving force in the evolution of stereoscopy in early primates (see also Heesy et al. 2011). Indeed, tarsiers (*Tarsius* spp., Crompton 1995) and slender lorises (*Loris lydekkerianus*, Nekaris 2005) are able to detect motionless insects visually in densely packed, complex-shaded forest environments. By contrast, wild mouse lemurs in short-term captivity hardly attacked prey when only stationary visual cues were available (Siemers et al. 2007), whereas moving prey clearly attracted their attention. Captive-born mouse lemurs could detect motionless mealworms using visual information (Piep et al. 2008); conceivably, the low diversity of prey types they encountered, coupled with the rather simple structure of the laboratory environment, might have allowed them to build up an efficient visual search image. In the wild, the richly structured vegetational background will hide prey, and search image formation will be complicated by the large taxonomic and structural variety of potentially edible arthropods and vertebrate prey.

Olfactory Cues

When faced with the task of detecting a hidden mealworm by smell, laboratory raised mouse lemurs performed just around the threshold of statistical significance (Piep et al. 2008), whereas olfactory detection of fruit (banana) is an easy task for mouse lemurs (Siemers et al. 2007). This difference can be explained by differential sensitivity to odorants emanating from insects and fruit and, more importantly, by different cue strengths. The importance of cue strength receives support from an experiment with greater galagos (*Ottolemur garnettii*), which performed poorly in trials with one mealworm but had no problem localizing ten noiseless, hidden mealworms using olfaction (B. M. Siemers, A. Wetzhold and I. Kaipf, unpublished data). Shrews (Churchfield 1990), the New Zealand short-tailed bat (*Mystacina tuberculata*, Jones et al. 2003) and several other insect-eating mammals effectively use olfaction for close-range detection and location of arthropods. In primates, however, the role of olfaction for the detection of animal prey is less clear. Data gathered by Piep et al. (2008) indicated that odor emanating from mealworms gives a weak, but still informative, prey cue to mouse lemurs. Nekaris (2005) observed that wild slender lorises occasionally use olfaction for finding prey, chiefly in their search for repellent, strong-smelling beetles and for slugs. It thus appears that arthropod odors,

in sufficiently high concentration, can play a role in directing prosimians to their prey, at least over short distances. Further studies are needed to identify the odorants emanating from insects and to characterize prosimian olfactory sensitivity to them. Generally, the olfactory sense of strepsirrhine primates is regarded as well developed and scent is important for intraspecific communication in strepsirrhines (e.g., Palagi et al. 2004) and also in tarsiers (Gursky-Doyen 2010).

Tactile Cues

The tap-scanning movements of the aye-aye, probing logs and tree trunks with its elongated third finger to find wood-boring insects, are surely the most pre-eminent example of prosimian tactile foraging. In a series of experiments, Erickson (1991, 1994) and Erickson et al. (1998) investigated the aye-aye's "percussive foraging" and suggested that both tactile and auditory cues resulting from the finger-tapping play a part. Muchlinski (2010; Chap. 25) examined the size of the infraorbital foramen as a measure of rostral touch acuity. The infraorbital nerve, which conveys tactile information from the vibrissae (whiskers), passes through this foramen. Muchlinski (Chap. 25) found that prosimians do not have enlarged infraorbital foramina compared with anthropoids, concluding that prosimians—as for primates in general—may have reduced maxillary mechanoreception.

Use of Multimodal Information

Many different groups of animals additively use or integrate different sensory modalities for vital behavioral tasks like foraging, spatial orientation, or mate choice (von der Emde and Bleckmann 1998; Uetz and Roberts 2002; Cochran et al. 2004). Sensory ecology data indicate that this also applies to foraging prosimians. Different sensory channels are likely to operate for prey perception over different distances (Dominy et al. 2001). Conceivably, acoustic cues first draw the animal's attention to prey at long range, while visual cues are used for precise localization at closer range, and olfactory cues are used at very close range to abandon attacks on unpalatable arthropods (Piep et al. 2008).

The Role of Sensory Ecology for Prey Selection and Resource Partitioning

Prey cues and the specific structuring of animal sensory systems constrain both foraging behavior and access to food (Endler 1991; Faure and Barclay 1992; Siemers and Schnitzler 2004). Apparent selectivity and specialization on a certain prey type

can to some degree be explained by the conspicuousness of the prey to the foragers' sensory systems (Siemers and Güttinger 2006; Siemers and Swift 2006; Safi and Siemers 2010). From a functional ecological perspective, food availability in the field should be viewed through a prosimian eye and ear in order to understand the role sensory bias plays in shaping their diets.

A number of studies on closely related animal species have identified morphological differences (e.g., canine or beak size) which lead to differential mechanical access to food (for a summary, see Schluter 2000). Less attention has been paid to interspecific differences in the senses used by animals to detect food and their contribution to resource partitioning within animal communities (e.g., Bernays and Wcislo 1994; Siemers and Schnitzler 2004; Siemers and Swift 2006; Safi and Siemers 2010). If a given prey type is easily detectable by one predator species but not by another, this means the same prey is differentially available, even if the predators forage in the same habitat. Sensory performance is crucial for foraging efficiency in prosimians, and comparative studies of prosimian sensory capacities would allow an exploration of their importance in niche differentiation within prosimian communities. This would augment a growing awareness in primatology of the importance of the evolution and ecology of sensory adaptation. For example, changes in sensory ecology and brain organization have recently been highlighted as crucial in setting the stage for the emergence of the human lineage (Williams et al. 2010).

Acknowledgments I thank the following colleagues for cooperation and support in researching the sensory ecology of mouse lemurs: Holger Goerlitz, Marcus Piep, Eric Robsomanitrandrasana, Jörg Ganzhorn, Ute Radespiel, Sabine Schmidt, Elke Zimmermann, Jean-Baptiste Ramanamanjato, Daniel Rakotondravony, Olga Ramilijaona, and Manon Vincelette. This work and associated discussions and reading provided the basis for this summary chapter. Thanks to Nathaniel Dominy for organizing the "sensory and cognitive ecology symposium" with me at Ithala and for many inspiring discussions. I am grateful to Judith Masters for making the splendid conference and this volume possible. Bakri Nadhurou provided the French translation of the summary.

References

Bernays EA, Wcislo WT (1994) Sensory capabilities, information processing and resource specialization. Q Rev Biol 69:187–204

Cartmill M (1972) Arboreal adaptations and the origin of the order primates. In: Tuttle R (ed) The functional and evolutionary biology of the primates. Aldine Atherton, Chicago, pp 97–122

Cartmill M (1974) Rethinking primate origins. Science 184:436–443

Cartmill M (1992) New views on primate origins. Evol Anthropol 1:105–111

Charles-Dominique P, Martin RD (1972) Behaviour and ecology of nocturnal prosimians: field studies in Gabon and Madagascar. Parey, Berlin

Churchfield S (1990) The natural history of shrews. Comstock, Ithaca

Charles-Dominique P (1977) Ecology and behaviour of nocturnal primates. Columbia University Press, New York

Cochran B, Mouritsen H, Wikelski M (2004) Migrating songbirds recalibrate their magnetic compass daily from twilight cues. Science 304:405–408

Coleman MN, Ross CF (2004) Primate auditory diversity and its influence on hearing performance. Anat Rec A Discov Mol Cell Evol Biol 281A:1123–1137
Crompton RH (1995) Visual predation, habitat structure and the ancestral primate niche. In: Alterman L, Doyle GA, Izard MK (eds) Creatures of the dark: the nocturnal prosimians. Plenum, New York, pp 11–30
Dkhissi-Benyahya O, Szel A, Degrip WJ, Cooper HM (2001) Short and mid-wavelength cone distribution in a nocturnal strepsirhine primate (*Microcebus murinus*). J Comp Neurol 438:490–504
Dominy NJ, Lucas PW, Osorio D, Yamashita N (2001) The sensory ecology of primate food perception. Evol Anthropol 10:171–186
Doyle GA (1974) Behavior of prosimians. In: Schrier AM, Stollnitz F (eds) Behavior of nonhuman primates. Academic, New York, pp 155–353
Endler JA (1991) Interactions between predators and prey. In: Krebs JR, Davies NB (eds) Behavioural ecology: an evolutionary approach, 3rd edn. Blackwell, Oxford, pp 169–196
Erickson CJ (1991) Percussive foraging in the aye-aye, *Daubentonia madagascarensis*. Anim Behav 41:793–801
Erickson CJ (1994) Tap-scanning and extractive foraging in aye-ayes, *Daubentonia madagascarensis*. Folia Primatol 62:125–135
Erickson CJ, Nowicki S, Dollar L, Goehring N (1998) Percussive foraging: stimuli for prey location by aye-ayes (*Daubentonia madagascarensis*). Int J Primatol 19:111–122
Faure PA, Barclay RMR (1992) The sensory basis of prey detection by the long-eared bat, *Myotis evotis*, and the consequences for prey selection. Anim Behav 44:31–39
Goerlitz HR, Siemers BM (2007) Sensory ecology of prey rustling sounds: acoustical features and their classification by wild Grey Mouse Lemurs. Funct Ecol 21:143–153
Goerlitz HR, Greif S, Siemers BM (2008) Cues for acoustic detection of prey: insect rustling sounds and the influence of walking substrate. J Exp Biol 211:2799–2806
Gursky-Doyen SL (2010) The function of scentmarking in spectral tarsiers. In: Gursky SL, Supriatna J (eds) Indonesian primates. Springer, New York, pp 359–369
Heesy CP, Kamilar JM, Willms J (2011) Retinogeniculostriate pathway components scale with orbit convergence only in primates and not in other mammals. Brain Behav Evol 77:105–115
Hladik CM (1979) Diet and ecology of prosimians. In: Doyle GA, Martin RD (eds) The study of prosimian behavior. Academic, New York, pp 307–357
Howe HF, Smallwood J (1982) Ecology of seed dispersal. Annu Rev Ecol Syst 13:201–228
Jones G, Webb PI, Sedgeley JA, O'Donnell CFJ (2003) Mysterious *Mystacina*: how the New Zealand short-tailed bat (*Mystacina tuberculata*) locates insect prey. J Exp Biol 206: 4209–4216
Kirk CE (2004) Comparative morphology of the eye in primates. Anat Rec A Discov Mol Cell Evol Biol 281A:1095–1103
MacKinnon J, MacKinnon K (1980) The behaviour of wild spectral tarsiers. Int J Primatol 1:361–379
Martin RD (1972) A preliminary field-study of the lesser mouse lemur (*Microcebus murinus* J. F. Miller 1777). In: Charles-Dominique P, Martin RD (eds) Behaviour and ecology of nocturnal prosimians. Field studies in Gabon and Madagascar. Parey, Berlin, pp 43–85
Muchlinski MN (2010) Ecological correlates of infraorbital foramen area in primates. Am J Phys Anthropol 141:131–141
Nekaris KAI (2005) Foraging behaviour of the slender loris (*Loris lydekkerianus lydekkerianus*): implications for theories of primate origins. J Hum Evol 49:289–300
Niemitz C (1979) Outline of the behavior of *Tarsius bancanus*. In: Doyle GA, Martin R (eds) The study of prosimian behavior. Academic, New York
Obrist MK, Fenton MB, Eger JL, Schlegel PA (1993) What ears do for bats: a comparative study of pinna sound pressure transformation in Chiroptera. J Exp Biol 180:119–152
Palagi E, Telara S, Tarli SMB (2004) Reproductive strategies in *Lemur catta*: balance among sending, receiving, and countermarking scent signals. Int J Primatol 25:1019–1031

Piep M, Radespiel U, Zimmermann E, Schmidt S, Siemers BM (2008) The sensory basis of prey detection in captive-born grey mouse lemurs (*Microcebus murinus*). Anim Behav 75:871–878

Ramsier MA, Dominy NJ (2010) A comparison of auditory brainstem responses and behavioral estimates of hearing sensitivity in *Lemur catta* and *Nycticebus coucang*. Am J Primatol 72:217–233

Safi K, Siemers BM (2010) Implications of sensory ecology for species coexistence: biased perception links predator diversity to prey size distribution. Evol Ecol 24:703–713

Schluter D (2000) The ecology of adaptive radiation. Oxford University Press, Oxford

Ross CF (2000) Into the light: the origin of Anthropoidea. Annu Rev Anthropol 29:147–194

Siemers BM, Schnitzler HU (2004) Echolocation signals reflect niche differentiation in five sympatric congeneric bat species. Nature 429:657–661

Siemers BM, Güttinger R (2006) Prey conspicuousness can explain apparent prey selectivity. Curr Biol 16:R157–R159

Siemers BM, Swift SM (2006) Differences in sensory ecology contribute to resource partitioning in the bats *Myotis bechsteinii* and *Myotis nattereri* (Chiroptera: Vespertilionidae). Behav Ecol Sociobiol 59:373–380

Siemers BM, Goerlitz HR, Robsomanitrandrasana E, Piep M, Ramanamanjato JB, Rakotondravony D, Ramilijaona O, Ganzhorn JU (2007) Sensory basis of food detection in wild *Microcebus murinus*. Int J Primatol 28:291–304

Uetz GW, Roberts JA (2002) Multisensory cues and multimodal communication in spiders: insights from video/audio playback studies. Brain Behav Evol 59:222–230

Von der Emde G, Bleckmann H (1998) Finding food: senses involved in foraging for insect larvae in the electric fish *Gnathonemus petersii*. J Exp Biol 201:969–980

Williams BA, Kay RF, Kirk EC (2010) New perspectives on anthropoid origins. Proc Natl Acad Sci USA 107:4797–4804

Chapter 29
Evolution of Auditory Sensitivity Among Strepsirhine Primates

Marissa A. Ramsier

Abstract Hearing is a crucial element of primate behavior and ecology. Beginning in 1969, traditional behavioral testing methods produced comparable audiograms for five strepsirhine taxa. Variation in this relatively small data set can be explained in part by head size, but relationships with social behavior and ecology have been elusive. Recently, with the use of auditory brainstem response (ABR) methods, standardized audiograms have been published for eleven strepsirhine species. Within this data set, social complexity explains a significant amount of the variation in auditory sensitivity, possibly because sociality favored an enhanced ability to detect conspecific vocalizations such as high frequency alarm calls. These findings shed light on the comparative biology of primate hearing and enable a reconstruction of the ancestral strepsirhine audiogram.

Resume L'audition est un élément essentiel de l'éco-éthologie des primates. Depuis 1969, les méthodes comportementales utilisées pour obtenir des audiogrammes comparables ont produits des résultats pour cinq taxa de strepsirhines. Les variations observées sur ce relativement petit échantillon s'expliquent en partie par l'effet de la taille de la tête, mais leurs relations avec la socio-écologie de ces animaux restent mystérieuses. Récemment, avec l'utilisation de la méthode de la Réponse Evoquée Auditive du tronc cérébral (REA), des audiogrammes standardisés ont été publiés pour onze espèces de strepsirhines. La variation de sensibilité auditive observée dans ce jeu de données s'explique par la complexité sociale, peut-être parce que la socialité favorise une capacité accrue à détecter les vocalisations spécifiques comme les alarmes émises à haute fréquence. Ces résultats éclairent la biologie comparée de l'audition des primates, et permettent de reconstruire un audiogramme ancestral des strepsirhines.

M.A. Ramsier (✉)
Department of Anthropology, Humboldt State University, Arcata, CA 95521, USA
e-mail: marissa.ramsier@humboldt.edu

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_29,

Introduction

Audition is central to primate survival and reproduction, and it can reasonably be assumed that natural selection has favored auditory sensitivities that vary as a function of socioecological parameters, yet progress has been slow and few adaptive relationships have been demonstrated. Initial data on the hearing sensitivities of primates were gathered by traditional behavioral methods during the 1960s and 1970s. Due in part to logistical and financial constraints, including limited access to species amenable to months of training and testing in laboratory settings, only five comparable audiograms are available for strepsirhine primates: *Galago senegalensis* (Heffner et al. 1969), *Nycticebus coucang* (Heffner and Masterton 1970), *Perodicticus potto* (Heffner and Masterton 1970), *Lemur catta* (Gillette et al. 1973), and *Phaner furcifer* (Niaussat and Molin 1978). Behavioral audiograms of two other species, *Eulemur fulvus* and *E. macaco* (Mitchell et al. 1971), are not comparable for methodological reasons (Coleman 2009).

The challenge of collecting behavioral audiograms drove researchers to develop alternative methods. Physiology-based techniques avert the need for subject training and are cost efficient. For example, in addition to constructing a behavioral audiogram for *Phaner furcifer*, Niaussat and Molin (1978) also used the auditory cortical response (ACR) method to test the auditory sensitivity of this species. Subsequently, Niaussat and Petter (1980) used the ACR method to construct audiograms for two more nocturnal strepsirhines, *Microcebus murinus* and *M. rufus*. Unfortunately, the comparative value of this method is difficult to assess. In *P. furcifer*, the ACR-derived audiogram was significantly elevated compared to the behavioral audiogram. Perhaps as a result of such inconsistencies, as well as the invasive nature of inserting electrodes directly into the auditory cortex, few subsequent studies have employed the ACR method for constructing primate audiograms. Another early physiology-based audiogram reported by Peterson et al. (1968) is problematic because subjects were sedated with barbiturates and their pinnae and cartilaginous external auditory meatus were removed—factors that affect auditory sensitivity (Belknap and Suthers 1982; Coleman and Ross 2004).

The absence of new comparative data over the past 30 years has frustrated efforts to understand how and why the hearing of strepsirhine primates varies (Heffner 2004; Coleman 2009; Kirk and Gosselin-Ildari 2009; Coleman and Colbert 2010). For four decades, head size has been viewed as the variable that best explains variation in high frequency hearing (Masterton et al. 1969; Heffner 2004). According to this model, species with larger interaural distances are better able to localize sound via interaural timing and spectral/intensity cues across a broad frequency spectrum. Smaller headed species, by contrast, experience shorter travel times between the ears and are less able to use interaural timing for localization; they must rely on higher frequencies (with shorter wavelengths) for localization via spectral/intensity cues. Strepsirhine primates generally fit this model; when compared with larger haplorhine species, they are more adept at detecting high frequencies and less so at detecting low frequencies. However, a smaller head does not always limit the detection of

low frequencies (Webster and Webster 1975), and there is substantial variation in primate behavioral audiograms that cannot be explained by head size (Coleman 2009).

Auditory Brainstem Response Method

Recently, Ramsier and Dominy (2010) tested the efficacy of the minimally invasive auditory brainstem response (ABR) method for constructing primate audiograms safely and efficiently, and without the need for invasive surgeries or subject training. Comparing behavioral and ABR-derived audiograms for a wide range of species, including *Lemur catta* and *Nycticebus coucang*, we found that the two methods produce audiograms with similar shapes, and that the frequency of best sensitivity (the frequency the subject can detect at the lowest level) and the high-frequency limit (the highest frequency detectable at 60 dB SPL) are comparable. Thus, the ABR method has emerged as an attractive alternative to behavioral testing.

Most significantly, the ABR method is portable and can be used to generate large, standardized data sets safely and efficiently. Ramsier et al. (2012) used ABR to generate new audiograms for eleven strepsirhine species. After controlling for phylogenetic relatedness, they found that variation in social group size explained a significant amount of the variation in enhanced auditory sensitivity, especially at higher frequencies. This result can partly be explained by a model of social drive, wherein the adaptive advantages of sociality have favored an enhanced ability to hear and respond to conspecific vocal signals. Although further testing of the concept is needed, it represents a significant theoretical advance in our understanding of primate audition. It also facilitates an ancestral character state analysis. To highlight this potential and fuel future research, I have used all comparable behavioral and ABR-derived data to reconstruct the audiogram of the ancestral strepsirhine. Although such an analysis is at best provisional, it is relevant to models of the adaptive origins of primates.

Methods

For the ABR-derived data set, threshold values for species average audiograms were taken from Ramsier et al. (2012) for 500 Hz and half-octave steps from 1.0 to 64.0 kHz. For the behavioral data set, species average audiograms were estimated for the five species with comparable audiograms (see above). Threshold values for the tested frequencies were taken directly from, or estimated from audiograms within, the original sources. For *Galago senegalensis*, *Nycticebus coucang*, and *Perodicticus potto*, these values were checked against supplemental information made available by Heffner (http://homepages.utoledo.edu/rheffne/). In the behavioral data set, different frequencies were tested for each species; to control for this

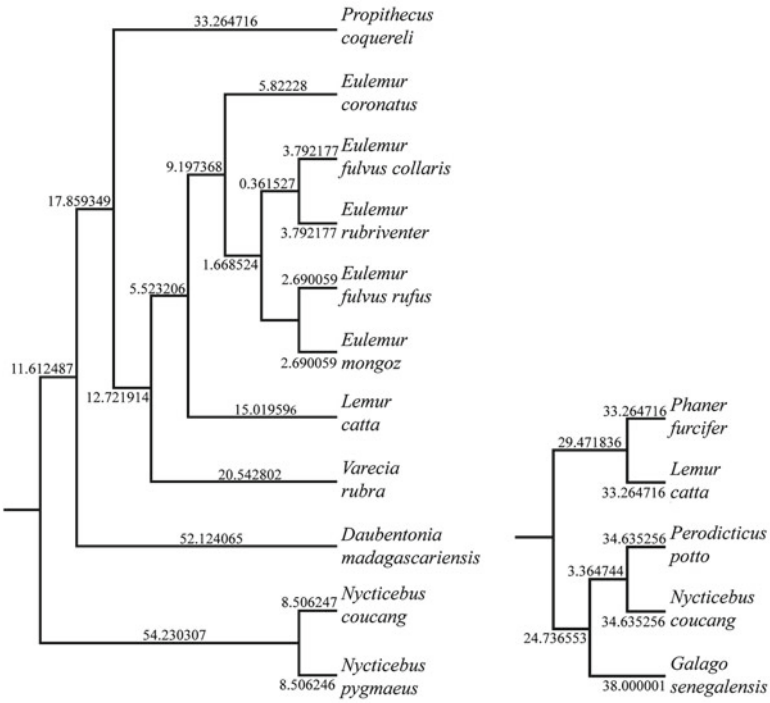


Fig. 29.1 Phylogenetic trees and branch lengths used for reconstruction of ancestral states

inconsistency, I estimated thresholds for 125, 250, and 500 Hz and half-octave steps from 1.0 to 64.0 kHz. I used these calculated thresholds to estimate the ancestral condition.

For both the behavioral and ABR-derived data sets, I reconstructed the ancestral condition (squared parsimony model; Finarelli and Flynn 2006) based on the species level phylogenies (Fig. 29.1) available in the 10kTrees project, version 3 (Arnold et al. 2010) and the PDAP:PDTREE module (Milford et al. 2008) of Mesquite v. 2.72, build 528 (Tucson, USA) (Maddison and Maddision 2010). For the ABR data, I log transformed branch lengths to account for lack of fit to the tip data (Milford et al. 2008).

Results and Discussion

Figure 29.2 illustrates the reconstructed ancestral audiograms from the behavioral and ABR-derived data sets. As expected, the absolute thresholds for the ABR-derived ancestral audiogram are elevated compared to the behavioral data

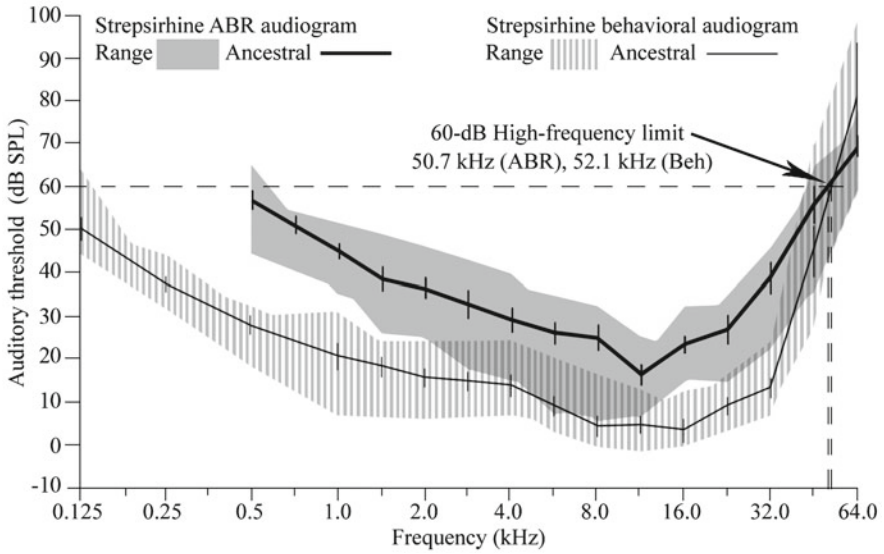


Fig. 29.2 Strepsirhine primate audiograms, including the range of all species (for calculated half-octave steps), and the reconstructed ancestral audiogram with standard error

(cf. Ramsier and Dominy 2010). This elevation is highly consistent, resulting in congruent shapes between the methods; an exception is the apparently elevated 64 kHz threshold for the behavioral audiogram, which can be explained by our high threshold estimate for *Perodicticus potto* (the highest frequency tested, 45.3 kHz, already had a threshold of 66 dB). For both data sets, the reconstructed ancestral audiogram has a region of enhanced sensitivity centered on ca. 11.3 kHz. Compellingly, the 60-dB high frequency limit is also a close match (ABR: 50.7 kHz and behavioral: 52.1 kHz) despite the fact that the data sets overlap in only two species. Such a remarkable level of agreement in the two most widely used auditory sensitivity parameters suggests that the ancestral strepsirhine was tuned to frequencies in the range of 8–16 kHz, and that the high frequency limit was ca. 51 kHz.

The reconstructed ancestral high frequency limit of ca. 51 kHz is most similar to the pygmy slow loris (*Nycticebus pygmaeus*), suggesting that the ancestral strepsirhine may have lived in relatively small groups of 1–3 individuals (Ramsier et al. 2012). Future research into the evolution of primate auditory sensitivities will benefit from methodological consistency, a broader exploration of habitat acoustics, and consideration of a wider range of audiometric parameters.

Acknowledgments I thank Nathaniel J. Dominy and Björn M. Siemers inviting me to participate in a symposium on the sensory and cognitive ecology of foraging in prosimians in the Prosimians 2007 International Congress. I thank Judith Masters and Fabien Génin for inviting me to contribute the present chapter. I am grateful to Nathaniel J. Dominy, the editors, and an anonymous reviewer for constructive comments.

References

Arnold C, Matthews LJ, Nunn CL (2010) The 10kTrees website: a new online resource for primate phylogeny, version 3. Evol Anthropol 19:114–118

Belknap DB, Suthers RA (1982) Brainstem auditory evoked responses to tone bursts in the echolocating bat, *Rousettus*. J Comp Physiol A 146:283–289

Coleman MN (2009) What do primates really hear? A meta-analysis of all known nonhuman primate behavioral audiograms. Int J Primatol 30:55–91

Coleman MN, Colbert MW (2010) Correlations between auditory structures and hearing sensitivity in non-human primates. J Morphol 271:511–532

Coleman MN, Ross CF (2004) Primate auditory diversity and its influence on hearing performance. Anat Rec 281A:1123–1137

Finarelli JA, Flynn JJ (2006) Ancestral state reconstruction of body size in the Caniformia (Carnivora, Mammalia): the effects of incorporating data from the fossil record. Syst Biol 55:301–313

Gillette RG, Brown R, Herman P, Vernan S, Vernon J (1973) The auditory sensitivity of the lemur. Am J Phys Anthropol 38:365–370

Heffner HE, Masterton B (1970) Hearing in primitive mammals: slow loris (*Nycticebus coucang*) and potto (*Perodicticus potto*). J Comp Physiol Psychol 71:175–182

Heffner HE, Ravizza RJ, Masterton B (1969) Hearing in primitive mammals, IV: Bushbaby (*Galago senegalensis*). J Aud Res 9:19–23

Heffner RS (2004) Primate hearing from a mammalian perspective. Anat Rec 281A:1111–1122

Kirk EC, Gosselin-Ildari AD (2009) Cochlear labyrinth volume and hearing abilities in primates. Anat Rec 292A:765–776

Maddison WP, Maddision DR (2010) Mesquite: a modular system for evolutionary analysis, Version 2.72, build 528. http//mesquiteproject.org/

Masterton B, Heffner H, Ravizza R (1969) The evolution of human hearing. J Acoust Soc Am 45:966–985

Milford PE, Garland T, Maddison WP (2008) PDAP Package of Mesquite, Version 1.14. http://mesquiteproject.org/

Mitchell CR, Vernon J, Herman P (1971) What does the lemur really hear? J Acoust Soc Am 50:710–711

Niaussat MM, Molin D (1978) Hearing and vocalization in a Malagasy lemur: *Phaner furcifer*. In: Chivers DJ (ed) Recent advances in primatology, vol 1: Behavior. Academic, London, pp 821–825

Niaussat MM, Petter J-J (1980) Etude de la sensibilité auditive d'un lémurien malgache: *Microcebus murinus* (J.-F. Miller, 1777). Mammalia 44:553–558

Peterson EA, Wruble SD, Ponzoli VI (1968) Auditory responses in tree shrews and primates. J Aud Res 8:345–355

Ramsier MA, Cunningham AJ, Finneran JJ, Dominy NJ (2012) Social drive and the evolution of primate hearing. Philos Trans R Soc Lond B Biol Sci 367(1597):1860–1868

Ramsier MA, Dominy NJ (2010) A comparison of auditory brainstem responses and behavioral estimates of hearing sensitivity in *Lemur catta* and *Nycticebus coucang*. Am J Primatol 72:217–233

Webster DB, Webster M (1975) Auditory systems of the Heteromyidae: functional morphology and evolution of the middle ear. J Morphol 146:343–376

Chapter 30
Vocalizations of Red Slender Lorises (*Loris tardigradus tardigradus*) in Masmullah Proposed Forest Reserve, Sri Lanka

Lilia Bernede, Robert Davies, K. Anne-Isola Nekaris, Asoka Gunawardene, and Simon K. Bearder

Abstract During a radio-tracking study of *L. t. tardigradus* in Masmullah Proposed Forest Reserve, Sri Lanka, we recorded the animals' vocalizations and associated behaviors. The 1,720 calls we heard in the field fell into five call types: whistle (97.7%), chitter (2.0%), monosyllabic chitter (0.2%), "krik" and "zic" calls (0.1%). We provide a preliminary account of the contextual use of these vocalizations, with an emphasis on qualitative variation in the loud "whistle" call, by far the most common call type. Whistles vary greatly in their contextual use, structure, and usage frequency. Synchronous calls are uttered by mothers and infants in the context of infant parking and pick up. The average number of calls per hour was highest between 19:00 and 20:00 (1.9 calls/h) and lowest between 6:00 and 7:00 (<0.01 calls/h).

Resume Au cours d'une étude par radio-pistage de *L. t. tardigradus* à Masmullah, une zone proposée pour un classement en Réserve Forestière, au Sri Lanka, nous avons construit le répertoire vocal de ces animaux et observé des comportements associés. Les 1720 vocalisations entendues sur le terrain entraient dans cinq [sept] types de cris : sifflement (97.7%), pépiement (2.0%), pépiement monosyllabique (0.2%), «kric» et «zic» (0.1%). Nous proposons un rapport préliminaire des

L. Bernede (✉)
Applied Road Ecology Group, Environmental Futures Centre and Griffith School of Environment, Griffith University, Nathan, QLD 4111, Australia
e-mail: l.bernede@griffith.edu.au

R. Davies • K. Anno-Isola Nekaris • S.K. Bearder
Nocturnal Primate Research Group, School of Social Sciences and Law, Oxford Brookes University, Oxford OX3 0BP, UK
e-mail: seivadtrebor@gmail.com; anekaris@brookes.ac.uk; skbearder@brookes.ac.uk

A. Gunawardene
Department of Animal Science, Faculty of Agriculture, University of Ruhuna, Mapalana, Kamburupitiya, Sri Lanka
e-mail: asokag@ansci.ruh.ac.lk

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_30,

contextes d'utilisation de ces vocalisations, en insistant sur les variations qualitatives observées sur le « sifflement » fort, de loin la plus commune des catégories de cris. Les sifflements montrent de grandes variations de contexte d'utilisation, de structure, et de fréquence d'utilisation. Des cris sont émis en synchronie par les mères et leurs jeunes, dans le contexte de parking et déplacements des jeunes. La fréquence moyenne des cris (1.9 cris par heure) était la plus grande entre 19 :00 et 20 :00 et la plus faible entre 6:00 et 7:00 (< 0.01 cris par heure).

Introduction

Two species of slender loris occur in India and Sri Lanka: *Loris tardigradus tardigradus* and *L. lydekkerianus*. To date, little is known of *L. t. tardigradus* vocal communication, but an extensive laboratory study of *L. lydekkerianus nordicus* vocalizations described nine call types and their contextual use (Schulze and Meier 1995). These data were augmented by one long-term study of the vocal repertoire of *L. l. lydekkerianus* (Bearder et al. 2002), and two short-term comparative studies of the acoustic repertoires and structure of the loud "whistle" calls produced by *L. t. tardigradus* and *L. l. nordicus* revealed interspecific differences (Nekaris and Jayewardene 2003, Coultas 2002).

We conducted a radio-tracking study of *L. t. tardigradus* to describe its behavior and ecology in Masmullah Proposed Forest Reserve (MPFR) (Bernede 2009; Chap. 9). Slender lorises sleep in small groups, sometimes in pairs, and have overlapping ranges exclusive of members of other groups. Affiliative interactions occur primarily between members of a sleeping group while direct agonistic interactions are rare.

This chapter describes the vocal repertoire and behavior of *L. t. tardigradus*, with emphasis on qualitative variation in the loud "whistle" call (hereafter referred to as the whistle) and provides a preliminary account of the contextual use of the vocalizations.

Methods

We collected data on vocal behavior from 2004 to 2006 and recorded calls opportunistically between 2005 and 2006 on a Marantz PMD tape recorder (40–14,000 Hz) with an AudioTechnica (20–20,000 Hz) microphone. On hearing a call, we noted the following information: sex and identity of caller, identity of tracked animal, call type, time of call, and context. For whistles, we noted the number and length of tones (units) making up the call. We allocated calls to one of three broad contextual categories: exchanges between conspecifics, calls uttered by only one animal, and calls uttered in the presence of predators (Table 30.1).

Table 30.1 Table showing the frequency (%) at which each call type was heard in different contexts

	Context (*n*)						
Call type (*n*)	Unidentified animals	♀–♂ Nonpair	♀–♀or ♂–♂	♀–♂ pair	Adult–young	Spacing/traveling	Predator presence
1t (147)	23.8	5.4	8.2	42.2	3.4	15.7	1.4
2t (255)	34.9	3.5	1.2	36.5	2.4	20.8	0.8
3t (86)	20.9	8.1	1.2	22.1	0.0	47.7	0.0
>4t (27)	5.0	31.4	0.0	6.4	0.0	57.3	0.0
1tp (11)	54.6	0.0	0.0	18.2	27.3	0.0	0.0
2tp (14)	21.4	14.3	0.0	35.7	0.0	28.6	0.0
3tp (10)	30.0	0.0	0.0	10.0	30.0	30.0	0.0
>4tp (25)	0.0	0.0	0.0	5.8	2.5	91.7	0.0
Chitter (12)	23.3	55.0	0.0	16.7	5.0	0.0	0.0
Zic (1)	0.0	0.0	0.0	0.0	100.0	0.0	0.0
Krik (1)	0.0	0.0	0.0	100.0	0.0	0.0	0.0

Whistles are classified according to the number of tones making up the call (1t, 2t, 3t, or >4t) and whether "peeps" were included (1tp, 2tp, etc.)

We digitized 180 whistles using Audacity 1.2.6. (SoundForge 2006) with a sampling rate of 44,000 Hz. We obtained sonographic displays using Sound Ruler (Gridi-Papp 2004), which we used to categorize qualitatively different whistles based on visual features. We collected recordings and contextual data from 14 adults and 1 infant.

We used SPSS for Windows (v. 13., SPSS Inc., Chicago, IL) for statistical analyses, comparing average calling rate intersexually using the Mann–Whitney test and intrasexually using the Kruskal–Wallis test. Tests were two tailed and significance set at $P<0.05$.

Results

Vocal Repertoire and Behavior

We heard five call types in the field ($n=1{,}720$): whistle (97.7%), chitter (2.0%), monosyllabic chitter (0.2%), "krik," and "zic" calls (0.1%). Whistles consisted of long tones only or a mixture of long tones and "peeps". The number of tones per call varied as follows: one tone (26.9%), two (49.2%), three (15.4%), four (4.2%), five (1.4%), six (0.3%), seven (0.24%), and eight (0.24%). Calls comprising long tones only accounted for the majority of whistles (92.2%), with the remainder made up of peeps and long tones. We heard calls consisting of a peep only 11 times (<1%). Examination of sonograms revealed nine types of one-tone whistles and eleven

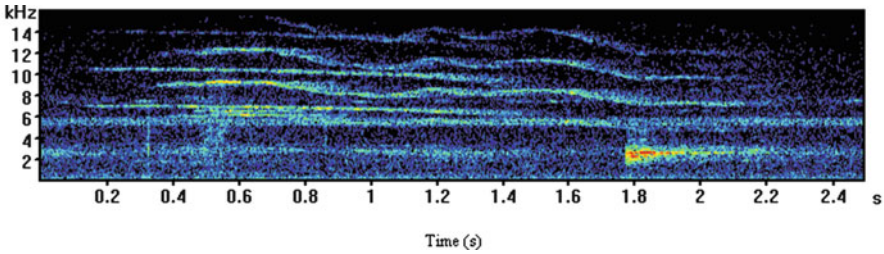


Fig. 30.1 Sonograms of synchronous calls uttered by a mother (long, one-tone whistle) and her infant (short, one-tone whistle)

types of two-tone whistles based on visual characteristics of call structure and pattern (Davies 2006). Further analysis of acoustic parameters would be required to qualify these whistle type variants as distinct calls. Seven calls described in the field were in fact two animals calling synchronously and, as a result, only one of the whistles could be heard. Sonograms revealed two kinds of synchronous calls: those with two whistles of different length (a long one-tone whistle and a short one-tone whistle; Fig. 30.1) and those consisting of two long whistles of striking visual similarity and length.

We heard a total of 1,720 whistle calls at an average of 0.82 calls/h (±1.2) (median = 0.8) with a maximum of 30 calls in 1 h and 85 in a 6-h night, uttered in the context of a female in estrus. Of the 1,016 calls heard while radio tracking, we heard an average of 1.10 calls/h ± 2.37 in the presence of females compared with 1.06 calls/h ± 2.19 in the presence of males ($U = 3{,}678.0$; $P = 0.397$). Based on the data set of identified callers ($n = 268$), females uttered an average of 0.25 calls/h ± 0.53 and males 0.25 calls/h ± 0.63 ($U = 3{,}889.0$; $P = 0.814$). The average number of calls per hour differed across the night and was the highest between 19:00 and 20:00 (1.9 calls/h) and the lowest between 6:00 and 7:00 (<0.01 calls/h). We heard no calls before 18:00 and after 7:00 (Fig. 30.2).

Context

The context in which lorises uttered different whistle types was determined for 55.5% of calls heard during the radio-tracking period ($n = 1{,}016$). Of these, 32.3% were between known paired animals, 27.7% occurred prior to or during traveling and were not returned by other loris calls, 27.2% were between animals whose identities were unknown or between a radio-collared animal and at least one other animal whose identity was unknown, 6.1% were between an unpaired male and female, 2.7% between females or between males, 3.2% between mother and infant, and 0.7% in the presence of a predator.

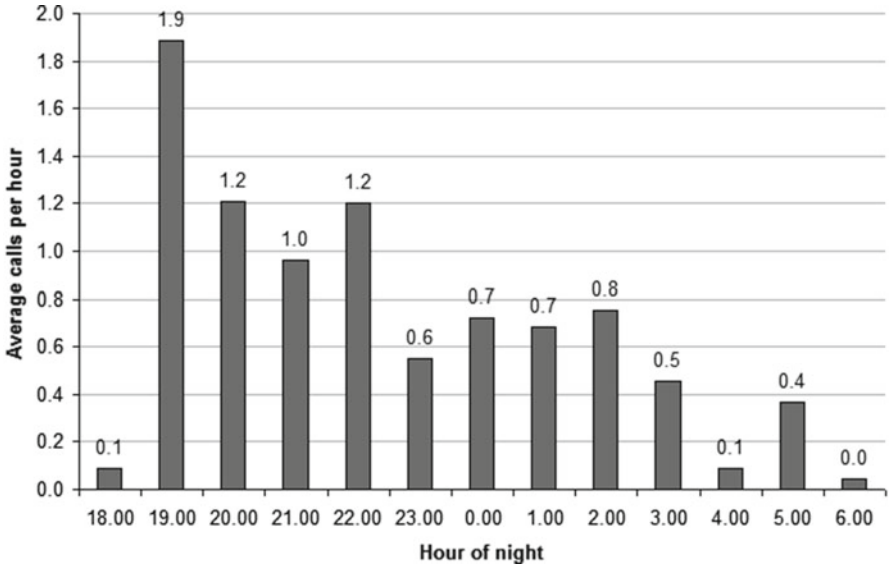


Fig. 30.2 Graph showing the average number of calls uttered hourly over the radio-tracking period ($n = 221$ nights)

Table 30.1 shows the contexts in which different whistle types were uttered. Whistles with more than four tones and including "peeps" were more frequently uttered within the context of traveling and were associated mainly with females moving around the peripheries of their home ranges. We heard one-peep calls mostly in exchanges between mothers and infants and between paired males and females. Lorises uttered one-tone whistles between two females or two males in the context of territoriality, or between males over a female in estrus. Sonograms of whistles uttered in the mother–infant context ($n = 32$) revealed seven cases of two overlapping whistles heard exclusively in the context of a mother parking its infant or picking it up. We heard these calls while observing a 1-month-old infant and all synchronous calls recorded in the field as one call appear to have come from the mother.

The "chitter" and monosyllabic chitter calls occurred in the context of a female rejecting a male's advances to groom, during estrus or during rough play. This call never occurred between adults of the same sex but did occur between adults and juveniles. The "krik" call was uttered by a female sitting within the home range border of one of the males. At the time of the call, the male was within 5 m and moving away. Schulze and Meier (1995) described this call in captivity as an appeasement call by an animal that has just been threatened or rejected. Wild male *L. l. lydekkerianus* surrounding a copulating couple uttered this call. The "zic" call was heard once while observing a noncollared female. The source of the call was within 5 m of the female, who immediately moved towards it, and may have been an infant calling for its mother, as described by Schulze and Meier (1995) and Nekaris (2003).

Discussion

The main findings from this study are (1) slender lorises at MPFR utter five qualitatively different call types, all of which have been described for other slender loris taxa; (2) they use the loud whistle more frequently than any other call; (3) whistles vary greatly in their contextual use, structure, and usage frequency; and (4) synchronous calls are uttered by mothers and infants in the context of infant parking and recontact.

Some of our results are consistent with previous findings. Five of the nine call types used by *L. l. nordicus* in captivity (Schulze and Meier 1995) were heard in this study (whistle—including the 'peep' whistle–chitter, monosyllabic chitter, zic, and krik). Four of these also were used by *L. l. lydekkerianus* in the wild (whistle, zic, krik, and chitter; Bearder et al. 2002; Nekaris 2003). As has been reported in *L. lydekkerianus*, whistles were the most frequent calls and can be multitonal (up to six tones in *L. l. lydekkerianus*: Bearder et al. 2002; up to three tones in *L. l. nordicus*: Coultas 2002).

The extent of variation in whistle calls, however, had until now been underestimated. In our study, 15 variants could be identified by sound, based on the number and length of tones alone, while spectrographic analysis of one-tone and two-tone whistles revealed additional variations (nine variants and eleven variants, respectively). Whistles of more than four tones were uttered in the context of traveling with no other lorises within visible distance. This may have been an animal marking territorial boundaries or a female advertising her reproductive status. The repetition of tones is common in long distance advertisement calls, as it enhances the call's probability of detection in dense vegetation and above insect noise (Snowdon 1986; Masters 1991; Brown et al. 1995; Zimmermann 1995).

In the open scrub forests of India, Bearder et al. (2002) could not discern the identity of the callers, and only on rare occasions could they see an animal calling. Therefore, no concrete interpretations could be made about the social functions of the loud whistle. At MPFR, radio tracking made it possible to identify the whistlers, and the majority of whistles occurred between members of a sleeping group. In a dense rainforest, acoustic recognition mechanisms and higher variation in whistle types may facilitate communication (as in *Lemur catta*, Oda 2002).

Chitter calls were uttered by *L. l. lydekkerianus* only during intrasexual fights, and peep calls were not documented. In captivity, *L. l. nordicus* was reported to use a "low whistle" in an affiliative context (Schulze 1995). No reference has been made to *L. l. lydekkerianus* emitting whistles in the context of infant parking (Radhakrishna and Singh 2004; Nekaris 2003) and the use of synchronous calls has never been reported in either taxon. The fact that these calls only occurred in this context may reflect a strategy that has evolved as a result of high predation pressure and the vulnerability of parked infants when calling, or simply, an age-related characteristic (Fitch and Hauser 1995; Theis et al. 2007).

Conclusion

Our study of the vocal repertoire of *L. t. tardigradus* in Masmullah Proposed Forest Reserve reveals strong similarities to, as well as novel differences from, the vocal repertoires that have been reported for *L. lydekkerianus* subspecies, as well as other conspecific populations. As with all slow and slender lorises, by far the most frequently used call is the loud whistle, which shows remarkable variation according to the context within which it is emitted and the identity of the caller. It is also likely to convey information on individual identity in the MPFR populations. Synchronous calls were recorded for the first time, uttered by mothers and infants in the context of baby parking and pick up. This chapter adds to our understanding of the complexity of slender loris vocal behavior and raises questions concerning inter- and intraspecific differences, the effects of social organization and environmental conditions on call structure, and the evolutionary pressures that have led to such diversity.

Acknowledgments We thank the Departments of Forest, Wildlife Conservation, and Telecommunications for providing permits, A. Beresford and K. Davey for field and laboratory assistance, and Oxford Brookes University, the Primate Society of Great Britain Conservation Working Party, Cleveland Metroparks Zoo, People's Trust for Endangered Species, National Geographic, Columbus Zoo, and the L.S.B. Leakey Foundation for financial assistance.

References

Bearder SK, Nekaris KAI, Buzzell CA (2002) Dangers in the night: are some nocturnal primates afraid of the dark? In: Miller L (ed) Eat or be eaten: predator sensitive foraging in primates. Cambridge University Press, Cambridge, pp 21–40

Bernede L (2009) A study of the social and behavioural ecology of the red slender loris (*Loris tardigradus tardigradus*) in Masmullah Proposed Forest Reserve, Sri Lanka. Unpublished PhD Thesis, Oxford Brookes University, Oxford

Brown CH, Gomez R, Waser PM (1995) Old world monkey vocalizations: adaptation to the local habitat? Anim Behav 50:945–961

Coultas D (2002) Bioacoustic analysis of the loud call of two species of slender loris (*Loris tardigradus* and *L. lydekkerianus nordicus*) from Sri Lanka. Unpublished MSc dissertation, Oxford Brookes University, Oxford

Davies R (2006) Bioacoustical analysis of free-ranging slender loris (*Loris tardigradus tardigradus*) whistles: their role in loris communication and some factors influencing their production. Unpublished MSc Dissertation. University College, London

Fitch WT, Hauser MD (1995) Vocal production in nonhuman primates: acoustics, physiology, and functional constraints on "honest" advertisement. Am J Primatol 37:191–219

Gridi-Papp M (2004) SoundRuler: acoustic analysis for research and teaching. http://soundruler.sourceforge.net

Masters JC (1991) Loud calls of *Galago crassicaudatus* and *G. garnettii* and their relation to habitat structure. Primates 32:153–167

Nekaris KAI (2003) Observations on mating, birthing and parental behaviour in three subspecies of slender loris (*Loris tardigradus* and *Loris lydekkerianus*) in India and Sri Lanka. Folia Primatol 74:312–336

Nekaris KAI, Jayewardene J (2003) Pilot study and conservation status of the slender loris (*Loris tardigradus* and *Loris lydekkerianus*) in Sri Lanka. Primate Conserv 19:83–90

Oda R (2002) Individual distinctiveness of the contact calls of ring-tailed lemurs. Folia Primatol 73:132–136

Radakrishna S, Singh M (2004) Infant development in the slender loris. Curr Sci 86:1121–1141

Schulze H, Meier B (1995) Behavior of captive *Loris tardigradus nordicus*: a qualitative description, including some information about morphological bases of behavior. In: Alterman LA, Doyle GA, Izard MK (eds) Creatures of the dark: the nocturnal prosimians. Plenum, New York, pp 221–250

Snowdon CT (1986) Vocal communication. In: Mitchell G, Irwin J (eds) Comparative primate biology, vol. 2a: conservation and ecology. Alan R. Liss, New York, pp 495–530

SoundForge (2006) Audacity 1.2.6. http://audacity.sourceforge.net/

Theis KR, Greene KM, Benson-Amram SR, Holekamp KE (2007) Sources of variation in the long-distance vocalizations of spotted hyenas. Behaviour 144:557–584

Zimmermann E (1995) Loud calls in nocturnal prosimians: structure, evolution and ontogeny. In: Zimmermann E, Newman JD, Jürgens U (eds) Current topics in primate vocal communication. Plenum, New York, pp 47–72

Chapter 31
Variation in Strepsirhine Infant Isolation Calls and Its Evolutionary Implications

John D. Newman, Catherine D. Depeine, and Michelle L. Becker

Abstract Infant cries (isolation calls) are ubiquitous among mammals. Their contribution to infant survival suggests a strong role for natural selection, making it appropriate to consider the cries of strepsirhine infants in an evolutionary context. Infants provide an opportunity to study vocal mechanisms without the complications of hormonal factors or complex vocal repertoires. The isolation calls of strepsirhine infants exhibit a diverse array of acoustic features, and infants of some species produce short-duration "click" vocalizations indicative of vocal tract specializations unique among primates. We report on several subtypes of vocalizations produced by infant strepsirhines when separated. The clade-specific nature of some of these subtypes leads us to propose that the isolation calls of infant prosimians constitute a particularly useful behavioral category for comparative studies.

Resume Les cris des jeunes (cris d'isolement) existent chez la plupart des mammifères. Leur contribution à la survie des jeunes suggère un rôle important de la sélection naturelle, qui rend appropriée l'étude des cris d'isolement des jeunes strepsirhines dans un contexte évolutif. Les jeunes offrent l'opportunité d'étudier les mécanismes vocaux sans la complication de facteurs hormonaux ou de répertoires vocaux complexes. Les cris d'isolement des jeunes strepsirhines ont des propriétés acoustiques diverses, et chez certaines espèces, comportent des « clics » qui indiquent la présence de spécialisations de l'appareil auditif uniques chez les primates. Nous reportons plusieurs sous-types de vocalisations produites par les jeunes strepsirhines isolés. Quelques-uns de ces sous-types se séparent en clades, ce qui montre la grande utilité des cris de jeunes que nous proposons comme nouvelle catégorie pour les études comparatives.

J.D. Newman (✉) • C.D. Depeine • M.L. Becker
Laboratory of Comparative Ethology, Eunice Kennedy Shriver National Institute of Child Health and Human Development, National Institutes of Health, Poolesville, MD 20837, USA
e-mail: jdnewman@helix.nih.gov; jdnewman@rocketmail.com; cdepeine@hotmail.com; monkey67@gmail.com

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_31,

Introduction

Part of our fascination with prosimian primates lies in the great variety of their physical and ecological characteristics (Martin 2000). Evolutionary primatologists use diverse tools to assess the origins and significance of this variation, including analyzing vocal repertoires. A small number of investigators have contributed the major part of our current knowledge of strepsirhine vocal communication, particularly Elke Zimmermann (1995, 1996, Chap. 32), but infant vocalizations have received little attention to date, no doubt because of the difficulties associated with recording infant sounds in both the field and the laboratory. Infant cries (isolation calls) are ubiquitous among mammals (Newman 2007) and likely to be under strong selection because of their survival value. Hence, it is appropriate to consider the cries of prosimian infants in an evolutionary context.

The mechanisms by which primates produce vocalizations have been studied at several levels, including the vocal tract, brain, and hormonal control. Not much is known about prosimian vocal tract or brain mechanisms (see Chap. 36, for an exception), and the situation is exacerbated for infant vocalizations. Infants provide an opportunity to learn about vocal mechanisms without the potential complication of hormonal factors. In addition, they tend to have smaller vocal repertoires than adults do, hence determining mechanisms with respect to particular vocalizations may be simpler.

The first step towards understanding vocal mechanisms is to understand the animals' behavior. Strepsirhine infants differ from haplorhines in that some species produce short-duration "click" vocalizations, which require quite different vocal tract specializations from those generating longer duration, tonal or noisy vocalizations. Here we report on several subtypes of vocalizations produced by infant strepsirhines when separated, suggesting a dynamic vocal evolutionary history. We present examples and argue that the isolation calls of infant prosimians constitute a particularly useful behavioral category for comparative studies.

Methods

Sound recordings were made at the Duke Lemur Center during 1981, 1982, 1985, and 1986. A Uher reel-to-reel recorder (recording at 19 cm/s) with a Uher microphone (40–18,000 Hz frequency response) or a Marantz PDM 430 cassette recorder with a Sony microphone (20–20,000 Hz frequency response) was used to record isolation calls. Depending on the species, infants were housed either in small family groups or in larger social groups. Individuals were separated from their groups and transported in a small cage to a quiet room. Recording sessions for each animal averaged 15–20 min. Immediately following the recording sessions, animals were returned to their home compounds. In some cases, animals failed to vocalize on the first recording attempt and were retested on another day. Infants were 1–4 months of age at the time of recording, except for *Cheirogaleus* and *Otolemur*, which were 1–3 weeks of age. Vocalizations were digitized with Raven 1.2 software (Cornell

University, Ithaca, New York), and sound spectrogram displays were created with Syrinx software (John Burt, http://www.syrinxpc.com). In total, 110 recorded cuts (90 cassette and 20 reel to reel) were digitized. High quality displays—those showing clear, sharp images and a lack of background noise—were copied to Microsoft PowerPoint software for graphic presentation. Sound spectrograms from at least two infants of each species were analyzed.

Results

Examination of the sound spectrograms suggested a natural grouping into five subtypes of isolation calls (1) click like; (2) broad frequency range, "noisy"; (3) tonal, minimal frequency modulation; (4) low fundamental, only upper harmonics present giving a "nasal" quality; and (5) rapidly frequency modulated. Table 31.1 lists the types of isolation calls we recorded in different strepsirhine species. Spectrograms of each isolation call subtype are shown in Figs. 31.1, 31.2, 31.3, 31.4, and 31.5.

Table 31.1 The five subtypes of infant isolation calls identified in selected prosimian species

Tonal	Broad band, "noisy"	Nasal	Rapid frequency modulation	Clicks
Lemur catta	*Eulemur mongoz*	*E. sanfordi*	*Cheirogaleus medius*	*Otolemur garnettii*
	E. albifrons	*E. coronatus*		*Otolemur crassicaudatus*
	E. fulvus			*Microcebus murinus*
	E. collaris			*Loris tardigradus*
	E. macaco			*Galago senegalensis*

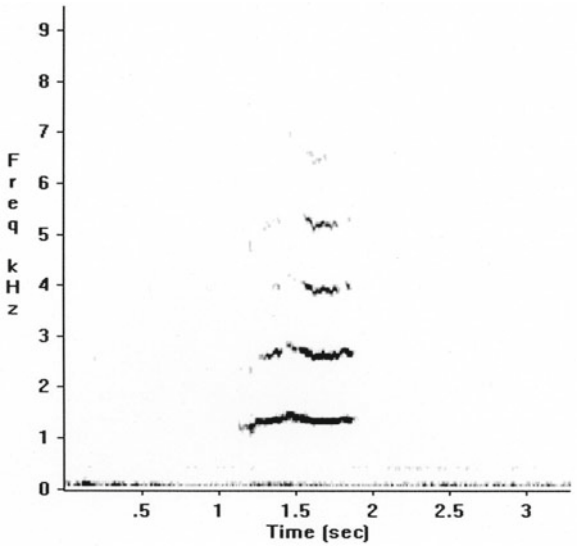


Fig. 31.1 Example of tonal infant isolation call (*Lemur catta*)

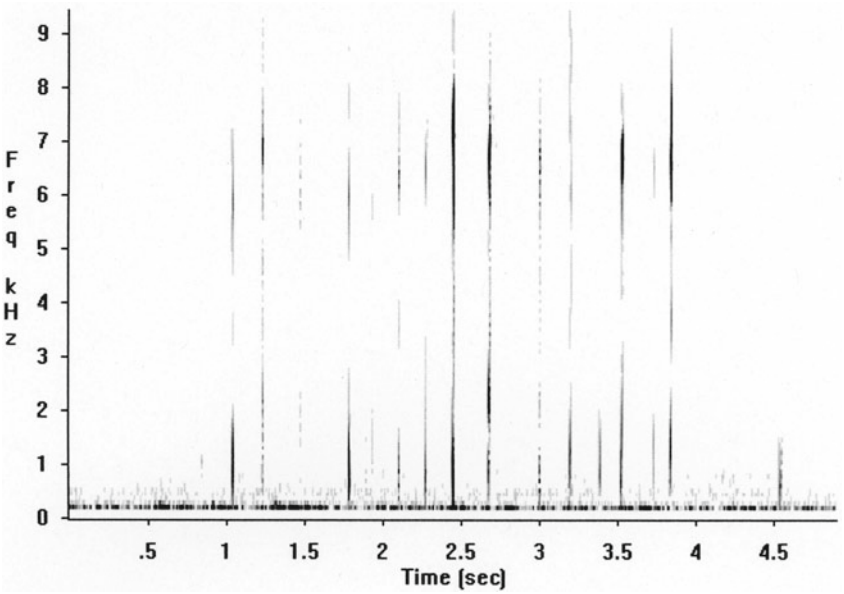


Fig. 31.2 Example of click infant isolation call (*Otolemur crassicaudatus*)

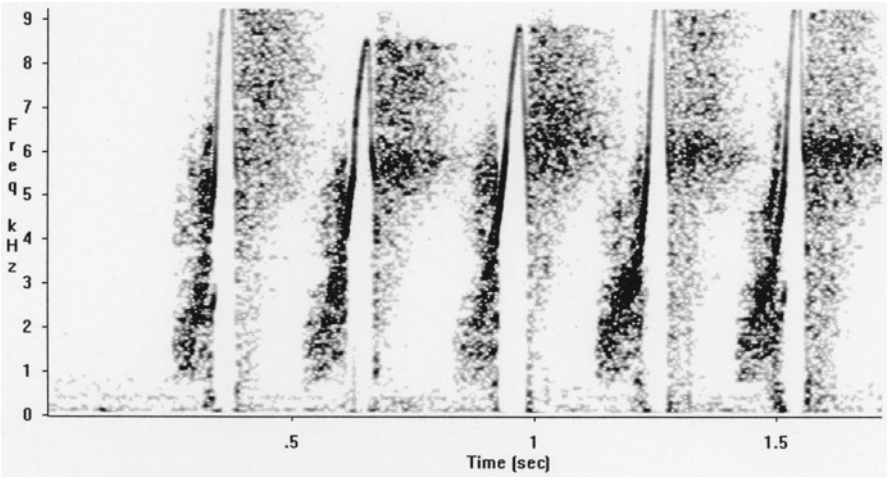


Fig. 31.3 Example of high-pitched tonal infant isolation call (*Cheirogaleus medius*)

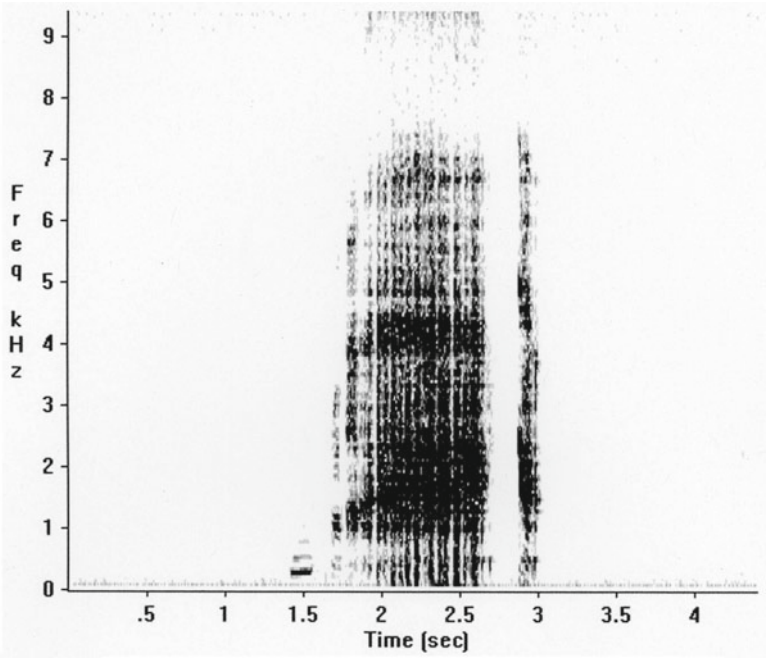


Fig. 31.4 Example of low harmonic infant isolation call (*Eulemur fulvus*)

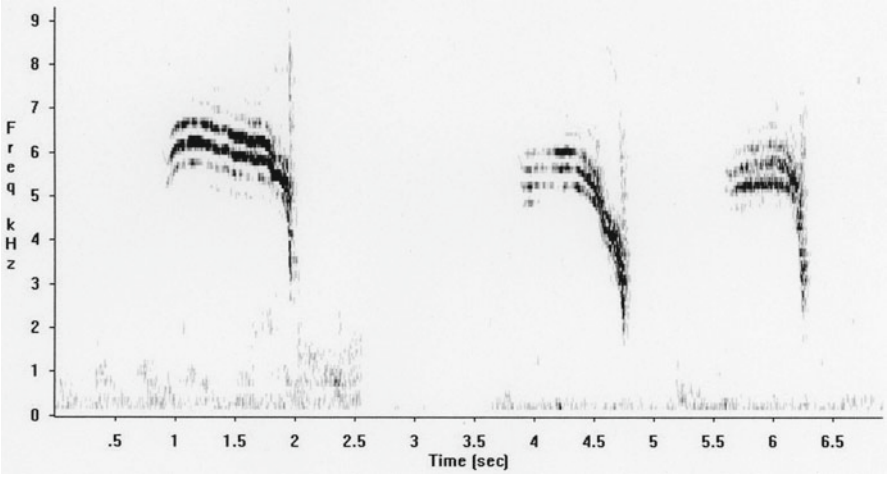


Fig. 31.5 Example of nasal infant isolation call (*Eulemur coronatus*)

Discussion

In striking contrast to the isolation calls of other primate infants, which show a widespread uniformity in their basic structure (Newman 1985, 1992), the isolation calls of strepsirhine infants exhibit a diverse array of acoustic features. Only *Lemur catta* infants produce isolation calls that fit the typical simian morphology of a slowly modulated, tonal call.

The click-like sounds produced by *Otolemur garnettii* and other lorisoids resemble those described for *O. crassicaudatus* and slow lorises (*Nycticebus coucang*) by Ehrlich (1973) and may represent a general isolation call subtype common to all lorisiform infants (Mascagni and Doyle 1993; Becker et al. 2003). These calls are acoustically very different from the "loud calls" of adults of the same species (Zimmermann 1995). Whether clicks are laryngeal in origin remains to be determined, but the peripheral mechanism producing them must be categorically different from the laryngeal structure found in simians, given the differences in acoustic morphology. Information on the laryngeal anatomy of prosimians is sparse. Negus (1962), in his classic monograph, illustrated and briefly described the larynx of several strepsirhines. However, the lack of detail presented precludes any conclusions regarding specializations for producing clicks. A detailed analysis of lorisiform laryngeal structure would ideally follow the careful studies of some New World primate larynges by Schön-Ybarra (1995). Lorisiforms are nocturnal, and it has been argued that transient sounds lasting a few milliseconds, like clicks, provide localization cues for mothers trying to locate lost or separated infants (Brown 1982), where visual cues are largely absent. However, other nocturnal primates, including some prosimians, produce tonal isolation calls (Newman 1992).

The isolation calls of *Eulemur* present a puzzle. Their broad-banded acoustics should make them readily localizable, although appropriate behavioral studies have yet to be performed. *Eulemur* species are cathemeral (Donati and Borgognini-Tarli 2006), and broad-banded sounds of relatively long duration would be adaptive for both nocturnal and diurnal patterns, if predation is not high (Brown 2003). The isolation calls of *E. sanfordi* and *E. coronatus* have a low fundamental but, probably due to pharyngeal and nasal filtering, the lower frequencies are absent, giving the calls a "nasal" character. This suggests supralaryngeal specializations that deserve further study. In *Lemur catta*, the tonal infant isolation calls are strikingly similar to the tonal calls used by older individuals in social contact (Macedonia 1993). It is unknown what the limits on laryngeal structure are that permit tonal vocalization, or how similar the larynx of *Lemur catta* is to that of simians producing tonal isolation calls.

Evolution of Infant Isolation Calls

The range of infant isolation calls in the strepsirhine species reported here prompts comparison with the isolation calls found in other mammalian species. Across a

wide range of mammalian families, infants have been found to make characteristic vocalizations when separated from their mothers or home environments. Typically, the acoustic form of these vocalizations is tonal, with only a moderate amount of frequency modulation or noisy components. This is the case whether the calls are ultrasonic, as in chiropteran bats (Gould 1971, 1975) and murid rodents (Brudzynski et al. 1999; Sales and Smith 1976; Smith and Sales 1980), or in the range of human hearing, such as cetaceans (Sayigh et al. 1990; Smolker et al. 1993), pinnipeds (Trillmich 1981; Petrinovich 1974), ungulates (Kiley 1972), or felids (Brown et al. 1978; Haskins 1977). There is a basic *bauplan* to the acoustic structure of mammalian infant isolation calls (Newman 2004). Newman (1985, p. 308) stated: "The many parallels between the vocal patterns of human infants and the infants of nonhuman primates suggest a conservative evolutionary history across the entire primate order regarding infant sound production and its underlying neural mechanisms." This makes the acoustic subtypes of some strepsirhine isolation calls all the more remarkable and indicates that there could be considerable value in infant isolation calls for phylogenetic reconstruction.

Acknowledgments This study would not have been possible without the assistance of the staff of the Duke Lemur Center (DLC) in Durham, North Carolina. This is DLC publication number 1138. The research was funded by the Division of Intramural Research, Eunice Kennedy Shriver National Institute of Child Health and Human Development, National Institutes of Health, Bethesda, MD. We dedicate this chapter to the memory of Deborah Bernhards, long-time research assistant in our laboratory, who died on July 8, 2009.

References

Becker M, Buder E, Bakeman R, Price M, Ward J (2003) Infant response to mother call patterns in *Otolemur garnettii*. Folia Primatol 74:301–311

Brown CH (1982) Auditory localization and primate vocal behavior. In: Snowdon CT, Brown CH, Petersen MR (eds) Primate communication. Cambridge University Press, Cambridge, pp 144–164

Brown CH (2003) Ecological and physiological constraints for primate vocal communication. In: Ghazanfar AA (ed) Primate audition: ethology and neurobiology. CRC, Boca Raton, pp 127–149

Brown KA, Buchwald JS, Johnson JR, Mikolich D (1978) Vocalization in the cat and kitten. Dev Psychobiol 11:559–570

Brudzynski SM, Kehoe P, Callahan M (1999) Sonographic structure of isolation-induced ultrasonic calls of rat pups. Dev Psychobiol 34:195–204

Donati G, Borgognini-Tarli SM (2006) Influence of abiotic factors on cathemeral activity: the case of *Eulemur fulvus collaris* in the littoral forest of Madagascar. Folia Primatol 77:104–122

Ehrlich A (1973) Infant development in two prosimian species: greater galago and slow loris. Dev Psychobiol 7:439–454

Gould E (1971) Studies of maternal-infant communication and development of vocalizations in the bats *Myotis* and *Eptesicus*. Commun Behav Biol A 5:263–313

Gould E (1975) Neonatal vocalizations in bats of eight genera. J Mammal 56:15–29

Haskins R (1977) Effect of kitten vocalizations on maternal behavior. J Comp Physiol Psychol 91:830–838

Kiley M (1972) The vocalizations of ungulates, their causation and function. Z Tierpsychol 31:171–222
Macedonia JM (1993) The vocal repertoire of the ringtailed lemur (*Lemur catta*). Folia Primatol 61:186–217
Martin RD (2000) Origins, diversity and relationships of lemurs. Int J Primatol 21:1021–1049
Mascagni O, Doyle GA (1993) Infant distress vocalizations in the southern African lesser bushbaby (*Galago moholi*). Int J Primatol 14:41–60
Negus VE (1962) The comparative anatomy and physiology of the larynx. Hafner Publishing Co., New York (reprint of 1949 edition published by William Heinemann Medical Books, Ltd., London)
Newman JD (1985) The infant cry of primates: an evolutionary perspective. In: Lester BM, Boukydis CFZ (eds) Infant crying: theoretical and research perspectives. Plenum, New York, pp 307–323
Newman JD (1992) The primate isolation call and the evolution and physiological control of human speech. In: Wind J, Chiarelli B, Bichakjian B, Nocentini A (eds) Language origins: a multidisciplinary approach, vol 61, NATO ASI Series D. Kluwer Academic, Dordrecht, pp 301–321
Newman JD (2004) The primate isolation call: a comparison with precocial birds and non-primate mammals. In: Rogers LJ, Kaplan G (eds) Comparative vertebrate cognition: are primates superior to non-primates? Kluwer Academic/Plenum, New York, pp 171–187
Newman JD (2007) Neural circuits underlying crying and cry responding in mammals. Behav Brain Res 182:155–165
Petrinovich L (1974) Individual recognition of pup vocalizations by northern elephant seal mothers. Z Tierpsychol 34:308–312
Sales GD, Smith JC (1976) Comparative studies of the ultrasonic calls of infant murid rodents. Dev Psychobiol 11:595–619
Sayigh LS, Tyack PL, Wells RS, Scott MD (1990) Signature whistles of free-ranging bottlenose dolphins *Tursiops truncatus*: stability and mother-offspring comparisons. Behav Ecol Sociobiol 26:247–260
Schön-Ybarra MA (1995) A comparative approach to the non-human primate vocal tract: implications for sound production. In: Zimmermann E, Newman JD, Jürgens U (eds) Current topics in primate vocal communication. Plenum, New York, pp 185–198
Smith JC, Sales GD (1980) Ultrasonic behavior and mother-infant interactions in rodents. In: Bell RW, Smotherman WP (eds) Maternal influences and early behavior. Spectrum Publications, New York, pp 105–133
Smolker RA, Mann J, Smuts BB (1993) Use of signature whistles during separation and reunions by wild bottlenose dolphin mothers and infants. Behav Ecol Sociobiol 33:393–402
Trillmich F (1981) Mutual mother-pup recognition in Galapagos fur seals and sea lions: cues used and functional significance. Behaviour 78:2142
Zimmermann E (1995) Loud calls of nocturnal prosimians: structure, evolution and ontogeny. In: Zimmermann E, Newman JD, Jürgens U (eds) Current topics in primate vocal communication. Plenum, New York, pp 47–72
Zimmermann E (1996) Castration affects the emission of an ultrasonic vocalization in a nocturnal primate, the grey mouse lemur (*Microcebus murinus*). Physiol Behav 60:693–697

Chapter 32
Primate Serenades: Call Variation, Species Diversity, and Adaptation in Nocturnal Strepsirhines

Elke Zimmermann

Abstract Interspecific divergence in acoustic signaling systems is a major focus of biodiversity and evolutionary research, but empirical data for primates are rare. Our research team compared communication calls of four cryptic, genetically defined mouse lemur (*Microcebus*) species uttered in comparable social situations. We found that calls vary interspecifically to different extents depending on the context. The acoustic pattern of calls given in the startle context was conserved across species, whereas calls given in agonistic and mating contexts showed significant interspecific variation. Uniformity in the acoustic pattern of calls across species can be explained by similar physiological and environmental constraints; and divergences have been explained by several hypotheses including natural and sexual selection. Because of remarkable species-specific differences in frequency contours, advertisement calls are the most useful diagnostic tools for noninvasive species and subspecies identification.

Resume La divergence interspécifique des signaux acoustiques est un sujet central pour la recherche sur la biodiversité et l'évolution, mais peu de données empiriques sont disponibles pour les primates. Chez quatre espèces jumelles de microcèbes (*Microcebus*) définies génétiquement, nous avons comparé les vocalisations émises dans des contextes sociaux comparables. Nos résultats montrent différents degrés de variation interspécifique dépendant du contexte. La structure des vocalisations émises dans un contexte de tressaillement est la même chez toutes les espèces, alors que les vocalisations émises dans un contexte agonistique ou sexuel montrent des différences interspécifiques marquées. L'uniformité interspécifique des structures sonores des vocalisations peut s'expliquer par des contraintes physiologiques et environnementales similaires; et les divergences par des hypothèses variées, comme la sélection naturelle et la sélection sexuelle. La remarquable diversité des contours

E. Zimmermann (✉)
Institute of Zoology, Veterinary University, Bünteweg 17, 30539 Hannover, Germany
e-mail: elke.zimmermann@tiho-hannover.de

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_32,

de fréquence des cris d'avertissement est aussi le meilleur caractère d'identification, non invasif, des espèces et des sous-espèces.

Introduction

A central question in biodiversity and evolutionary research is how vocalizations diverge during speciation. Comparative studies in sound-producing animals (crickets, cicadas, frogs, birds, bats, and pinnipeds) suggest that ecological factors like predation pressure, habitat acoustics, interspecific interactions in sound-producing communities, social systems, and physiological constraints influence divergences in acoustic communication (Foster and Endler 1999). Until recently, comparable empirical data for primates were rare and restricted to a few species (e.g., Delgado 2007; Braune et al. 2008; Wich et al. 2008).

Mouse lemurs (*Microcebus*) are an excellent group for studying the evolution of vocal communication during speciation. They are a speciose genus, and the animals have large mobile ears, show high auditory sensitivity, are highly vocal, and have evolved an elaborate set of social calls extending into the ultrasonic range, comparable to microchiropterans, cetaceans, and some rodents and frogs. Specific call types are used in the context of infant isolation, startle (e.g., grunt), disturbance (e.g., short whistle), aggression/submission (e.g., tsaks), and social cohesion (e.g., trill; Zimmermann 2009; Scheumann et al. 2007a, b). Mouse lemurs are the smallest extant primates and live in dispersed social systems (Radespiel et al. 2001; Weidt et al. 2004; Radespiel 2006). Vocal activity is higher during the mating season (Zimmermann and Lerch 1993) when males actively search for estrous females (Craul et al. 2004). At present, 18 genetically characterized species are known, some of which are difficult to distinguish noninvasively in the field on external characteristics (Olivieri et al. 2007; Mittermeier et al. 2010).

I review interspecific bioacoustic and morphological variation in four cryptic, genetically defined mouse lemur species (Pastorini et al. 2001; Olivieri et al. 2007), three of which belong to the "rufous" group (*M. ravelobensis, M. berthae*, and *M. lehilahytsara*), which also contains species in eastern Madagascar (Fig. 32.1). The fourth species, the gray mouse lemur (*M. murinus*), is widely distributed in the west and its range overlaps the respective ranges of the incumbent rufous species in north-western and western Madagascar. I studied gray mouse lemurs at two localities separated by 500 km (Ampijoroa and Kirindy) and at two sites 1.5 km apart within the same locality. *M. murinus* from the two study locations formed separate clades in a tree based on mtDNA (Pastorini et al. 2001) and I thus regarded them as subspecies. In analyzing the acoustic signals of the four species, I identified shared traits inherited from a common ancestor and potential phylogenetic constraints, as well as species-specific traits that may have evolved by adaptation to different environments (Paterson 1985). Species-specific acoustic signals are of special importance for biodiversity research and conservation, since they allow the noninvasive identification of cryptic species in groups like nocturnal primates (Masters 1993).

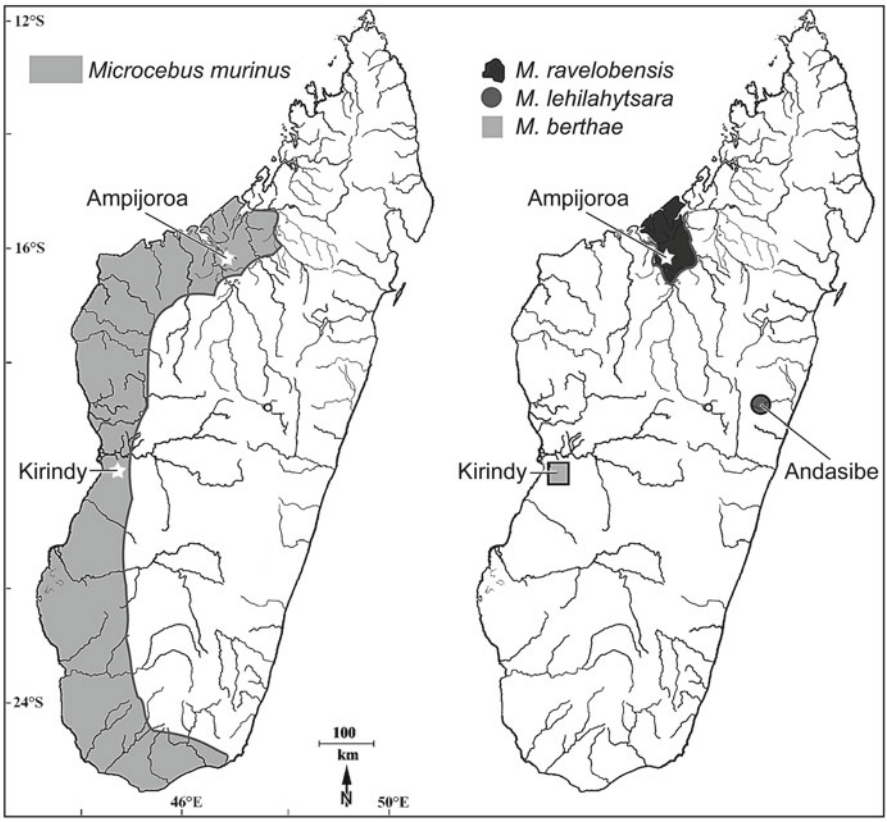


Fig. 32.1 Distribution map and localities of the mouse lemur populations studied: (*left*) the gray mouse lemur (*Microcebus murinus*) with subspecies in Kirindy and Ampijoroa and (*right*) the rufous mouse lemur species

Contextualized Inter- and Intraspecific Call Variation: Conserved and Labile Acoustic Traits

A prerequisite for assessing interspecific acoustic variation is the comparison of calls uttered in similar contexts. My research team conducted experiments in which we manipulated the calling behavior of caged members of four mouse lemur species (Zimmermann 1996; Hafen et al. 1998; Braune et al. 2008). We simulated three contexts: startle, agonistic, and mating contexts and compared them visually (by spectrograms) as well as statistically, using multiparametric acoustic and multivariate methods.

Startle Context

When a mouse lemur occupying a sleeping site (tree, nest, and nest box) is threatened by an intruder, it lunges forward uttering a series of loud, plosive, and noisy grunts (Fig. 32.2a) until the intruder withdraws. All four species produced noisy sounds covering the same broadband frequency range. There was no interspecific variation in sound quality, the number of clicks, or call duration (Kruskal–Wallis ANOVA, $N_{\text{murinusAmpijoroa}}=21$, $N_{\text{murinusKirindy}}=12$, $N_{\text{ravelobensis}}=9$; $N_{\text{berthae}}=3$), and calls given in the startle context are phylogenetically conservative.

Agonistic Context

We conducted social encounter experiments in which we paired males and females during the mating season. Under these circumstances, males were always motivated to court females, whereas females were more selective (Craul et al. 2004). If a male approached an unwilling female, she expressed her reluctance by aggressive staring and tsak-calls. If the male continued in his approach, the female attacked and chased him. The chased male usually withdrew, emitting submissive tsak calls. In the four species, tsak calls sounded similar and had similar, chevron-shaped frequency contours (Fig. 32.2b). When analyzed statistically, they were not significantly different in the two *M. murinus* subspecies, while seven out of the eight interspecific comparisons differed significantly (Fig. 32.3): calls varied quantitatively between species in maximum fundamental frequency and bandwidth.

Mating Context

During approaches to females in the social encounter experiments, males emitted trill/advertisement calls which had the most complex acoustic structure of the four species' vocal repertoires. Despite the fact that there was no significant difference in absolute frequency range and bandwidth of the heterospecific trill calls, they sounded quite different and showed remarkably different frequency contours (Fig. 32.2c). Calls of gray mouse lemurs were the longest, of variable duration, and showed statistical variation within the frequency contours that could convey individual, group (different sites at the same location), and subspecies information (Hafen et al. 1998; Leliveld et al. 2011). Individual and group specificity was also indicated for the calls of two rufous mouse lemur species (Braune et al. 2005). Advertisement calls in the mating context exhibit the highest inter- and intraspecific variation of all call types, indicating both stabilized and variable elements.

Our experiments showed that the acoustic patterns of mouse lemur calls varied interspecifically to varying extents depending on the context. The acoustic pattern of calls given in the startle context is conserved across the four species, whereas

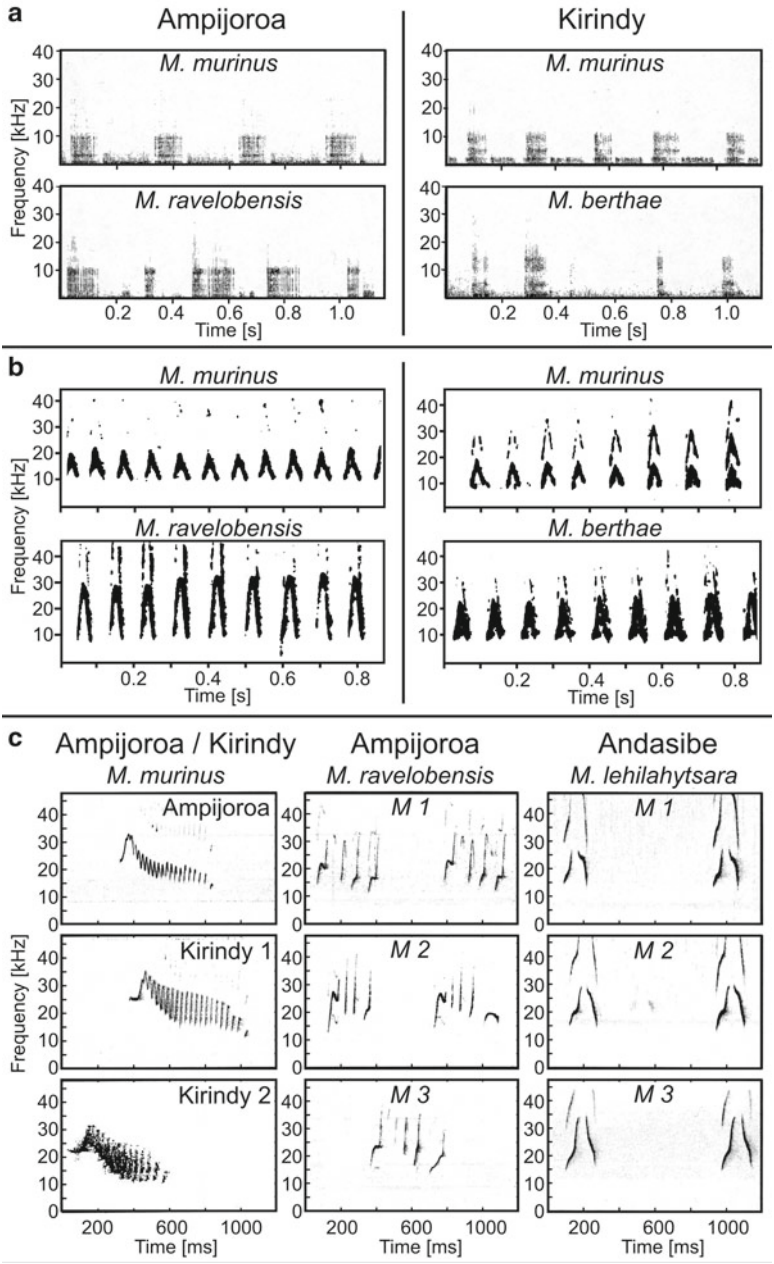


Fig 32.2 Sonagrams of communication calls evoked in three different contexts reflecting variation on different scales (**a**) grunt calls given in startle contexts, fixed across species; (**b**) chevron shaped tsak calls given in agonistic contexts, variable in certain frequency parameters between species but not between subspecies; (**c**) loud advertisement calls or trill calls, given during mating and for social cohesion, variable in frequency contours between species, subspecies, and within one species at two different sites at the same locality. Trill calls of male *M. murinus* were recorded at two geographic localities (Ampijoroa and Kirindy, respectively; Zietemann 2000; Braune et al. 2008) and at two different sites within the same locality (Kirindy; Hafen et al. 1998). Trill calls of the two rufous mouse lemur species represented were emitted by three different males at the same locality (M1–M3)

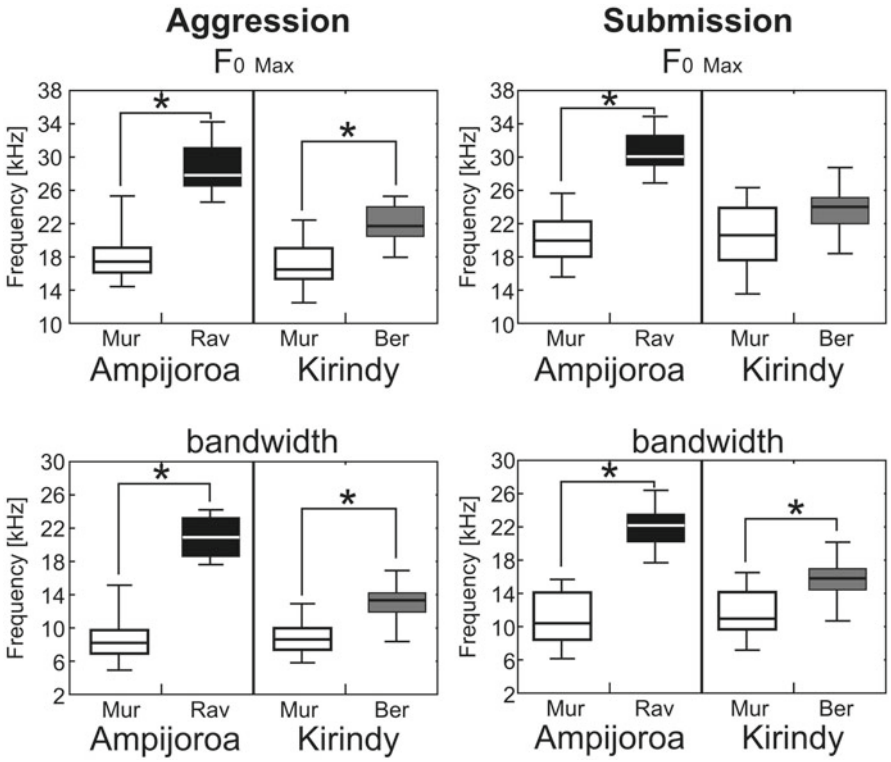


Fig. 32.3 Quantitative differences between species and subspecies in frequency parameters of chevron shaped tsak calls given during agonistic encounters. Significant differences (*) occurred in F_{omax} and bandwidth (Tukey HSD test, $P<0.05$; $N_{murinusAmpijoroa}=31$, $N_{murinusKirindy}=37$, $N_{ravelobensis}=47$; $N_{berthae}=16$; Zietemann 2000). Mur = *M. murinus*, Rav = *M. ravelobensis*, Ber = *M. berthae*. F_{omax} = maximum fundamental frequency, bandwidth = $F_{omax} - [(F_{ostart} + F_{oend})]/2$

calls given in the agonistic and mating contexts display high interspecific acoustic variation. Due to the remarkable species-specific differences in frequency contours, advertisement calls represent the most useful diagnostic tool for noninvasive species and subspecies identification in mouse lemurs.

Evolutionary Divergence of Acoustic Traits

The evolution of species-specific acoustic traits is driven by trade-offs among sound production and perception systems, predation, environment, and mate choice criteria (Endler 1992). Our bioacoustic comparison of vocalizations in mouse lemurs revealed varying degrees of interspecific acoustic variation depending on

social context. All four taxa used a series of plosive, low frequency, noisy broadband sounds in the startle context during sleeping site defense. Similarity may be explained by similar predation pressures, physiological constraints (Fitch et al. 2002), or convergent selection (Gautier 1989; Masters 2007). Sounds with similar acoustic characteristics are widespread among strepsirhines that rest in nests or holes (Zimmermann 1985a, b; Scheumann et al. 2007a) as well as in other hole-dwelling mammals (Binz and Zimmermann 1989), probably because of their effectiveness in evoking escape responses in intruders (Owren and Rendall 2001). Convergent selective forces may thus have favored conservative acoustic patterns across species and genera.

Similar chevron-shaped frequency contours were observed across species in calls conveying aggression/submission in the agonistic context. Comparable frequency contours have been found in a wide range of different mammalian and bird lineages (Morton 1977). Both the highest interspecific variation (i.e., in frequency contours) and intraspecific variation (i.e., broadband frequency modulations in the same frequency range) were found in advertisement calls, which play an important role in mouse lemur courtship (Braune et al. 2008). Broadband, frequency-modulated signals provide advantages for sound localization, while uniformity in frequency range may be a result of similar morphological constraints and predation pressures. The species-specific acoustic contour of these calls is likely to reflect selection for specific-mate recognition, as advertisement calls were the only calls to vary qualitatively between species. This acoustic differentiation also suggests that advertisement calls evolve much more rapidly than other kinds of calls, as predicted by Masters (2007) on the basis of the genomic dynamics of speciation. Adaptation to different microhabitats (Paterson 1985; Alcock 2005; Blumstein 2007) may further have driven divergence in mouse lemur advertisement calls. Rufous mouse lemur species, inhabiting the rain forest and more humid parts of the dry deciduous forest, produce rapidly repeated, relatively short calls with slow frequency modulations, characteristics common to calls transmitted over long distances in dense, humid environments. In contrast, both gray mouse lemur subspecies, living in dry deciduous forests, utter longer calls consisting of short, rapidly repeated, frequency-modulated elements, adapted to transmission in more open habitats.

As predicted by Paterson's (1985) Recognition Concept, the frequency signature of advertisement calls remains uniform in the two gray mouse lemur subspecies, despite geographical separation by several major rivers and subsequent genetic divergence, whereas it is highly variable between the rufous species, which are also separated by major rivers (Olivieri et al. 2007). Gray mouse lemurs seem to have a younger phylogenetic age than the rufous species (Kappeler et al. 2005), and the lack of divergence in calls may be due to their recent speciation and dispersion. On the other hand, this pattern is exactly what would be predicted if calls involved in specific-mate recognition were subject to stabilizing selection over space and time and underwent rapid and extensive change during speciation (Paterson 1985; Masters 1993).

Conclusion

The presence of clearly distinguishable species-specific calls provides a rapid and noninvasive tool for the clarification of systematic identities and relationships among cryptic nocturnal prosimians like *Microcebus*, but only if the calls compared have been uttered in comparable social contexts. An understanding of the behavior and vocal repertoires of populations, and of their variability, adds considerably to the information deriving from genetics, in our quest to comprehend the strepsirhine radiation.

Acknowledgments I thank Judith Masters and her coworkers for organizing an inspiring prosimian conference in Ithala 2007, and Ute Radespiel, Sabine Schmidt and the DFG-Research Group 499 for many stimulating discussions.

References

Alcock J (2005) Animal behavior. An evolutionary approach. Sinauer, Sunderland

Binz H, Zimmermann E (1989) The vocal repertoire of adult tree shrews (*Tupaia belangeri*). Behaviour 109:142–162

Blumstein DT (2007) The evolution, function, and meaning of marmot alarm communication. Adv Study Behav 37:371–401

Braune P, Schmidt S, Zimmermann E (2005) Spacing and group coordination in a nocturnal primate, the golden brown mouse lemur (*Microcebus ravelobensis*): the role of olfactory and acoustic signals. Behav Ecol Sociobiol 58:587–596

Braune P, Schmidt S, Zimmermann E (2008) Acoustic divergence in communication of cryptic species of nocturnal primates (*Microcebus* spp.). BMC Biol 6:19. doi:10.1186/1741-7007-6-19

Craul M, Zimmermann E, Radespiel U (2004) First experimental evidence for female mate choice in a nocturnal primate. Primates 45:271–274

Delgado RA Jr (2007) Geographic variation in the long calls of male orangutans (*Pongo* spp.). Ethology 113:487–498

Endler JA (1992) Signals, signal conditions, and the direction of evolution. Am Nat 139:S125–S153

Fitch WT, Neubauer J, Herzel H (2002) Calls out of chaos: the adaptive significance of nonlinear phenomena in mammalian vocal production. Anim Behav 63:407–418

Foster SA, Endler JA (1999) Geographic variation in behavior: perspectives on evolutionary mechanisms. Oxford University Press, New York

Gautier J-P (1989) Interspecific affinities among guenons as deduced from vocalizations. In: Gautier-Hion A, Bourlière F, Gautier J-P, Kingdon J (eds) A primate radiation: evolutionary biology of the African guenons. Cambridge University Press, Cambridge, pp 194–226

Hafen T, Neveu H, Rumpler Y, Wilden I, Zimmermann E (1998) Acoustically dimorphic advertisement calls separate morphologically and genetically homogenous populations of the grey mouse lemur (*Microcebus murinus*). Folia Primatol 69(Suppl 1):342–356

Kappeler PM, Rasoloarison RM, Razafimanantsoa L, Walter L, Roos C (2005) Morphology, behavior and molecular evolution of giant mouse lemurs (*Mirza* spp.) Gray,1870, with description of a new species. Primate Rep 71:3–26

Leliveld LMC, Scheumann M, Zimmermann E (2011) Acoustic correlates of individuality in the vocal repertoire of a nocturnal primate (*Microcebus murinus*). J Acoust Soc Am 129:2278–2288

Masters JC (1993) Primates and paradigms: problems with the identification of genetic species. In: Kimbel WH, Martin LB (eds) Species, species concepts, and primate evolution. Plenum, New York, pp 43–64

Masters JC (2007) Taking phylogenetics beyond pattern analysis: can models of genome dynamics guide predictions about homoplasy in morphological and behavioral data sets? J Hum Evol 52:522–535

Mittermeier RA, Louis EE Jr, Richardson M, Schwitzer C, Langrand O, Rylands AB, Hawkins F, Rajaobelina S, Ratsimbazafy J, Rasoloarison R, Roos C, Kappeler PM, Mackinnon J (2010) Lemurs of Madagascar, 3rd edn. Conservation International, Washington, DC

Morton ES (1977) On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. Am Nat 111:855–869

Olivieri G, Zimmermann E, Randrianambinina B, Rasoloharijaona S, Rakotondavony D, Guschanski K, Radespiel U (2007) The ever-increasing diversity in mouse lemurs: three new species in north and northwestern Madagascar. Mol Phylogenet Evol 43:309–327

Owren MJ, Rendall D (2001) Sound on the rebound: bringing form and function back to the forefront in understanding nonhuman primate vocal signaling. Evol Anthropol 10:58–71

Pastorini J, Martin RD, Ehresmann P, Zimmermann E, Forstner MRJ (2001) Molecular phylogeny of the lemur family Cheirogaleidae (Primates) based on mitochondrial DNA sequences. Mol Phylogenet Evol 19:45–56

Paterson HEH (1985) The recognition concept of species. In: Vrba ES (ed) Species and speciation. Transvaal Museum Monographs, Pretoria, pp 21–29

Radespiel U (2006) Ecological diversity and seasonal adaptations of mouse lemurs (*Microcebus* spp.). In: Gould L, Sauther ML (eds) Lemurs: ecology and adaptation. Springer, New York, pp 211–233

Radespiel U, Sarikaya Z, Zimmermann E, Bruford M (2001) Sociogenetic structure in a free-living nocturnal primate population: sex-specific differences in the grey mouse lemur (*Microcebus murinus*). Behav Ecol Sociobiol 50:493–502

Scheumann M, Rabesandratana A, Zimmermann E (2007a) Predation, communication and cognition in lemurs. In: Gursky SL, Nekaris KAI (eds) Primate anti-predator strategies. Springer, New York, pp 100–126

Scheumann M, Zimmermann E, Deichsel G (2007b) Context-specific calls signal infants' needs in a strepsirrhine primate, the gray mouse lemur (*Microcebus murinus*). Dev Psychobiol 49:708–718

Weidt A, Hagenah N, Randrianambinina B, Radespiel U, Zimmermann E (2004) Social organization of the golden brown mouse lemur (*Microcebus ravelobensis*). Am J Phys Anthropol 123:40–51

Wich SA, Schel AM, de Vries H (2008) Geographic variation in Thomas langur (*Presbytis thomasi*) loud calls. Am J Primatol 70:566–574. doi:10.1002/ajp. 20527

Zietemann V (2000) Artendiversitaet bei Mausmakis: die Bedeutung der akustischen Kommunikation. Unpubl. PhDthesis, University of Hannover, Hannover

Zimmermann E (1985a) The vocal repertoire of the adult Senegal bushbaby (*Galago senegalensis senegalensis*). Behaviour 94:211–233

Zimmermann E (1985b) Vocalizations and associated behaviours in adult slow loris (*Nycticebus coucang*). Folia Primatol 44:52–64

Zimmermann E (1996) Castration affects the emission of an ultrasonic vocalization in a nocturnal primate, the grey mouse lemur (*Microcebus murinus*). Physiol Behav 60:693–697

Zimmermann E (2009) Vocal expression of emotion in a nocturnal prosimian group, mouse lemurs. In: Brudzynski SM (ed) Handbook of mammalian vocalization. Academic, Oxford, pp 215–225

Zimmermann E, Lerch C (1993) The complex acoustic design of an advertisement call in male mouse lemurs (*Microcebus murinus*, Prosimii, Primates) and sources of its variation. Ethology 93:211–224

Chapter 33
Noises in the Dark: Vocal Communication in *Lepilemur ruficaudatus* and Other Nocturnal Pair-Living Primates

Claudia Fichtel and Roland Hilgartner

Abstract Although the number of pair-living species is higher in nocturnal than in diurnal primates, less is known about the communicative function of their vocalizations. One striking feature of vocal communication in diurnal pair-living primates is that partners exchange vocalizations in coordinated duets. Several functions have been attributed to duets, including mate attraction, advertizing and strengthening the pair bond, and territorial defense. To assess whether these functions can also be attributed to vocalizations of pair-living nocturnal primates, we studied the communicative function of vocalizations of red-tailed sportive lemurs (*Lepilemur ruficaudatus*). Social interactions between partners were equally often accompanied by vocal exchanges or not. Half of these vocal interactions included mutual but not coordinated exchanges of vocalizations between partners. In addition, playback experiments with vocalizations of the respective partner did not elicit vocal responses. Thus, exchanges of vocalizations might function to regulate spacing and interactions within pairs rather than to advertize or strengthen pair bonds. Since *Lepilemur ruficaudatus* interacted more often vocally with partners than with neighbors, and also vocalized when alone, we conclude that calling serves to signal an animal's presence in its territory and to regulate spacing among conspecifics. Because vocalizations seem to serve in territorial defense in most nocturnal pair-living primates, cohesiveness between partners may have been the initial driving force behind the evolution of duets.

C. Fichtel (✉)
Behavioral Ecology and Sociobiology Unit, German Primate Center, CRC "Evolution of Social Behavior", University of Göttingen, Kellnerweg 4, Göttingen 37077, Germany
e-mail: claudia.fichtel@gwdg.de

R. Hilgartner
Behavioral Ecology and Sociobiology Unit, German Primate Center, University of Göttingen, Kellnerweg 4, Göttingen 37077, Germany

Department of Experimental Ecology, University of Ulm, Ulm, Germany
e-mail: hilgartner@gmx.de

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_33,

Resume Bien que les Primates nocturnes vivent plus souvent en couples que les diurnes, la fonction communicative de leurs vocalisations est moins bien connue. Une caractéristique frappante de la communication vocale des primates vivant en couples est que ceux-ci échangent des vocalisations émises en duos coordonnés. Plusieurs fonctions ont été attribuées à ces duos, comme l'attraction de partenaires sexuels, l'expression publique et le renforcement des liens entre partenaires, ainsi que la défense territoriale. Afin de déterminer la fonction attribuable aux vocalisations émises par les primates nocturnes vivant en paires, nous avons étudié la fonction communicative des vocalisations du Lépilémur à queue rousse (*Lepilemur ruficaudatus*). Les interactions sociales entre partenaires étaient ou non accompagnées de vocalisations, dans les mêmes proportions. La moitié des interactions vocales étaient mutuelles, mais non coordonnées. De plus, les expériences de repasse de vocalisations du partenaire respectif n'ont entraîné aucune réponse. Donc, les échanges vocaux pourraient réguler l'espacement et les interactions entre partenaires, plutôt que de servir à la publicité ou aux renforcements des liens entre partenaires. Comme les animaux interagissent plus souvent entre partenaires d'une même paire qu'entre voisins, et vocalisent aussi quand ils sont seuls, nous concluons que les vocalisations servent de signaux marquant la présence des animaux dans leur territoire et régulant leur espacement. Parce que les vocalisations de la plupart des primates nocturnes vivant en couple semblent être territoriales, la cohésion entre partenaires pourrait être la raison initiale de l'évolution des duos.

Introduction

The last decade of research on nocturnal primates has revealed them not to be as solitary as was previously believed, and several species are pair living (*Cheirogaleus medius*: Müller 1998; Fietz 1999; *Lepilemur edwardsi*: Rasoloharijaona et al. 2006; Thalmann 2001; *Avahi occidentalis*: Thalmann 2003; *Phaner furcifer*: Schülke and Kappeler 2003; *Lepilemur ruficaudatus*: Zinner et al. 2003) or exhibit even more complex types of social organization (*Tarsius spectrum*: Gursky 2000). Most of these species emit conspicuous loud calls in communicating with partners and neighbors. Although the number of pair-living species is higher in nocturnal than in diurnal primates (Kappeler and Heymann 1996), less is known about the communicative function of their vocalizations. A striking feature of vocal communication in diurnal pair-living primates is that partners exchange vocalizations in coordinated duets (Thalmann et al. 1993; Cowlishaw 1992; Geissmann 1999; Müller and Anzenberger 2002; Geissmann and Mutschler 2006). Numerous functional roles have been attributed to these duets, including mate attraction, advertizing and strengthening the pair bond, and territorial defense and spacing among groups. We investigated whether nocturnal, pair-living *Lepilemur ruficaudatus* also exchange vocalizations in coordinated duets, and whether the functions attributed to duets in

diurnal pair-living primates can also be ascribed to vocalizations of *L. ruficaudatus* and, by implication, other nocturnal pair-living primates.

Methods

We observed eight pairs of *Lepilemur ruficaudatus* regularly during a 24-month field study in Kirindy Forest CFPF, western Madagascar (Zinner et al. 2003; Hilgartner 2006; Hilgartner et al. 2008). Pair partners were observed simultaneously, i.e., two observers followed the male and female of a given pair at the same time using focal animal sampling. The exact location as well as the behavior (feeding, resting, and locomotion) of the focal animal were recorded instantaneously at 5-min intervals. All vocalizations and social interactions were noted *ad libitum*.

A duet is defined as the joint vocalization of two individuals, coordinated in time and/or in emission of distinct notes (Wickler 1980). To investigate whether *L. ruficaudatus* pairs duet, we analyzed how often social interactions between partners were accompanied by vocalizations and whether vocalizations were exchanged in a coordinated manner. Another approach to identifying duets in nonhuman primates is to conduct playback experiments with vocalizations of the respective partner (Raemaekers and Raemaekers 1985; Nietsch and Kopp 1998). The frequency of vocalizations and approaches towards the speaker can be used as a proxy to identify duets. We therefore conducted playback experiments in which we presented the female and male of 8 pairs with vocalizations of their respective partners (5 bouts of vocalization separated by 4 s of silence with an average total length of 85 s, presented at a distance of about 10 m, when the respective partner was out of sight).

Results

We identified six call types produced by *Lepilemur ruficaudatus* (Fig. 33.1). Three call types (snores, screams, and alarm barks) were given by both sexes; double chucks were given by females only, whereas woofs and chucks were given by males only. Because alarm barks and screams are given during predatory contexts and aggressive interactions with conspecifics (Fichtel 2007), we explored only the functions of female double chucks and snores and male woofs, chucks, and snores.

The median of the frequency of social encounters between partners was 0.5/h (Table 33.1). Half of these encounters (median: 57%) were accompanied by vocal exchanges (Wilcoxon test: $z = -0.980$, $P = 0.327$). In 42% of interactions both partners vocalized and in 58% of interactions only one partner vocalized (Table 33.1, Wilcoxon test: $z = -1.407$, $P = 0.159$). If interactions were accompanied by vocalizations by only one partner, females vocalized significantly more often than males

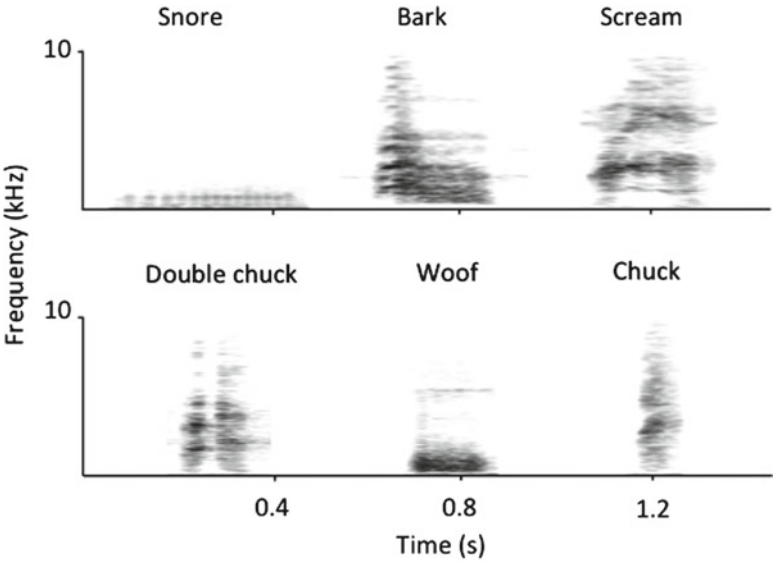


Fig. 33.1 Vocal repertoire of *Lepilemur ruficaudatus*. Snores, barks, and screams are produced by both sexes, while double chucks are given by females only and woofs and chucks by males only

(females: median = 33%, IQR = 20%; males: median = 4%, IQR = 5%; Mann–Whitney $U = 2.5$; $P = 0.002$). Thus, a median of 27% (IQR = 9%) of social encounters provoked vocalizations by both partners.

During vocal exchanges between partners ($N = 50$ recordings), females usually started with a series of double chucks and males responded with a series of woofs, snores, or chucks. During such vocal interactions, females and males exchanged calls on average once (median = 1; IQR = 2). Female and male calls sometimes overlapped and sometimes not, so there was no typical pattern of successive calls, and *L. ruficaudatus* did not seem to coordinate their vocalizations. In response to playback experiments with vocalizations of the respective partner, *L. ruficaudatus* never vocalized or approached the speaker (binomial test: $P = 0.001$) and responded solely with a change of gaze direction in median 10 scans (IQR = 16). We conclude that *L. ruficaudatus* do not coordinate their vocalizations into duets.

To explore whether *L. ruficaudatus* vocalizations serve in territorial defense, we analyzed how often sportive lemurs were engaged in vocal interactions with territorial neighbors. Both sexes were significantly more often involved in mutual vocal exchanges with their partners than with neighbors (Table 33.1, Wilcoxon test: females: $z = -2.54$; $P = 0.012$; males: $z = -2.53$; $P = 0.012$). The solo calling rate of both sexes was higher than the duet calling rate, so vocalizations may serve as a location marker to advertize the animals' presence in the territory (Table 33.1, Wilcoxon test: females: $z = -1.92$; $P = 0.23$; males: $z = -1.12$; $P = 0.26$).

Table 33.1 Average rates and percentages of vocalization bouts within a 2-h period given by red-tailed sportive lemurs during social interactions between pair partners ($N=8$ pairs), other conspecifics, or in the absence of conspecifics

	Rate of social encounters between partners within 2 h	Percentage of social encounters between partners including vocalizations	Percentage of social encounters between partners including vocalizations of both partners	Percentage of social encounters between partners including vocalizations of one partner
Median	0.1	57	42	58
1. Quartile	0.7	49	35	54
3. Quartile	1.2	66	46	65

	Female calling rate/2 h with mutual exchange of vocalizations with		Male calling rate/2 h with mutual exchange of vocalizations with		Female solo calling rate/2 h	Male solo calling rate/2 h
	partner	others	partner	others		
Median	0.5	0.1	0.5	0.1	0.8	0.7
1. Quartile	0.4	0.1	0.4	0	0.6	0.4
3. Quartile	0.6	0.1	0.6	0.1	1.1	1.4

Discussion

Our results show that *Lepilemur ruficaudatus* pairs exhibit a low rate of mutual vocal exchanges, and vocal exchanges were not coordinated. Playback experiments with vocalizations of the respective pair partner did not elicit either vocalizations or approaches towards the speaker. Thus, vocal exchanges may function to regulate social interactions between pair partners but not to advertize or strengthen their pair bond.

Observations of *Lepilemur edwardsi*, which also form dispersed pairs, revealed that this species regularly exchanges vocalizations at specific places such as sleeping or feeding sites, indicating that antiphonal calling might be used to signal the pair bond (Rasoloharijaona et al. 2006). Because *L. edwardsi* partners regularly share the same sleeping tree whereas *L. ruficaudatus* pairs rarely do so (Zinner et al. 2003), cohesiveness between partners may be higher in *L. edwardsi*, and the frequency of mutual exchanges of vocalizations may be a function of pair cohesiveness.

Detailed observations of intrapair communication are lacking for most other nocturnal pair-living primates. Observations of captive fat-tailed dwarf lemurs revealed that they do not produce duets and vocalizations do not function to advertize or strengthen their pair bond (Stanger 1993). However, preliminary observations of other nocturnal pair-living primates suggest that *Phaner pallescens* and *Avahi* spp. produce joint vocalizations as a means of communication between partners (Petter and Charles-Dominique 1979; Harcourt 1991; Thalmann 2003). Duets in nocturnal primates have been reported in detail only for *Tarsius spectrum* and

T. dianae (Nietsch 2003). In tarsiers, males and females form a social unit in which interactions occur regularly (Gursky 2000). Both sexes contribute to duets to defend territories, as well as to attract and defend mates (Nietsch and Kopp 1998; Nietsch 2003). Partners in species that exhibit either antiphonal calling or duets seem to form sleeping groups regularly (*L. edwardsi*: Rasoloharijaona et al. 2006; *Avahi* spp.: Norscia and Borgognini-Tarli 2008) or engage in affiliative interactions outside the mating season (*Tarsius* spp.: Gursky 2000; *Phaner pallescens*: Schülke and Kappeler 2003). Thus, the available data on intrapair communication in nocturnal primates suggest that antiphonal calling or duetting occurs in species in which partners are more closely associated than in *L. ruficaudatus* and may, thus, reflect the cohesiveness or sociality of a pair.

A territorial function for vocalizations is inferred when vocalizations accompany encounters with neighbors (Geissmann 1999; Nietsch 2003). *L. ruficaudatus*, however, vocalized more often during interactions with partners than with neighbors. In response to playback experiments in which we simulated a strange territorial intruder, *L. ruficaudatus* rarely responded with vocalizations or approached the speaker (Hilgartner 2006). Since *L. ruficaudatus* vocalized regularly without social interactions throughout their activity period, we conclude that calling serves as a location marker to signal their presence in the territory, and thus to regulate spacing between partners and neighbors. In other nocturnal pair-living species, a territorial function for vocalizations has been suggested for *L. edwardsi* in which antiphonal calling serves as a cooperative display of territory defense (Rasoloharijaona et al. 2006). Captive *Cheirogaleus medius* males match the frequency of whistles of other males, a display addressed directly to other males (Stanger 1995). *Phaner pallescens* not only regularly vocalizes during departure or reunion at the sleeping site but also in joint duets during vocal interactions with neighbors (Petter and Charles-Dominique 1979). Moreover, *Avahi* spp. use loud calls in territorial contexts (Harcourt 1991; Thalmann 2003). Thus, loud calling as a territorial defense, either directly during interactions with neighbors or less directly as location markers, seems to be present in all nocturnal pair-living strepsirhines studied so far.

Conclusion

Intrapair communication in nocturnal primates varies from no duets (*Lepilemur ruficaudatus*) through antiphonal calling (*L. edwardsi*) to duets (*Tarsius* spp.). Since antiphonal calling and duets share the functions suggested for diurnal pair-living primates, the degree of coordinated vocal exchange might reflect the cohesiveness or sociality of a pair. Vocalizations of pair-living nocturnal primates may serve in territorial defense and spacing among groups, irrespective of whether or not they are coordinated as duets. Thus, cohesiveness between partners may have been the initial driving force for the evolution of duets, but more comparative data are required for a rigorous test of this hypothesis.

Acknowledgments We thank Professors Ramilijaona and Rakotondravony, University of Antananarivo, the Commission Tripartite de Direction des Eaux et Forêts and the CNFEREF/ Morondava for authorizing this study. We also thank Mario Heriniaina Ramohavelo for assistance during data collection in the field, Peter Kappeler for comments on the manuscript, and J. Masters, M. Gamba, and F. Génin for editing this volume. Financial support was provided by the German Science foundation (DFG, Ka1082/6-1; Fi929/1-2).

References

Cowlishaw G (1992) Song function in gibbons. Behaviour 121:131–153

Fichtel C (2007) Avoiding predators at night: antipredator strategies in red-tailed sportive lemurs *(Lepilemur ruficaudatus)*. Am J Primatol 69:611–624

Fietz J (1999) Monogamy as a rule rather than exception in nocturnal lemurs: the case of the fat-tailed dwarf lemur, *Cheirogaleus medius*. Ethology 105:259–272

Geissmann T (1999) Duet songs of siamang, *Hylobates syndactylus*: II. Testing the pair-bonding hypothesis during a partner exchange. Behaviour 136:1005–1039

Geissmann T, Mutschler T (2006) Diurnal distribution of loud calls in sympatric wild indris *(Indri indri)* and ruffed lemurs *(Varecia variegata)*: implications for call functions. Primates 47:393–396

Gursky S (2000) Sociality in the spectral tarsier, *Tarsius spectrum*. Am J Primatol 51:89–101

Harcourt CS (1991) Diet and behaviour of a nocturnal lemur, *Avahi laniger*, in the wild. J Zool 223:667–674

Hilgartner R (2006) Living apart together: pair-living in red-tailed sportive lemurs (*Lepilemur ruficaudatus*). Unpublished PhD Thesis, University of Ulm

Hilgartner R, Zinner D, Kappeler PM (2008) Life history traits and parental care in *Lepilemur ruficaudatus*. Am J Primatol 69:1–15

Kappeler PM, Heymann EW (1996) Nonconvergence in the evolution of primate life history and socio-ecology. Biol J Linn Soc 59:297–326

Müller AE (1998) A preliminary report on the social organisation of *Cheirogaleus medius* (Cheirogaleidae; Primates) in north-west Madagascar. Folia Primatol 69:160–166

Müller AE, Anzenberger G (2002) Duetting in the titi monkey *Callicebus cupreus*: structure, pair specificity and development of duets. Folia Primatol 73:104–115

Nietsch A (2003) Outline of the vocal behavior of *Tarsius spectrum*: call features, associated behaviors and biological functions. In: Wright P, Simons EL, Gursky S (eds) Tarsiers: past, present, and future. Rutgers University Press, New Brunswick, pp 166–220

Nietsch A, Kopp M-L (1998) Role of vocalization in species differentiation of Sulawesi tarsiers. Folia Primatol 69(Suppl 1):371–378

Norscia I, Borgognini-Tarli SM (2008) Ranging behavior and possible correlates of pair-living in southeastern avahis (Madagascar). Int J Primatol 29:153–171

Petter J-J, Charles-Dominique P (1979) Vocal communication in prosimians. In: Doyle GA, Martin RD (eds) The study of prosimian behavior. Academic, New York, pp 247–305

Raemaekers JJ, Raemaekers PM (1985) Field playback of loud calls to gibbons (*Hylobates lar*): territorial, sex-specific and species-specific responses. Anim Behav 33:481–493

Rasoloharijaona S, Randrianambinina B, Braune P, Zimmermann E (2006) Loud calling, spacing, and cohesiveness in a nocturnal primate, the Milne Edwards' sportive lemur (*Lepilemur edwardsi*). Am J Phys Anthropol 129:591–600

Schülke O, Kappeler P (2003) So near and yet so far: territorial pairs but low cohesion between pair-partners in a nocturnal lemur, *Phaner furcifer*. Anim Behav 65:331–343

Stanger K (1993) Structure and function of the vocalizations of nocturnal prosimians (Cheirogeleidae). (PhD-thesis: Univ Tübingen, Germany)

Stanger K (1995) Vocalizations of some cheirogaleid prosimians evaluated in a phylogenetic context. In: Alterman L, Doyle GA, Izard MK (eds) Creatures of the dark: the nocturnal prosimians. Plenum, New York, pp 353–376

Thalmann U (2001) Food resource characteristics in two nocturnal lemurs with different social behavior: *Avahi occidentalis* and *Lepilemur edwardsi*. Int J Primatol 22:287–324

Thalmann U, Geissmann T, Simona A, Mutschler T (1993) The indris of Anjanaharibe-Sud, Northeastern Madagascar. Int J Primatol 14:357–381

Thalmann U (2003) *Avahi*, woolly lemurs, *Avahy*, *Fotsy-fe*, *Ampongy*, *Tsarafagitra*, *Daintsifaky*. In: Goodman SM, Benstead JP (eds) The natural history of Madagascar. University of Chicago Press, Chicago, pp 1340–1342

Wickler W (1980) Vocal dueting and the pair bond I. Coyness and partner commitment. A hypothesis. Z Tierpsychol 52:201–209

Zinner D, Hilgartner RD, Kappler PM, Pietsch T, Ganzhorn JU (2003) Social organization of *Lepilemur ruficaudatus*. Int J Primatol 24:869–888

Chapter 34
Artificial Neural Networks: A New Tool for Studying Lemur Vocal Communication

Luca Pozzi, Marco Gamba, and Cristina Giacoma

Abstract Previous studies have applied Artificial Neural Networks (ANNs) successfully to bioacoustic problems at different levels of analysis (individual and species identification, vocal repertoire categorization, and analysis of sound structure) but not to nonhuman primates. Here, we report the results of applying this tool to two important problems in primate vocal communication. First, we apply a supervised ANN to classify 222 long grunt vocalizations emitted by five species of the genus *Eulemur.* Second, we use an unsupervised self-organizing network to identify discrete categories within the vocal repertoire of black lemurs (*Eulemur macaco*). Calls were characterized by both spectral (fundamental frequency and formants) and temporal features. The result show not only that ANNs are effective for studying primate vocalizations but also that this tool can increase the efficiency, objectivity, and biological significance of vocal classification greatly. The advantages of ANNs over more commonly used statistical techniques and different applications for supervised and unsupervised ANNs are discussed.

Resume Des études antérieures ont appliqué avec succès les Réseaux Neuronaux Artificiels (RNA) aux questions bioacoustiques (reconnaissance individuelle et inter-spécifique, catégorisation des répertoires vocaux, et analyse des structures sonores), mais pas sur les primates non-humains. Ici nous appliquons cet outil à

L. Pozzi (✉)
Department of Anthropology, Center for the Study of Human Origins, New York University, 25 Waverly Place, New York 10003, NY, USA
e-mail: luca.pozzi@nyu.edu

M. Gamba • C. Giacoma
Dipartimento di Biologia Animale e dell'Uomo, Università degli Studi di Torino, Via Accademia Albertina, 13, 10124 Torino, Italy
e-mail: marco.gamba@unito.it; cristina.giacoma@unito.it

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_34,

deux problèmes concernant la communication vocale des Primates. Premièrement, nous utilisons un modèle de RNA « supervisé » à la classification de 222 « grognements longs » émis par 5 espèces du genre *Eulemur*. Deuxièmement, nous utilisons un modèle auto-organisé « non supervisé » de RNA pour identifier des catégories discrètes dans le répertoire vocal du lémur Macaco (*Eulemur macaco*). Les vocalisations sont caractérisées par leurs propriétés spectrales (fréquence fondamentale et formant) et temporelles. Les résultats montrent que les RNA sont des outils efficaces pour l'étude des vocalisations des primates, mais aussi que cette méthode qui accroit l'efficacité, l'objectivité, et la signification biologique des classifications vocales. Les avantages des RNA sur d'autres méthodes communément utilisées, ainsi que différentes applications des RNA supervisées et non supervisées sont discutés.

Introduction

Identifying discrete categories is one of the most challenging problems in bioacoustics. In studies of animal communication, the classification of vocal signals into discrete categories is a preliminary step to comparing acoustic variability at different levels of analysis (definition of vocal repertoires, identification of species or individuals, analysis of call structure, etc.). Unfortunately, current statistical methods do not always give satisfactory results, particularly when the data are nonlinearly distributed (Demuth and Beale 1993). Moreover, most statistical techniques involve a number of a priori assumptions that may affect the objectivity of the classification and, therefore, the comparison of results between studies.

In recent years, many attempts have been made to develop mathematical tools for automatic and "objective" classification. Artificial Neural Networks (ANNs) have been widely used in the field of pattern recognition and have been applied successfully within the biological sciences to model complex functions and solve problems of classification, regression, and prevision (Ghirlanda and Enquist 1998).

The Theory of Artificial Neural Networks: Structure and Function

ANNs are computer simulations of biological nervous systems and mimic their fault-tolerance and learning capacity by modeling the low-level structure of the brain. Although this technique cannot reach the complexity of most biological nervous systems, it provides a powerful classificatory tool on account of its ability to learn a specific classification scheme and deal with incomplete or noisy data.

ANNs can be classified into two main groups: s*upervised* and *unsupervised* neural networks. The operation of a supervised neural network can be divided into two phases (1) *learning*, in which the network is trained to recognize different output categories (*targets*) and (2) *generalization*, where the network autonomously

classifies a new set of previously unseen data according to the classification scheme acquired during the previous phase. Unlike supervised ANNs, unsupervised networks do not require a priori definition of output categories, and the process of classification is based on local information only. The network is thus able to self-organize data, to detect patterns in inputs autonomously, and to classify them into categories without requiring the number or types of categories to be predefined (Kohonen 1988).

Application of ANNs to Bioacoustic Problems

Because of their ability to model complex functions, ANNs have been used to address several issues in animal bioacoustics. The main applications of ANNs in this field have been to human speech, but they have also been applied to a variety of animal vocalizations. ANNs have been successfully applied to categorization of species' vocal repertoires (whales: Mercado and Kuh 1998; Murray et al. 1998), individual (sea lions: Campbell et al. 2002; deer: Reby et al. 1997; birds: Adi et al. 2010) and species identification (insects: Chesmore 2004; Chesmore and Ohya 2004; birds: Derégnaucourt et al. 2001; Lopes et al. 2011; bats: Parsons 2001; Jennings et al. 2008), and studies of the acoustic structure of vocalizations (birds: Dawson et al. 2006; Nickerson et al. 2006; whales: Green et al. 2011).

To date, the application of this computational technique in the study of nonhuman primate utterances has been extremely limited. Zimmermann (1995) suggested neural network modeling as a tool for the analysis and interpretation of primate sounds but did not perform any experimental studies using the technique. Recently, we applied ANNs to the study of the vocal repertoire of black lemurs, *Eulemur macaco* (Pozzi et al. 2010), and demonstrated the ability of supervised ANNs to classify lemur vocalizations into discrete categories with 94% correct prediction overall. In this chapter, we explore this approach further for classifying primate vocalizations, specifically (1) to differentiate the calls of different *Eulemur* species and (2) to categorize the vocal repertoire of black lemurs using unsupervised ANNS.

Materials and Methods

Application of Supervised ANNs to Differentiate Eulemur Species Vocalizations

A sample of 222 long grunts emitted by *Eulemur macaco* (115), *E. mongoz* (33), *E. coronatus* (23), *E. rubriventer* (16), and *E. fulvus* (35) was randomly selected

from a larger data set recorded between 1995 and 2005 [see Gamba and Giacoma (2005) for recording techniques]. This vocal type was chosen because (1) it is present in the vocal repertoire of all lemurid species (Macedonia and Stanger 1994; Gamba and Giacoma 2005); (2) it is emitted by all species at a high rate, providing a good sample for the analyses; and (3) previous studies have demonstrated that long grunts are species specific (Gamba and Giacoma 2005). The different rates of long grunt emission across the five species and the need for good sound quality biased the number of recordings included in the sample. However, ANNs are not influenced by unbalanced numbers in different groups, only by the number of inputs during the training phase (Pozzi et al. 2010).

Each vocalization was split into a series of very short duration (0.01 s) nonoverlapping time windows, and 30 windows were sampled at regular intervals. The average duration of each vocalization was 0.521 s (SD 0.145 s), meaning that most vocalizations had approximately 50 windows. Vocalizations shorter than 0.30 s were excluded from the analysis. The inputs for the ANNs were two-dimensional characterizations of long grunts, in which each signal was described by a combination of pitch (F0) and the first four formants (i.e., spectral peaks), F1–F4. Each vector was constructed by concatenating the five 30-element vectors into a single 150-element vector and served as inputs into a supervised artificial neural network using a back-propagation algorithm during the training phase. Neural network analyses were performed using Statistica Neural Networks 7.1 (StatSoft, Trajan Software Ltd 1996–2000).

Identification of Distinct Calls Within the Eulemur macaco Vocal Repertoire Using an Unsupervised ANN

A total of 311 vocalizations including seven different vocal types (alarm calls, grunted hoots, hoots, grunts, long grunts, long grunt clear calls, and tonal calls) described in previous studies (Gosset et al. 2002; Macedonia and Stanger 1994) was used in the study. Each vocalization was characterized by a 10-element vector: three elements each corresponding to measurements of fundamental frequency (F0) and the first two formants (F1 and F2) at three different points (at the beginning, middle and end of the signal), and one element corresponding to duration. These vectors were the inputs for an unsupervised ANN (Self-Organizing Neural Network or SONN). Analyses were performed using both Matlab 7.0 (Matlab Neural Network Toolbox, Demuth and Beale 1993) and Statistica Neural Networks 7.1 (StatSoft, Trajan Software Ltd, 1996–2000).

Because unsupervised ANNs do not require target categories to be defined a priori, the architecture of the network has been characterized as a trial-and-error procedure (protocol described in Murray et al. 1998). We tested 12 networks using different combinations of learning rate (0.01 and 0.03), numbers of iterations (5,000 and 10,000), and numbers of neurons (40, 20, and 10). The number of units in a

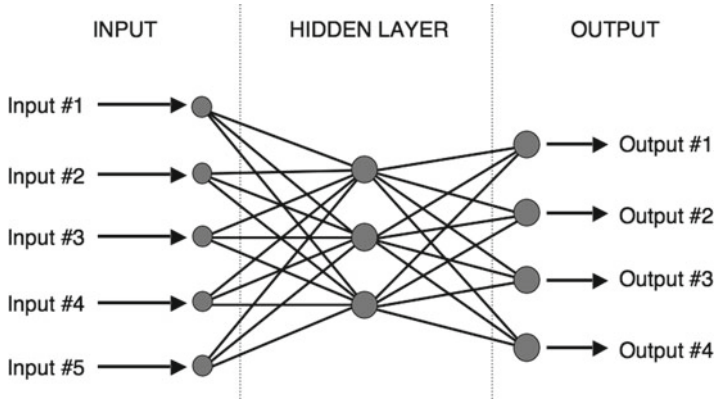


Fig. 34.1 Structure of the artificial neural network used in this study

SONN can be taken as the maximum number of potential categories that the network can identify during a training session. For each run, we analyzed the number of neurons activated that correspond to the number of categories recognized by the system of classification. The output neurons activated during the analysis represent the number of categories recognized by the network. To match these categories to the vocal types defined a priori for the black lemur vocal repertoire, we analyzed the weight vectors of each activated unit: the pattern of the spectral values (F0–F2) and the call durations were compared with the vocal repertoire description to assess concordance between the network results and the categories previously recognized.

Results

Application of Supervised ANNs to Differentiate Eulemur Species Vocalizations

We applied a one-hidden layer network with 70 units and 1,000 epochs (Fig. 34.1); this topology was the best network in the preliminary analyses, with 98% correct classifications in the training phase and 81% in the test.

The data set was randomly divided into a training (67% signals) and a test set (33%), and the analyses were run independently 15 times. The percentage correct prediction during the test phase varied from 67% in *E. coronatus* to 99% in *E. macaco*. The means and standard deviations for all vocal types analyzed are reported in Table 34.1: four out of five species were recognized with >80% correctly classified signals. The overall average reliability of the network was 89%.

Table 34.1 Number of signals, correct classifications (mean performance) and standard deviation for each of the five species within the genus *Eulemur* resulted in the application of the supervised neural network with 70 hidden units

	E. macaco	*E. fulvus*	*E. mongoz*	*E. coronatus*	*E. rubriventer*
N	115	35	33	23	16
Mean performance	99.42	84.44	80.00	66.67	84.00
Standard deviation	1.18	14.17	11.34	14.95	17.24

Identification of Distinct Calls Within the Eulemur macaco Vocal Repertoire Using an Unsupervised ANN

The weight vectors resulting from each activated unit in the analysis are shown in Fig. 34.2. The *x*-axis represents the ten elements making up the vectors, while the normalized *z*-scores are on the *y*-axis. Zero represents the mean, and values above and below zero are deviations from the mean. All networks but one identified five different categories. We thus compared the resulting five weight vectors with the sound structure of the different vocal types. The association between the weight vectors and the vocal categories recognized by the network is represented in Fig. 34.2. The five categories recognized by the unsupervised neural networks are:

1. *Alarm call*, represented by the weight vector W1, shows long duration and high frequency values in spectral parameters (above the mean).
2. *Long grunt,* represented by the vector W2, is characterized by low fundamental frequency and formant values and by long duration.
3. *Tonal* or *clear calls* (weight vector W3) have relatively high spectral values and average duration (around zero).
4. The composite vocalization *long grunt clear call* (W4) is made up of two parts: the first similar to the *long grunt* category (low spectral parameters) and the second with very high fundamental frequency and formant values.
5. A combined category including *hoot*, *grunt,* and *grunted hoot* (W5) has a spectral structure similar to the category 2 *long grunt* (low F0 and formant values) but is of much shorter duration.

Discussion

ANNs are widely used in bioacoustics to address numerous problems, but ours are the first applications of ANNs to nonhuman primate vocalizations. We applied different network typologies to address two common issues in the study of primate communication (1) the identification of closely related species and (2) the categorization of a species' vocal repertoire. The supervised network in the first case study distinguished five *Eulemur* species with an overall performance of almost 90%.

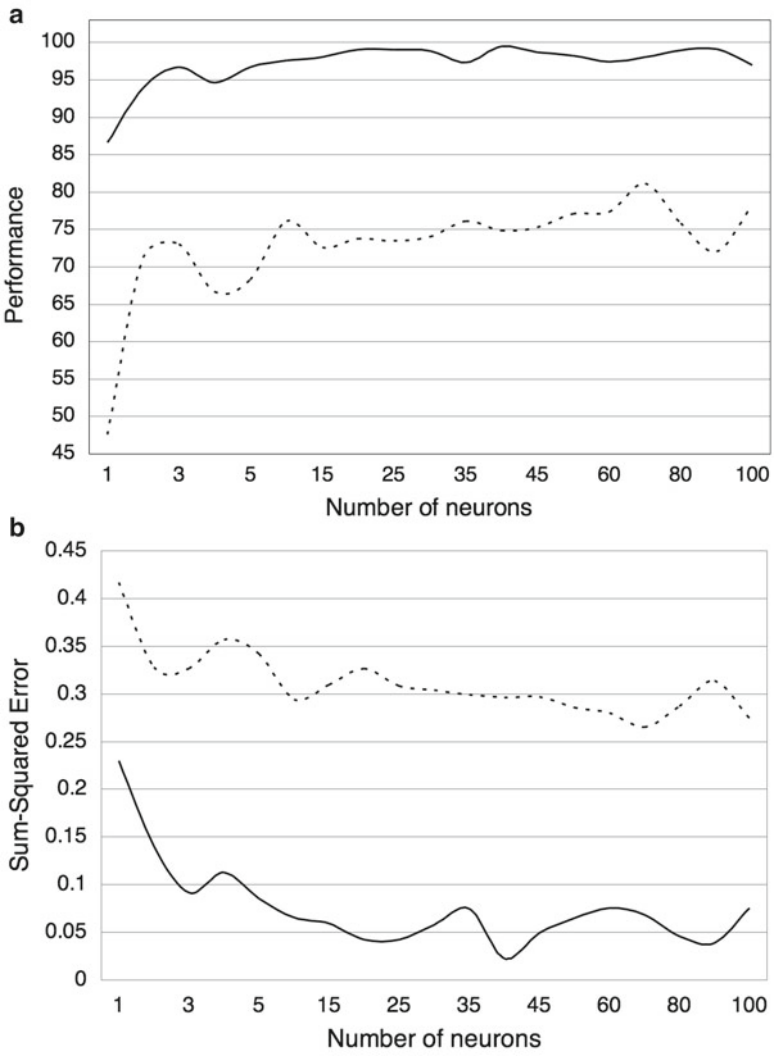


Fig. 34.2 Results of the SONN: the 10-element weight vectors of each of the five units resulting from the supervised network analysis. Zero (*y*-axis) represents the grand mean for each dimension (normalized *z* scores). Values above and below zero represent deviations from the mean. Each weight vector is associated with one or more of the call typologies recognized in this study (see the text for details). *LG* long grunt, *LGCC* long grunt clear call, *G* grunt, *GH* grunted hoot, *H* hoot

The unsupervised ANN used to categorize the black lemur vocal repertoire recognized five out of the seven vocal types defined a priori. The remaining two types (*grunted hoot* and *hoot*), with very similar structure, were merged under a larger category with *grunts*. This result is probably due to the relatively low number of appropriate signals in our sample.

Our study shows that ANNs provide an effective tool for acoustic categorization and have several advantages over other systems of classification. First, our approach requires fewer a priori assumptions than other statistical methods, reducing the degree of subjectivity in the classification procedure. Second, ANNs can deal with incomplete or noisy data, which is especially important in biological classification tasks, where unambiguous, discrete categories are often difficult to define. Finally, ANNs allow researchers to develop automatic or semiautomatic acoustic screening of animal vocalizations.

Our use of both supervised and unsupervised networks allows us also to draw some conclusions regarding their advantages and constraints for primate call classification. The application of supervised learning systems is obviously more efficient in recognizing discrete categories but requires the definition of a priori categories during the learning phase and is therefore more prone to subjective choices. Since ANNs are able to detect a classification rule autonomously during the learning phase and to reduce the noise in the signals, supervised ANNs are extremely powerful at classifying vocalizations into previously defined categories, even with low quality recordings (Placer and Slobodchikoff 2000). The main advantage of supervised ANNs is that these networks can be trained on a well-defined set of signals and then used to classify previously unseen records (Pozzi et al. 2010). Such networks are thus better suited to classification tasks where some aspect of pattern is already known. On the other hand, unsupervised ANNs (SONNs) are capable of detecting regularities and classifying inputs into discrete categories without numbers and types of outputs being defined a priori. Unsupervised neural networks reduce the role of the external operator in the classification process, increasing the objectivity of the classification system. SONNs are thus excellent for classification where no a priori knowledge of vocalizations is available (Murray et al. 1998).

The great potential of this approach indicates that more effort should be directed towards the development of neural networks to classify complex signals emitted by nonhuman primates. Such applications may be used to clarify various aspects of primate vocal behavior when discrete categories are hard to define using more conventional techniques. The integration of behavioral and statistical approaches with ANNs can increase greatly the efficiency, objectivity, and biological significance of vocal classification, and so advance our efforts to understand the evolution of vocal behavior in nonhuman primates.

Acknowledgments We thank Judith Masters for providing the opportunity to contribute to this volume. We also thank Cesare Avesani Zaborra and Parco Natura Viva for their continued support.

References

Adi K, Johnson MT, Osiejuk TS (2010) Acoustic censusing using automatic vocalization classification and identity recognition. J Acoust Soc Am 127:874–883

Campbell GS, Gisiner RC, Helweg DA, Milette LL (2002) Acoustic identification of female Steller sea lions (*Eumetopias jubatus*). J Acoust Soc Am 111:2920–2928

Chesmore D (2004) Automated bioacoustic identification of species. An Acad Bras Cienc 76:435–440

Chesmore ED, Ohya E (2004) Automated identification of field-recorded songs of four British grasshoppers using bioacoustic signal recognition. Bull Entomol Res 94:319–330

Dawson MR, Charrier I, Sturdy CB (2006) Using an artificial neural network to classify black-capped chickadee (*Poecile atricapillus*) call note types. J Acoust Soc Am 119:3161–3172

Demuth H, Beale M (1993) Neural network toolbox. The MathWorks, Inc., Natick, MA

Derégnaucourt S, Guyomarc'h J-C, Richard V (2001) Classification of hybrid crows in quail using artificial neural networks. Behav Proc 56:103–112

Gamba M, Giacoma C (2005) Key issues in the study of primate acoustic signals. J Anthropol Sci 83:61–87

Ghirlanda S, Enquist M (1998) Artificial neural networks as models of stimulus control. Anim Behav 56:1383–1389

Gosset D, Fornasieri I, Roeder J-J (2002) Acoustic structure and contexts of emission of vocal signals by black lemurs. Evol Commun 4:225–251

Green SR, Mercado E, Pack AA, Herman LM (2011) Recurring patterns in the songs of humpback whales (*Megaptera novaeangliae*). Behav Proc 86:284–294

Jennings N, Parsons S, Pocock MJO (2008) Human vs. machine: identification of bat species from their echolocation calls by humans and by artificial neural networks. Can J Zool 86:371–377

Kohonen T (1988) The 'neural' phonetic typewriter. Computer 21:11–22

Lopes MT, Gioppo LL, Higushi TT, Kaestner CAA, Silla Jr, CN, Koerich AL (2011) Automatic bird species identification for large number of species. IEEE international symposium on multimedia, pp. 117–122

Macedonia JM, Stanger KF (1994) Phylogeny of the Lemuridae revisited: evidence from communication signals. Folia Primatol 63:1–43

Mercado E, Kuh A (1998) Classification of humpback whale vocalizations using a self-organizing neural network. Proceedings of the 1998 IEEE joint conference on neural networks, pp 1584–1589. doi: 10.1109/IJCNN.1998.686014

Murray SO, Mercado E, Roitblat HL (1998) The neural network classification of false killer whale (*Pseudorca crassidens*) vocalizations. J Acoust Soc Am 104:3626–3633

Nickerson CM, Bloomfield LL, Dawson MR, Sturdy CB (2006) Artificial neural network discrimination of black-capped chickadee (*Poecile atricapillus*) call notes. J Acoust Soc Am 120:1111–1117

Parsons S (2001) Identification of New Zealand bats (*Chalinolobus tuberculatus* and *Mystacina tuberculata*) in flight from analysis of echolocation calls by artificial neural networks. J Zool 253:447–456

Placer J, Slobodchikoff CN (2000) A fuzzy-neural system for identification of species-specific alarm calls of Gunnison's prairie dogs. Behav Proc 52:1–9

Pozzi L, Gamba M, Giacoma C (2010) The use of artificial neural networks to classify primate vocalizations: a pilot study on black lemurs. Am J Primatol 72:337–348

Reby D, Lek S, Dimopoulos I, Joachim J, Lauga J, Aulagnier S (1997) Artificial neural networks as a classification method in the behavioural sciences. Behav Proc 40:35–43

Zimmermann A (1995) Artificial neural networks for analysis and recognition of primate vocal communication. In: Zimmermann E, Newman JO, Jürgens UWE (eds) Current topics in primate vocal communication. Plenum, New York, pp 29–46

Chapter 35
A Quantitative Description of the Vocal Types Emitted in the Indri's Song

Viviana Sorrentino, Marco Gamba, and Cristina Giacoma

Abstract The indri's song is composed of a series of roars uttered simultaneously by several members of a group, followed by a long modulated howl. The latter part consists of overlapping or successive notes emitted by different individuals. Previous qualitative studies have described four different kinds of notes. We provide the first quantitative acoustic investigation of the indri's song repertoire. After visual inspection of fundamental frequency (F_0) modulation and duration in 30 songs and 1995 notes emitted by 30 individuals, we distinguished nine different unit types (roar + 8 modulated units). For these nine putative types, we measured six F_0-related and three temporal parameters, which were then subjected to multivariate statistical analysis. Both discriminant analyses and cross-validation procedures classified the vocal types correctly with high reliability.

Resume Le chant de l'Indri est composé de séries de rugissements émis simultanément par plusieurs membres d'un groupe, suivi d'un long hurlement modulé. Cette dernière partie est composée de notes émises par différent individus qui se suivent ou se chevauchent. Des études précédentes ont décrit quatre types de notes sur des bases qualitatives. Nous présentons la première analyse acoustique quantitative du répertoire vocale des notes du chant de l'Indri. Après un examen visuel de 30 chants et 1995 notes émis par 30 individus, nous décrivons neuf différents types d'unités (rugissement + 8 unités modulées), en examinant la modulation et la durée de la Fréquence Fondamentale (F0). Pour ces 9 hypothétiques types, nous avons mesuré six paramètres liés à la F0 et six paramètres temporels, analysés à l'aide d'une méthode multi-variée, afin de valider notre hypothèse. L'analyse discriminante et l'analyse par validation croisée ont toutes deux classifié la plupart des vocalisations dans les catégories attendues.

V. Sorrentino (✉) • M. Gamba • C. Giacoma
Dipartimento di Biologia Animale e dell'Uomo, Università degli Studi di Torino,
Via Accademia Albertina, 13, 10123 Torino, Italy
e-mail: vivianasorrentino@yahoo.it; marco.gamba@unito.it; cristina.giacoma@unito.it

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_35,

Introduction

The indri (*Indri indri*) is a large, black and white lemur with a very short tail. Indris are arboreal and diurnal and live in groups of 2–6 individuals (Petter and Charles-Dominique 1979). Groups occupy nonoverlapping areas in the forest (Pollock 1979) and intergroup spacing is maintained by wailing cries that can be heard throughout the species' range from the Anosibe an'Ala Classified Forest in the south to the Anjanaharibe-Sud Special Reserve in the north (Pollock 1986; Mittermeier et al. 2010). The species is severely threatened by deforestation, logging, and slash-and-burn agriculture (Mittermeier et al. 2010).

The indri song is a vocal display in which one or more individuals emit a sequence of notes separated by short pauses (Pollock 1986). Songs last 40–250 s and are usually introduced by three or four "roars" uttered simultaneously by several members of a group (Maretti et al. 2010), and then, one at a time, or sometimes in pairs, group members produce a long "modulated howl" (Petter and Charles-Dominique 1979) or "song proper" (Pollock 1986). Previous investigations agree that the main functions of indri songs not only involve territorial announcement and defense (Petter et al. 1977; Petter and Charles-Dominique 1979; Pollock 1986; Geissmann and Mutschler 2006) but may also convey information about group composition (Giacoma et al. 2010).

The units, or notes, uttered during the "song proper" are variable (Gamba et al. 2011), but some authors have recognized a general pattern of three call types:

(1) *Type 1 calls* (Pollock 1986) or *long note sequences* (Thalmann et al. 1993) are twice as long as other calls (maximum duration 5.2 s), have a fundamental frequency (hereafter, F_0) of 750 Hz and little modulation. These units are given only by the adult male at the beginning of the song, just after the roars (Pollock 1986).

(2) *Type 2 calls* (Pollock 1986) are uttered by all singing individuals. They have duration of 1.2–2.0 s, are amplitude modulated, and always show an increase in the F_0 from the beginning to the end. The units may precede mirror units showing a constant decrease in F_0 and ending at the initial frequency of the preceding series (Pollock 1986).

(3) *Type 3 calls* (Pollock 1986) or *descending phrase sequences* (Thalmann et al. 1993) are emitted by all individuals and consist of a series of three or four successive units characterized by slight frequency modulation (Pollock 1986). These sequences, also called "phrases," usually begin with a very high frequency note, followed by one to four units of progressively lower starting frequencies (Thalmann et al. 1993). They have the same duration as *type 2 calls*, which they often follow in the song.

Our study aimed to provide a robust classification of indri calls based on quantitative acoustic descriptions.

Material and Methods

Definition of Terms

Previous studies have used different terminology to describe elements of the indri song [*modulated song* (*roar* + *song proper*): Pollock 1986; *plaintive call*, *howling call*, *plaintive howl* (*loud barks* + *modulated howl*): Petter et al. 1977; Petter and Charles-Dominique 1979; song (*waa notes* + *song proper*): Thalmann et al. 1993; *song*: Geissmann and Mutschler 2006]. We use "song" to refer to the complex of roar and song proper, and the elements constituting the song proper as "notes" or "units" (i.e., the *calls* or *howls* of Pollock 1986; the *howls* of Petter et al. 1977 and Petter and Charles-Dominique 1979; and the *notes* of Thalmann et al. 1993).

Subjects

We investigated the songs of indris inhabiting the forests around Andasibe, Madagascar. Seven groups of indris were recorded at the Analamazaotra Special Reserve of the National Park Andasibe-Mantadia and three at Station Forestière Mitsinjo in autumn in 2004 and 2005. The average number of calling individuals per group was 3 ± 0.82 (mean ± SD; range 2–5) at the Analamazaotra Reserve and 3 ± 1 (range 2–4) at the Station Forestière Mitsinjo. The 30 indris contributing to the study included both youngsters (4 individuals, 1.5–3 years old) and adults (26 individuals, over 3 years), 11 females, and 19 males. They were individually identified by pelage patch patterns.

Recording and Acoustic Analyses

Songs consisted of 19–181 notes. In total, 1995 notes emitted by 30 individuals were recorded during the daytime. Songs were spontaneously emitted in response to neighboring groups; nothing was done to provoke the utterances or modify the behavior of the animals.

Calls were recorded using Marantz PMD670 solid-state recorders on compact flash memory cards. Recorders were equipped with Sennheiser ME60 and ME66 shotgun microphones. Sounds were digitized at a sampling rate of 44.1 kHz and amplitude resolution of 16 bits.

Three song recordings per group were analyzed and segmented, separating the contribution of each individual using the autocorrelation pitch contour method in Praat (Boersma and Weenink 2006) and Akustyk (Plichta 2004). We processed each of the songs as follows (1) the F_0 contour of each note emitted by the focal animal was extracted ("to pitch cc": time step 0.01; silence threshold 0.10; minimum F_0

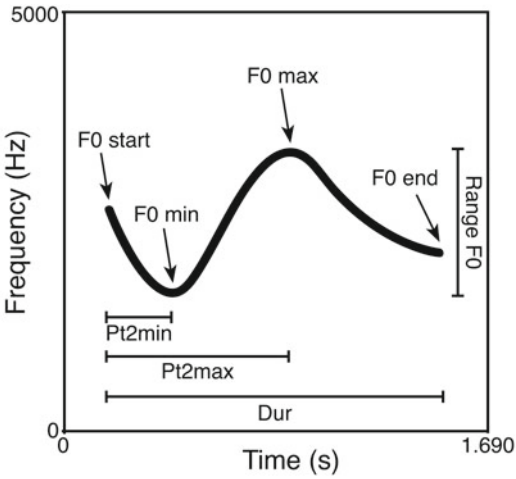


Fig. 35.1 Parameters extracted from the fundamental frequency contour of each note: total duration (Dur), percentage of time to the minimum F_0 (Pt2min), percentage of time to the maximum F_0 (Pt2max), starting frequency (F_0 start), ending frequency (F_0 end), minimum (F_0 min), maximum (F_0 max), and range (Range F_0) of the Fundamental frequency. Average F_0 (F_0 mean) was calculated across all analysis frames using Praat

150 Hz; maximum F_0 2,000 Hz); (2) nonfocal candidates were excluded from the contour manually; and (3) the data were saved to a separate file. These steps were repeated for all animals participating in the call. Using the F_0 contour, (4) we synthesized a new sound featuring one emitter's notes and then (5) segmented this utterance into files containing single notes. For each note, we extracted from the F_0 contour the following parameters: duration, percentage of time to maximum F_0 (Pt2max), percentage of time to minimum F_0 (Pt2min), F_0 start, F_0 end, maximum F_0, minimum F_0, range F_0, and F_0 mean (Fig. 35.1). The data output file was assembled in PRAAT and exported to an Excel spreadsheet (Gamba and Giacoma 2005).

Statistical Analyses

Following a preliminary visual classification of the notes according to overall modulation and relative position in the individual song's temporal structure, we used discriminant function analysis (DFA) to determine which variables contributed to the discrimination of the nine putative unit types.

Because individuals contributed disproportionately to our sampling of vocal types, we averaged the values of individuals per vocal type. We performed one DFA over the complete set and a series of additional DFAs over 25 permutated subsets to minimize the effect of pooled paired and independent data. In these additional DFAs, we randomly created a subset containing 70% of the cases and performed an external classification on the remaining 30% (Gamba and Giacoma 2007). Average classification and leave-one-out rates were calculated. In the leave-one-out cross-validation procedure, each case is classified by the functions derived from all cases except that one.

Results

Identification of Vocal Types

Elements comprising the indri's song were inspected visually using spectrograms. Sound spectrograms were made for all the songs, the resynthesized individual contributions, and the single notes. By considering the order in which calls were emitted in the choruses and a rough categorization of their frequency and time domain, it was possible to identify nine different call types. A spectrographic key to this harmonic vocalization is given in Fig. 35.2.

Statistical Classification of the Note Types Using DFA

Measures of the acoustic features (Table 35.1) were used to verify the extent to which the note types identified previously correspond to significantly different acoustic categories. DFA classified 79.9% of cases correctly using the whole set ($N = 169$, Wilks' lambda = 0.017, $F_{32,580} = 36.588$, $P < 0.001$).

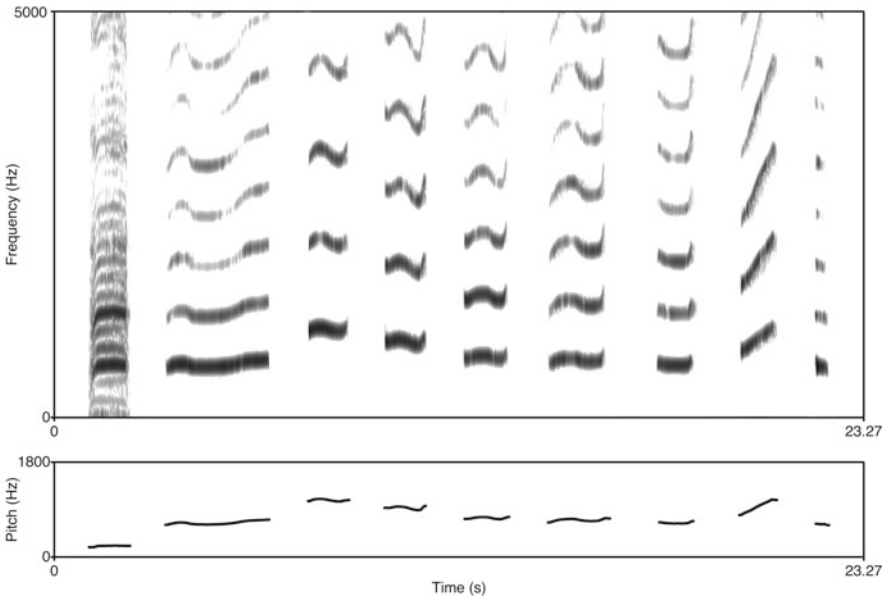


Fig. 35.2 Spectrogram of the nine unit types described here (from type 0 on the *right* to type 8 on the *left*). The spectrogram was generated in Praat with the following parameters: window length: 0.02 s, time range 0.0–23.27 s; frequency range: 0–5,000 Hz; maximum: 62 dB/Hz; dynamic range: 60 dB; preemphasis: 0.0 dB/Oct; dynamic compression: 0.0

Table 35.1 Mean and standard deviation of acoustic parameters per unit type

Unit type	*N*	Dur (s)	Pt2min (%)	Pt2max (%)	F_0 mean (Hz)	F_0 max (Hz)	F_0 min (Hz)	Range F_0 (Hz)	F_0 start (Hz)	F_0 end (Hz)
0	27	0.971 ± 0.342	31 ± 17	68 ± 16	677 ± 32	712 ± 36	639 ± 34	73 ± 34	655 ± 36	690 ± 35
1	30	2.354 ± 0.798	47 ± 15	55 ± 29	749 ± 46	838 ± 47	697 ± 54	141 ± 33	780 ± 60	793 ± 60
2	30	1.237 ± 0.210	43 ± 23	56 ± 26	1,056 ± 76	1,127 ± 73	996 ± 81	131 ± 46	1,041 ± 102	1,088 ± 65
3	30	1.298 ± 0.234	66 ± 7	29 ± 13	918 ± 57	981 ± 63	870 ± 60	111 ± 37	958 ± 69	921 ± 54
4	29	1.394 ± 0.232	59 ± 9	41 ± 19	773 ± 46	832 ± 54	734 ± 44	98 ± 27	795 ± 65	786 ± 41
5	21	1.361 ± 0.253	45 ± 26	58 ± 21	719 ± 40	777 ± 55	678 ± 51	99 ± 49	720 ± 59	734 ± 70
6	2	0.999 ± 0.000	61 ± 22	38 ± 45	694 ± 40	748 ± 47	668 ± 38	79 ± 10	733 ± 28	707 ± 79
7	11	1.149 ± 0.142	18 ± 13	85 ± 13	824 ± 48	936 ± 72	756 ± 34	181 ± 55	766 ± 28	929 ± 78
8	3	1.316 ± 0,224	95 ± 1	34+20	668 ± 68	703 ± 62	626 ± 86	77 ± 62	692 ± 65	627 ± 86

Columns report: number of individuals considered (*N*), duration in seconds (Dur), percentage of duration before minimum F_0 (Pt2min), percentage of duration before maximum F_0 (Pt2max), average fundamental frequency (F_0 mean), maximum fundamental frequency (F_0 max), minimum fundamental frequency (F_0 min), fundamental frequency range (Range F_0), starting Fundamental frequency (F_0 start), and final Fundamental frequency (F_0 end)

The set of variables that proved useful in predicting vocal type were identified on *F*-level loadings and were F_0 end, F_0 mean (which showed maximum correlation with the first DF, 0.903 and 0.895, respectively), Dur (which showed maximum correlation with the second DF, 0.818), and Pt2min (maximum correlation with the third DF, 0.992). Standardized Canonical Discriminant coefficients for the three functions showing statistical differences among vocal types were: DF1, F_0 end = 0.792, Dur = 0.340, F_0 mean = 0.312, Pt2min = 0.080; DF2, F_0 end = 1.257, Dur = 0.920, F_0 mean = −1.291, Pt2min = 0.469; and DF3, F_0 end = 0.055, Dur = −0.123, F_0 mean = −0.076, Pt2min = 1.044.

The classification matrix showed that cases (average individual mean for sounds ascribed *a priori* to one vocal type) were assigned to their appropriate group (vocal type) with percentages ranging between 62.1 and 100% for 7 out of 9 vocal types. Unit types 5 and 6 scored correct classifications of 57.1% and 50% respectively, still above the rate for correct classification due to chance.

An average of 80.5 ± 2.5% of the unit types comprising the songs were correctly classified in the permutated subsets ($P \leq 0.001$); for the permutated subsets, 75.7 ± 5.6% of cross-validated cases were correctly classified, and the external classification rate was 75.0 ± 2.1% correct.

Discussion

Previous studies identified four different classes of notes comprising the song of the indri, which was described as a sequence of roars, *long notes*, *type 2 notes*, and *descending phrases* (Pollock 1986; Thalmann et al. 1993). However, the level of analysis revealed several uncertainties in identifying the units, especially for the descending phrases. We identified nine different unit types (roar + eight modulated units), by visual inspection of the complete spectrograms of 30 indri songs, which we assumed had different acoustic structures. To test this assumption, we subjected temporal and frequency measurements taken from the nine putative unit types to multivariate statistical analyses. Both discriminant analyses and cross-validation procedures classified all nine vocal types with a high percentage of accuracy. The predictors chosen from the stepwise discriminant analysis showed that fundamental frequency values (F_0 end and F_0 mean), temporal (Dur) and modulation (Pt2min) parameters all contributed to assigning notes to unit types.

Unit Type 0 is the previously described roar that occurs at the beginning of the chorus (Pollock 1986; *waa notes* in Thalmann et al. 1993). Unit Type 1 (described as Type 1 by Pollock 1986, or *long notes* by Thalmann et al. 1993) always occurred at the beginning of the song, as in the work of other authors. Unit Types 2–6 are sounds occurring during the *descending phrase* (Thalmann et al. 1993; Type 3 in Pollock 1986). Unit Type 7 is preferable to Type 2 described by Pollock (1986) and it is emitted only by females. Unit Type 8, a short utterance given only by males shortly before the roar, is described for the first time.

Conclusions

Our results demonstrate that indri's song is made up of at least nine note types that can be distinguished on the basis of fundamental frequency variation, modulation, and duration, i.e., a harsh sounding roar and eight discrete variants of frequency-modulated song notes. This method of unit analysis and classification has proved be a valuable tool for understanding complex vocalizations and can serve as the basis for future comparative studies focusing on within- (e.g., age and sex differences) and between-group variability (e.g., geographic variation in relation to genetic and morphological correlates) in complex call structures.

Aknowledgments Our research was supported by the Università degli Studi di Torino and by grants from the Parco Natura Viva—Centro Tutela Specie Minacciate. We thank Association Nationale pour la Gestion des Aires Protégées Madagascar, Association Mitsinjo, Dr Cesare Avesani Zavorra, Dr Caterina Spiezio, Fanomezantsoa Andrianirina, and Lanto Rakotoarisoa for their help and support.

References

Boersma P, Weenink D (2006) Praat: doing phonetics by computer. http://www.praat.org

Gamba M, Giacoma C (2005) Key issues in the study of primate acoustic signals. J Anthropol Sci 83:61–87

Gamba M, Giacoma C (2007) Quantitative acoustic analysis of the vocal repertoire of the crowned lemur. Ethol Ecol Evol 19:323–343

Gamba M, Favaro L, Torti V, Sorrentino V, Giacoma C (2011) Vocal tract flexibility and variation in the vocal output in wild indris. Bioacoustics 20:251–266

Geissmann T, Mutschler T (2006) Diurnal distribution of loud calls in sympatric wild indri (*Indri indri*) and ruffed lemurs (*Varecia variegata*): implications for call functions. Primates 47:393–396

Giacoma C, Sorrentino V, Rabarivola C, Gamba M (2010) Sex differences in the song of *Indri indri*. Int J Primatol 31:539–551

Maretti G, Sorrentino V, Finomana A, Gamba M, Giacoma C (2010) Not just a pretty song: an overview of the vocal repertoire of *Indri indri*. J Anthropol Sci 88:151–165

Mittermeier RA, Louis EE Jr, Richardson M, Schwitzer C, Langrand O, Rylands AB, Hawkins F, Rajaobelina S, Ratsimbazafy J, Rasoloalison R, Roos C, Kappeller PM, Mackinnon J (2010) Lemurs of Madagascar, 3rd edn. Conservation International, Washington, DC

Petter J-J, Charles-Dominique P (1979) Vocal communication in prosimians. In: Doyle GA, Martin RD (eds) The study of prosimian behavior. Academic, New York, pp 272–282

Petter J-J, Albignac R, Rumpler Y (1977) Faune de Madagascar. Mammifères: Lémuriens, vol 44, pp 391–410

Plichta B (2004) Akustyk. http://www.msu.edu/plichtab

Pollock JI (1979) Spatial distribution and ranging behaviour in lemurs. In: Doyle GA, Martin RD (eds) The study of prosimian behavior. Academic, New York, pp 359–409

Pollock JI (1986) The song of indris (*Indri indri*; Primates, Lemuroidea): natural history, form and function. Int J Primatol 7:225–267

Thalmann U, Geissmann T, Simona A, Mutschler T (1993) The indris of Anjanaharibe-Sud, north-eastern Madagascar. Int J Primatol 14:357–381

Chapter 36
What Can Virtual Vocal Tracts Tell Us About Lemur Communication?

Marco Gamba, Jules Medard, Haingoson Andriamialison, Gilbert Rakotoarisoa, and Cristina Giacoma

Abstract Recent research emphasizes the importance of species-specific acoustic signals in primate vocal communication. We examine the potential of nasal tract resonance in generating these signals using anatomically based vocal tract computational modeling in lemurs. True lemurs (*Eulemur*) show a remarkable species diversity, and nasal vocalizations play a crucial role in their communication systems. The supralaryngeal cavities (glottal constriction, nasopharyngeal cavity, nasal chambers, and nostrils) of *E. coronatus*, *E. rufus*, *E. rubriventer*, *E. macaco*, and *E. fulvus* were approximated as fixed-length concatenated tubes, variable in number according to nasal tract length and varying in size according to anatomical measurements. Formants extracted from the acoustic response of the computational models showed that differences in morphological features between lemur taxa determine the structural characters of their vocalizations.

Resume Les recherches récentes sur la communication vocale des primates insistent sur l'importance des signaux acoustiques spécifiques. Nous examinons le potentiel de résonnance des voies nasales pour engendrer des signaux, en utilisant un modèle informatique basé sur l'anatomie de l'appareil vocal. Les vrais lémurs (*Eulemur*) montrent une diversité spécifique remarquable, et les vocalisations nasales jouent un rôle important dans leur système de communication. Les cavités supra-laryngiales (constriction de la glotte, cavité naso-pharyngiale, chambres nasales et narines) de *E. coronatus*, *E. rufus*, *E. rubriventer*, *E. macaco* et *E. fulvus* sont assimilés à

M. Gamba (✉) • C. Giacoma
Dipartimento di Biologia Animale e dell'Uomo, Università degli Studi di Torino,
Via Accademia Albertina, 13, 10124 Torino, Italy
e-mail: marco.gamba@unito.it; cristina.giacoma@unito.it

J. Medard • H. Andriamialison • G. Rakotoarisoa
Parc Botanique et Zoologique Tsimbazaza, Rue Fernand Kasanga,
Tsimbazaza, Antananarivo 101, Madagascar
e-mail: ahaingoson@yahoo.fr; gilbertrakotoarisoa@yahoo.com

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_36,

des tubes identiques connectés les uns aux autres, dont la taille et le nombre sont déterminés, pour chaque espèce, par les mesures anatomiques. Les formants extraits des réponses acoustiques des modèles montrent que les différences morphologiques de ces lémuriens déterminent la structure de leurs vocalisations.

Introduction

In humans and other primates (Fitch 1997; Riede et al. 2005) including lemurs (Gamba and Giacoma 2005), the anatomy and morphology of the vocal apparatus determine the acoustic characteristics of vocal emissions. A basic approach to the source–filter theory (Fant 1960) splits the production of vocal signals into two independent processes. The first, usually termed "voice source," takes place at a glottal level. Vocal fold vibration produces a complex periodic wave, and the spectrum of the source signal contains energy at the fundamental frequency of laryngeal vibration (F0) and at integer multiples of the fundamental frequency, termed harmonics. Above the larynx the second process, termed "filter," takes place. The vocal tract acts as a resonator, adjusting the relative intensities of the frequencies of the source. The column of air vibrates in a complex manner that is influenced by the length and the shape of the vocal tract. One or several resonant frequencies of the vocal tract correspond to prominent spectral peaks called "formants." The position and variation of the formants have been found to have a significant impact on the way we recognize speech sounds.

For many years, a model of vocal production based on the relationship between the vocal tract area function and the formant output has been the most common framework for understanding speech production in humans. From an acoustic and physiological point of view, human vocal communication is far better known than any other mammal communication system, and techniques from speech science have often been applied to the study of vocal production in other mammals, especially nonhuman primates. Our recent research has focused on the "filter" process (Gamba and Giacoma 2006, 2007; Gamba et al. 2011) and on the application of the vocal tract modeling in lemurs. Lemurs, having evolved into many different species, can allow crucial insights into the evolution of primate vocal communication systems.

In voice science, vocal tract modeling is used to simulate the formant characteristics of the various speech sounds. A vocal tract model is a computational method which generates formants simulating resonance into a tube of known shape and length. In this chapter, we examine the potential of the vocal tract to produce species-specific features in lemur vocal signals using vocal tract models. In nonhuman primates, resonance takes place alternatively in the oral or in the nasal tract (Fitch 1997, 2000). Like the oral tract, the nasal tract has its own resonant frequencies. Since lemurs often produce closed-mouth vocalizations, in which the column of air resonates in the nasal tract, we focused on nasal tract resonance, which has very limited flexibility and no articulation.

We investigated whether nasal tract models based on anatomical measurements of various *Eulemur* species produce different resonance patterns, and how morphological features of the nasal tract affect the vocal output in terms of formant location. We further generalized the results to understand the extent to which resonance cues remain distinct across species, when intra- and interspecific variation in body size (and thus in vocal tract length) is taken in account.

Methods

Subjects

Taxa belonging to the genus *Eulemur* were historically described as five distinct species *(E. coronatus*, *E. rufus*, *E. rubriventer*, *E. macaco*, and *E. fulvus*) and several subspecies. All *E. fulvus* and *E. macaco* subspecies were then elevated to species level (Groves 2001; Mittermeier et al. 2010; Chap. 2). We follow this nomenclature.

Casts of the nasal airways were made to describe the morphology of the nasal tract in five lemur species: *E. coronatus*, *E. rufus*, *E. rubriventer*, *E. macaco*, and *E. fulvus*. All specimens had died of natural causes and their bodies were stored in the Département Faune, Parc Botanique et Zoologique de Tsimbazaza, Antananarivo, Madagascar. For our study, cadavers were partially defrosted and tracheotomized. Casts were obtained by injecting a liquid silicone compound through the tracheal tube until the oral and nasal cavities were completely filled, bypassing the larynx (Gamba and Giacoma 2006). Linear measurements were taken directly from the casts using digital calipers (Mitutoyo, accurate to 0.01 mm), while cross sections of the vocal tracts (which were not circular) were measured in 3.5 mm increments and assembled in Microsoft Excel to calculate cross-section areas.

Modeling

The nasal tract was split into various concatenated tubes (hereafter tubes). The number of tubes varied with the measurements of the nasal tract cast of each specimen. Cross-sectional areas and lengths were used to build the nasal tract area function that provided the input for Matlab-based vocal tract modeling software using a frequency-domain model (Zhang and Espy-Wilson 2004). We applied the transmission-line model (Fant 1970; Stevens 1998), which had already proved successful in predicting vocal tract resonance in lemurs (Gamba and Giacoma 2006). For each model, the first three formants (F1, F2, and F3) from the computed acoustic response were considered.

In order to understand the extent to which shape and size influence the filtering properties of the nasal tract and, consequently, to evaluate the degree of species specificity of formant patterns, changes in vocal tract size were replicated in the model. Assuming that the vocal tract morphology of a single dead animal may represent a species, we modeled tubes in which areas and lengths were respectively increased and decreased by 10%, in accordance with the variability in crown size described in wild lemur populations (Zaonarivelo et al. 2007). We estimated that this accounts for body size variation of ~30%, which embraces the range of adult variation in nature (Harris et al. 2006).

Results

Vocal tract area functions derived from the anatomical measurements were used to generate computational concatenated tube models for the nasal tracts of *E. coronatus*, *E. rufus*, *E. rubriventer*, *E. macaco*, and *E. fulvus*. These tubes are approximations of the vocal tract, from the glottal constriction, through the nasopharyngeal cavity, to the nasal chambers and nostrils. The computational model for the supraglottal vocal systems of the five species comprises a nasal tract consisting of 20–28 concatenated tubes of 3.5 mm, corresponding to a total tract length ranging from 7.0 cm (*E. coronatus*) to 9.8 cm (*E. fulvus*) (Table 36.1). Vocal tract area functions and respective acoustic responses are shown in Fig. 36.1.

First formant estimates, 1,018 ± 63 Hz averaged across species, showed very limited variability. Second formants, 2,360 ± 437 Hz averaged across species, decreased with the increase of vocal tract length and showed remarkable differences between species. Third formants, with an average value of 4,863 ± 1,105 Hz, also showed remarkable differences between species, but did not vary with length of the vocal tract.

Table 36.1 First three formants (F1, F2, and F3) generated from the concatenated tube model of the vocal tract (M = males and F = females)

Species	Sex	Ghl (cm)	Nct	Ntl (cm)	F1 (Hz)	F2 (Hz)	F3 (Hz)
E. coronatus	M	8.41	20	7.0	1,126	2,911	6,526
E. rufus	M	9.28	22	7.7	996	2,646	4,706
E. rubriventer	M	8.56	24	8.4	961	2,371	5,221
E. macaco	F	9.88	26	9.1	1,011	2,036	4,271
E. fulvus	F	9.43	28	9.8	996	1,836	3,591
Mean					1,018	2,360	4,863
SD					63	437	1,105
CV					0.06	0.19	0.23

Greatest head length (Ghl), measured as the distance from the tip of the nose to the posterior margin of the head, is shown for all subjects. Number of fixed-length concatenated tubes (Nct), variable in cross-sectional area, changes in relation to nasal tract length (Ntl) across species. Formant frequencies averaged across species (mean) are also shown, as are standard deviation (SD) and coefficient of variation (CV)

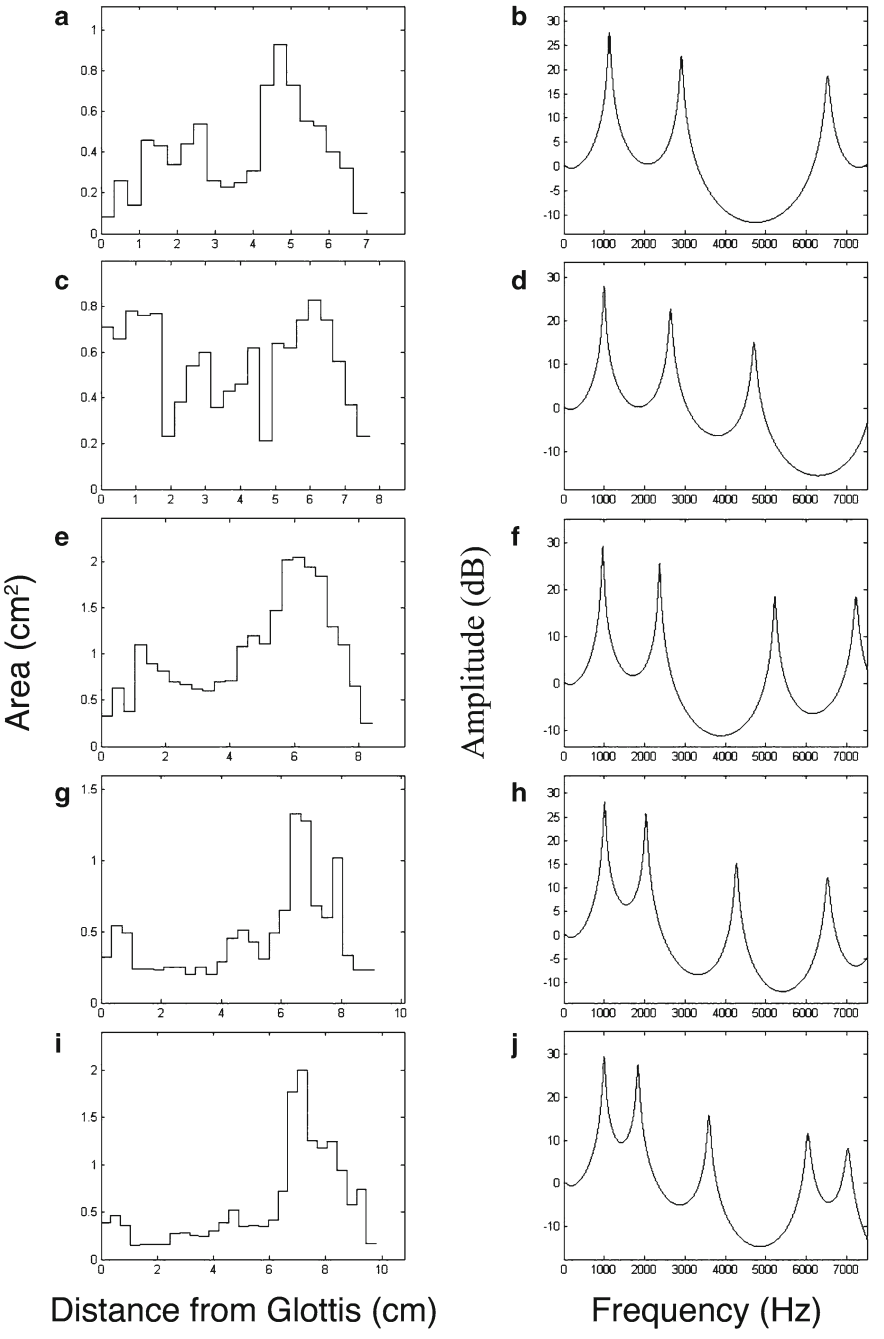


Fig. 36.1 The nasal tract area functions and their acoustic response calculated for the five study species. From the top: *E. coronatus*, *E. rufus*, *E. rubriventer*, *E. macaco*, and *E. fulvus*. Calculation options: frequency scale 0–7,500 Hz; frequency step 5 Hz; maximum length of tube subsection 0.35 cm

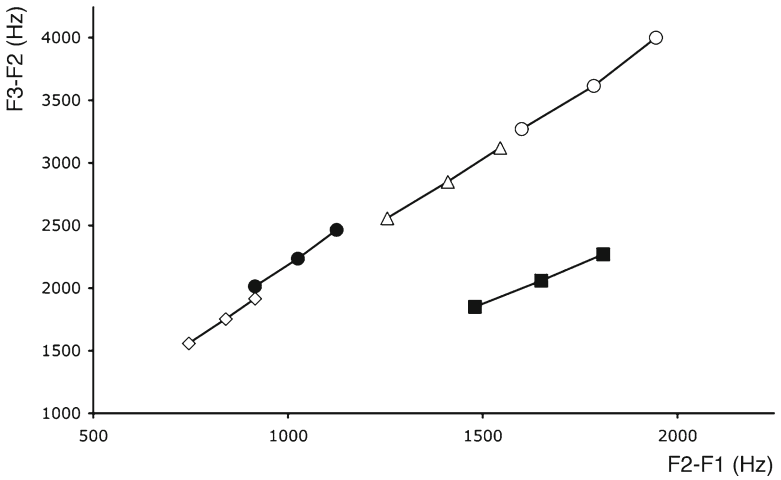


Fig. 36.2 Plot of F2–F1 distance on the *x*-axis and F3–F2 distance on the *y*-axis for *E. coronatus*, *E. rufus*, *E. rubriventer*, *E. macaco*, and *E. fulvus*. Formants generated from the tube models of the nasal tract showed minimal overlap between species, even when a 10% increase and decrease of the vocal tract length and cross-sectional areas were computed according to natural body size variation [*E. coronatus* (*open circle*), *E. rufus* (*filled square*), *E. rubriventer* (*open triangle*), *E. macaco* (*filled circle*), and *E. fulvus* (*open diamond*); *left* to *right* (+10%)-(measured)-(−10%)]

Concatenated tube models in which segments were increased or decreased by 10% in length and area (Fig. 36.2) exhibited the following peaks in the transfer function: *E. coronatus*: 1,026–1,226 Hz (F1), 2,626–3,171 Hz (F2), and 5,896–7,171 Hz (F3); *E. rufus*: 906–1,081 Hz (F1), 2,386–2,891 Hz (F2), and 4,236–5,161 Hz (F3); *E. rubriventer*: 881–1,046 Hz (F1), 2,136–2,591 Hz (F2), and 4,696–5,711 Hz (F3); *E. flavifrons*: 916–1,086 Hz (F1), 1,831–2,211 Hz (F2), and 3,846–4,676 Hz (F3); and *E. fulvus*: 911–1,091 Hz (F1), 1,656–2,006 Hz (F2), and 3,216–3,921 Hz (F3).

Discussion

We investigated the relevance of vocal tract morphology for determining differences in formant values and formant dispersion in the vocalizations of Malagasy lemurs using vocal tract modeling. Our particular focus was the study of resonances in the nasal airways. Working from one specimen per species and then estimating natural vocal tract length variation, we found that the differences in the formant output account for species-specific formant patterns in *E. coronatus*, *E. rufus*, *E. rubriventer*, *E. macaco*, and *E. fulvus*.

Modeling of nasal tract resonance in the genus *Eulemur* confirmed that morphology and tract length influence the pattern of formants. In our models, F1 showed small changes across all study species, probably because F1 is not correlated with vocal tract length but results from the passage of air through the constrictions in the nasal passage. The second formant predicted by the models showed remarkable differences between species and scaled inversely with vocal tract length. F2 emerged as a good parameter for future investigations of the relationship between vocal tract length and formant variation in nasal sounds. Variation in F3 did not show an obvious relationship with variation in tube length, which could indicate that the third formant is more strongly related to the shape and the volume of the nasal cavities, but this proposition needs to be examined in a larger sample of individuals.

To generalize our model calculations, we computed the resonance of vocal tracts in which lengths and cross-sectional areas of the tube sections were increased and decreased according to morphometric variation observed in other lemur species. We found that distances between formants effectively separated patterns according to species, even considering intraspecific size variation. Unfortunately, precise resolution of this variation was prevented by a lack of data documenting any disproportionate anatomical differences between males and females, or subadults and adults within a strepsirhine species (Ey et al. 2007).

Conclusion

Differences in nasal tract morphology among *E. coronatus*, *E. rufus*, *E. rubriventer*, *E. macaco*, and *E. fulvus* effectively determine distinctive formant patterns in their vocalizations and provide the potential for species-specific recognition. In fact, the resonance properties of the supralaryngeal tracts of lemurs determine formants, which are useful for investigating differences between species (Gamba and Giacoma 2005, 2008, 2010), vocalization types (Gamba and Giacoma 2005, 2006), and individuals (Gamba et al. 2011).

Vocal tract models showed that formant location in lemurs is influenced by vocal tract length, and thus influenced by body size, at least within species. However, discrepancies in vocal tract length do not explain differences between species completely. Areas of the laryngeal ventricle, vestibule, nasal tube, and nostrils also determine species-specific formant patterns. It is therefore likely that formants play an important role in conveying information to conspecifics for social organization and reproduction and to heterospecific individuals for reciprocal recognition during encounters in the forest.

Acknowledgments Our research was supported by the Università degli Studi di Torino and by grants from the Parco Natura Viva—Centro Tutela Specie Minacciate. We thank Drs Cesare Avesani Zavorra, Caterina Spiezio, and Zhaoyan Zhang for their help and support.

References

Ey E, Pfefferle D, Fischer J (2007) Do age- and sex-related variations reliably reflect body size in non-human primate vocalizations? A review. Primates 48:253–267

Fant G (1960) Acoustic theory of speech production. Mouton, The Hague

Fitch WT (1997) Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques. J Acoust Soc Am 102:1213–1222

Fitch WT (2000) The phonetic potential of nonhuman vocal tracts: comparative cineradiographic observations of vocalizing animals. Phonetica 57:205–218

Gamba M, Giacoma C (2005) Key issues in the study of primate acoustic signals. J Anthropol Sci 83:61–88

Gamba M, Giacoma C (2006) Vocal tract modeling in a prosimian primate: the black and white ruffed lemur. Acta Acust United Ac 92:749–755

Gamba M, Giacoma C (2007) Quantitative acoustic analysis of the vocal repertoire of the crowned lemur. Ethol Ecol Evol 19:323–343

Gamba M, Giacoma C (2008) Subspecific divergence in the black lemur's low-pitched vocalizations. Open Acoust J 1:49–53

Gamba M, Giacoma C (2010) Key issues in the study of primate acoustic signals, an update. J Anthropol Sci 85:215–220

Gamba M, Colombo C, Giacoma C (2011) Acoustic cues to caller identity in lemurs: a case study. J Ethol 30:191–196

Groves C (2001) Primate taxonomy. Smithsonian Institution Press, Washington, DC

Harris TR, Fitch WT, Goldstein LM, Fashing PJ (2006) Black and white colobus monkey (*Colobus guereza*) roars as a source of both honest and exaggerated information about body mass. Ethology 112:911–920

Mittermeier RA, Louis EE, Richardson M, Schwitzer C, Langrand O, Rylands AB, Hawkins F, Rajaobelina S, Ratsimbazafy J, Rasoloarison R, Roos C, Kappeler PM, Mackinson J (2010) Lemurs of Madagascar. Conservation International, Washington, DC

Riede T, Bronson E, Hatzikirou H, Zuberbuhler K (2005) Vocal production mechanisms in a non-human primate: morphological data and a model. J Hum Evol 48:85–96

Stevens KN (1998) Acoustic phonetics. MIT Press, Cambridge, MA

Zaonarivelo JR, Andriantompohavana R, Engberg SE, Kelley SG, Randriamanana JC, Louis EE, Brenneman RA (2007) Morphometric data for indri (Indri indri) collected from ten forest fragments in eastern Madagascar. Lemur News 12:19–23

Zhang ZY, Espy-Wilson CY (2004) A vocal-tract model of American English /I/. J Acoust Soc Am 115:1274–1280

Chapter 37
Cognitive Capacities of Captive Gray Mouse Lemurs as Evidenced by Object Manipulation

Alain Schilling

Abstract Observations using infrared photography have shown that captive *Microcebus murinus* are capable of manipulating various objects when appropriately motivated. I tested the capacity of ten adult males to reach a learning criterion to obtain a mealworm placed in a box that opened several ways, followed by a series of related but more complex tasks. Despite individual differences, the animals managed to solve all problems more and more rapidly; in particular, those requiring successive, simultaneous manipulations or changes of behavioral strategy. Additional tests indicated that learning could be achieved in very young subjects (4.5 months) and was retained long term (one year). In addition, video recordings demonstrate that learning criteria can be acquired progressively (notably by social imitation) or spontaneously (resulting from an "insight"). The facility with which mouse lemurs learn object manipulation indicates sophisticated cognitive abilities which probably contributed to their evolutionary success in Madagascar.

Resume Des observations par caméra infra-rouge ont montré qu'en captivité, *Microcebus murinus* pouvait manipuler différents objets à condition d'être suffisamment motivé. J'ai donc testé chez 10 mâles adultes leur capacité à satisfaire un critère d'apprentissage exigeant pour obtenir un ver de farine placé dans une boîte s'ouvrant de plusieurs façons; puis dans des présentoirs imposant des problèmes cognitifs plus complexes. Malgré des différences individuelles, les animaux ont appris à résoudre de plus en plus rapidement tous les problèmes posés; en particulier, les problèmes incluant des manipulations successives, simultanées ou des changements de stratégie comportementale. Des tests complémentaires prouvent que ces apprentissages peuvent s'acquérir chez de très jeunes sujets (4.5 mois) et être mémorisés à long terme (1 an). Par ailleurs, l'étude des enregistrements vidéos montre que ces apprentissages pouvaient s'acquérir de manière progressive

A. Schilling (✉)
Département d'Ecologie et Gestion de la Biodiversité, UMR CNRS/MNHN 7179, 4 avenue du Petit Chateau, 91800 Brunoy, France
e-mail: schillingal@gmail.com

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_37,

(notamment par imitation sociale) ou spontanée (à partir d'un hasard ou d'un «insight »). La facilité avec laquelle les microcèbes apprennent à manipuler témoigne de dispositions cognitives particulières ayant probablement joué un rôle dans leur succès évolutif à Madagascar.

Introduction

Against expectation, prosimians have been shown to perform as well as simian species in some cognitive areas (Ohta et al. 1984; Rumbaugh and Pate 1984). Recent studies have demonstrated that gray mouse lemurs (*Microcebus murinus*) can master reversal learning and delayed response tasks and have an excellent spatial memory (Picq 2000; Joly and Zimmermann 2007). Moreover, lemurs seem to share certain numerical abilities with other primates (Santos et al. 2005a). I became interested in the cognitive abilities of gray mouse lemurs when I observed them devising detours and manipulating objects when sufficiently motivated. Videotaped observations show mouse lemurs using their hands to catch mealworms suspended by a thread and retrieving them from the bottom of a glass bottle when the aperture is too narrow to accommodate the animal's mouth. The animals learned to pull a thread tied to a mealworm to extract the insect from a wire mesh cage or a box and to open several kinds of baited boxes using the nose or the hands, either by lifting the lids or by opening a drawer. These observations indicate that, despite anatomical limitations to their manipulative abilities (Torigoe 1985), prosimians can solve more complex manipulative problems than expected.

Object manipulation has been proposed as a precursor for tool use (Parker 1974), which requires behavioral flexibility, conceptual innovation, and sensorimotor coordination (Vauclair 1996) and has been reported under captive and wild conditions in apes, some Old World monkeys, a few New World monkeys (Santos et al. 2006; Cunningham et al. 2006) and in two lemur species (Santos et al. 2005b). In this light, I tested the ability of gray mouse lemurs, using a standardized procedure, to learn how to open a box in three different ways and then to perform a series of related, but more complex, tasks.

General Methods

All ten *M. murinus* subjects used in this study were captive-born males, 3.5–5 years old, and kept under controlled conditions (Perret 1992). The activity of this species is strongly influenced by photoperiod (Schilling et al. 2001), so all experiments were conducted during the animals' most active periods, i.e., during the dark phase ("night") of the long photoperiod (corresponding to the summer reproductive season). For the duration of the experiment, mouse lemurs were fed their normal diet, with mealworms serving only as rewards for successful trials. Animals were tested

individually, as learning can be impeded in some social contexts (Anderson et al. 1992). They were placed in a 1-m^3 cage in an isolated room, where I videotaped trials under dim red light, and recorded details of the manipulative behaviors and the duration of the trials from first contact with the manipulated object to the seizure of the worm. I conducted tests either daily or every second day, and animals were given no more than 60 trials for each task. During the training phase, each session was limited to 10 min; if the goal (obtaining a mealworm) was not attained within 2 min, I stopped the session and recorded it as 2 min. I considered learning to have begun (i.e., the testing phase) when trials lasted less than 120 s, and I defined the learning criterion as having been achieved when an animal performed the task three times in succession in a mean time of 12 s (i.e., 10% of the allowed testing time). All values presented are means ± S.E.

Results

Three Ways of Opening a Box: Testing the Ability to Solve a Task with Different Manipulative Solutions

After several unsuccessful attempts at opening the box, subjects selected and refined one of the three possible opening methods (Fig. 37.1a). Subjects improved their scores and reached the learning criterion more (970C) or less (983A) easily. Once the learning criterion had been attained, the preferred style of opening the box (e.g., raising the lid for seven subjects) was blocked, forcing the animal to seek a second method (e.g., pulling the drawer for six subjects). Once the second learning criterion had been attained, the second method was blocked, and the animal was thereby driven to find the third method.

All subjects mastered the three methods of opening the box (Fig. 37.1a). The mean number of trials was 50.8 ± 12.8, with notable variation among individuals (31–75 trials), corresponding to a mean total time of 29.6 ± 12.6 min (10.6–52.5 min) (Fig 37.1b). Raising the lid (11.3 ± 3.3 mean trials) and pulling the drawer (11.1 ± 4.2 mean trials) were learned much faster than pushing the drawer (27.8 ± 11.2 mean trials) (Fig 37.1c).

Complex Manipulations

The double cylinder: test involving two manipulative steps plus simultaneous actions. The subjects had to pull a cord to gain access to an inner container holding a mealworm attached by a thread, which they also had to pull (Fig. 37.2a). All subjects attained the learning criterion (Fig. 37.2b). As expected, they learned to pull the cord easily but experienced some difficulty learning how to tighten the cord to

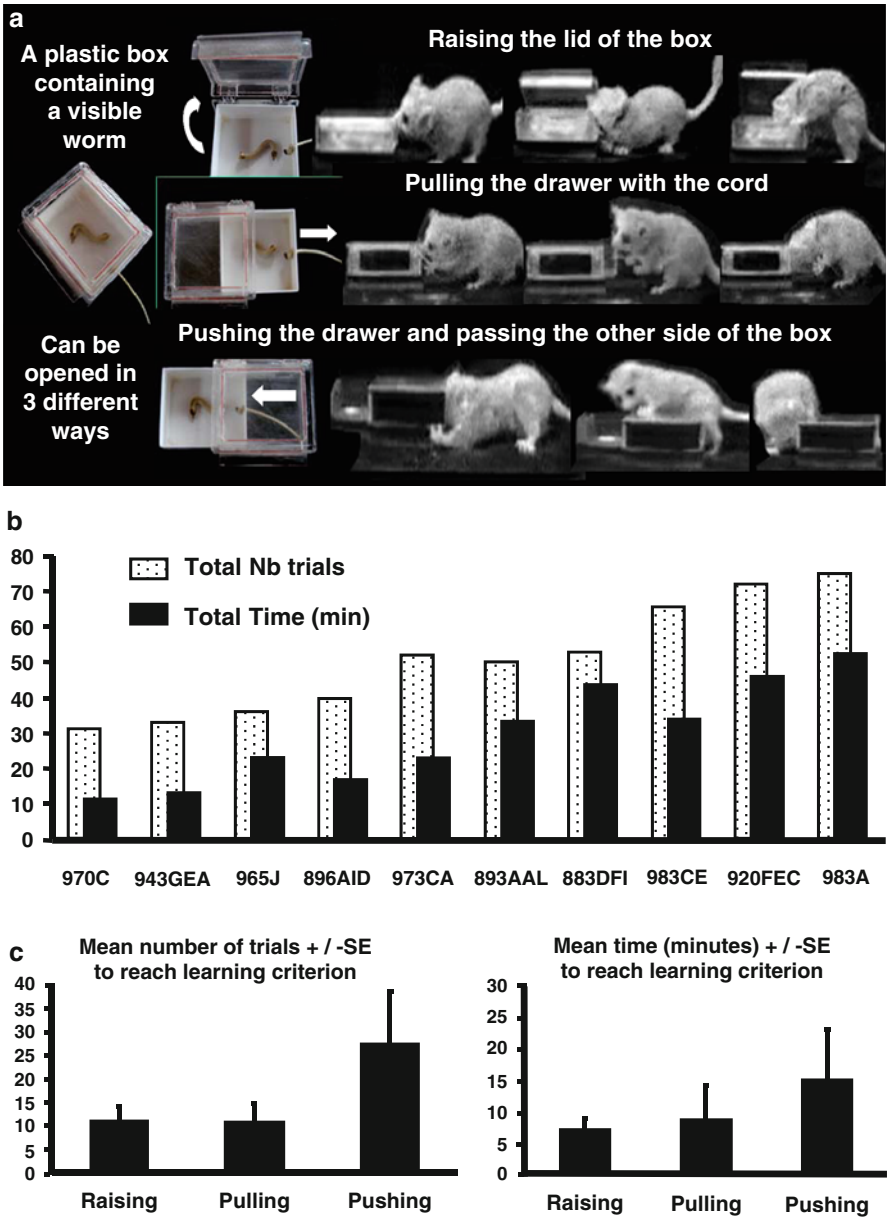


Fig. 37.1 (**a**) Three ways of opening a box. (**b**) Total number of trials and cumulative time to reach the three learning criteria for each subject. (**c**) Mean number of trials ± SE and mean time ± SE to reach the learning criteria for the three ways of opening the box

prevent the inner cylinder from moving backwards, while they seized the thread (usually with their teeth) attached to the mealworm. Comparing these trial durations with those of the previous test situation, the subjects learned this complex task faster

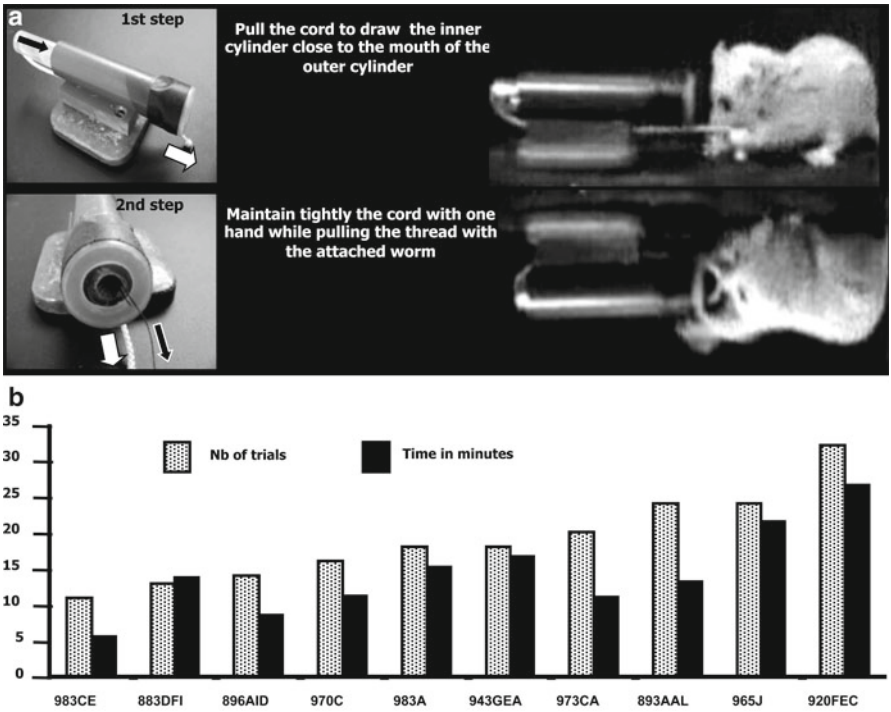


Fig. 37.2 (**a**) Double cylinder. (**b**) Number of trials and time to reach the learning criterion for each tested subject

than they learned to open the box by pushing the drawer [mean number of trials = 19 ± 6 (11–32); mean time = 14.4 ± 5.8 min (5.6–26.7 min)].

Using a mirror: testing the capacity to use the image of an object as a cue. The test situation is shown in Fig. 37.3a. In order to avoid bias due to spatial habituation, the worm was suspended at a different height for each trial. Of the eight animals tested, all were highly motivated in this task. All began by seeking the reward at the back of the device, but almost all learned to extend one or two hands into the device and to seize the mealworm behind the panel without seeing it directly. Six subjects reached the learning criterion easily, while one (896AID) attained it with difficulty, and one gave up after 30 trials (Fig. 37.3b). The mean number of trials to reach the learning criterion was 16.7 ± 3.1, corresponding to a mean time of 17.3 ± 6.2 min.

Alternate manipulation of a simple box: testing the capacity to adjust a learned response to new circumstances. To obtain a mealworm, subjects had to open a round box, the lid of which could turn only in one direction (Fig. 37.4a). All subjects tested ($N=8$) chose the same manipulative behavior, i.e., bringing the lid back toward themselves using their forepaws. They learned this task faster than the other manipulations, attaining the learning criterion within a mean of 10.2 ± 2.8 trials.

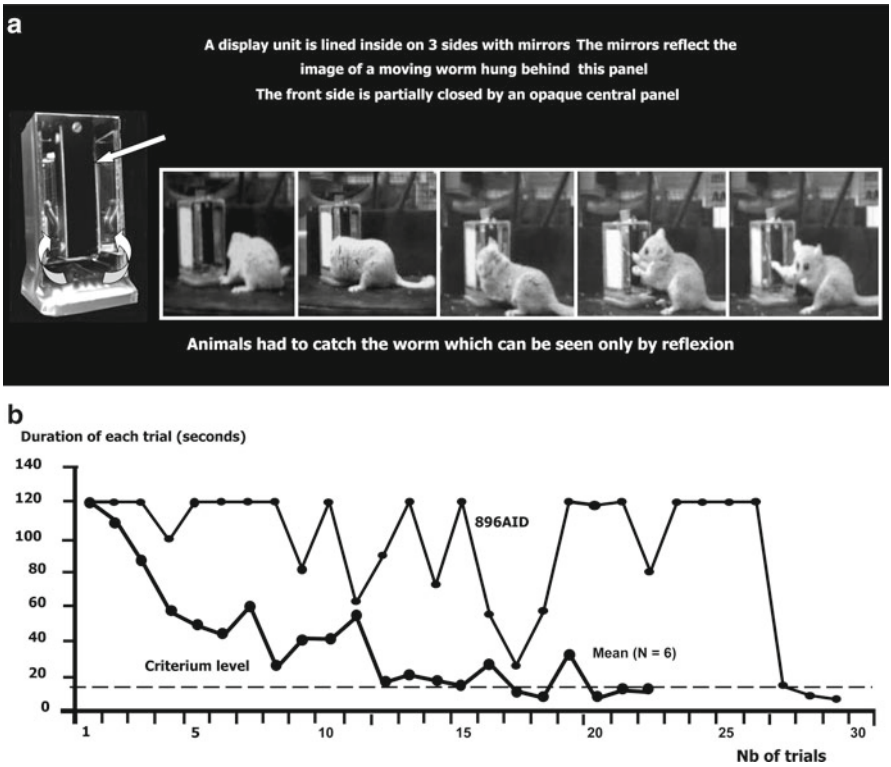


Fig. 37.3 (**a**) Manipulation in front of a mirror. (**b**) Results for seven subjects

The direction in which the lid could turn was then reversed (Fig. 37.4b); this did not change the spatial disposition of the box. The test subjects ($N=3$) learned again to push the lid in front of them using the forepaws or snout. They also learned to change their position on the box in order to maintain their previous strategy. The alternation of direction was repeated three times until the learning criterion was attained. In addition to the test subjects, a very young male (4.5 months old) was presented with the same task.

The results are shown in Fig. 37.4c. All subjects improved their scores at each change of direction, and the mean number of trials and mean time to reach the learning criterion decreased with each reversal. Moreover, animals needed fewer trials to learn how to handle the first change of direction than they did to learn the initial task. Surprisingly, the 4.5-month-old male completed the learning phase plus the five reversals in 33 trials (compared with 29, 34, and 42 trials in the adults), corresponding to 15.7 min (as opposed to 14.9, 23.3, and 23.7 min in the adults).

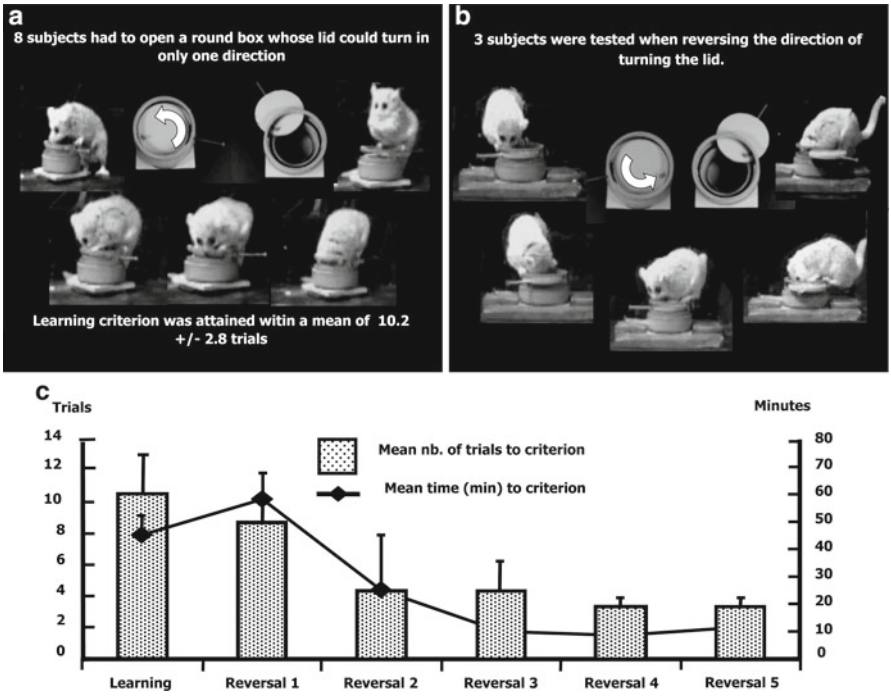


Fig. 37.4 (**a**) Learning to turn the lid of a round box. (**b**) Alternated manipulation of the same box. (**c**) Score improvements in three subjects learning the alternated manipulative task

Discussion and Conclusion

Despite large interindividual variations, the ten test subjects easily solved a manipulative problem involving three different solutions. They needed far more attempts and time to learn the pushing task than either raising the lid or pulling the drawer, which could be accounted for in one of two ways. First, captive mouse lemurs have been observed pulling objects (e.g., in the context of play) but never pushing them. A capacity for pulling objects is common in primates, whereas pushing is not (Torigoe 1985; Hauser et al. 1999). Second, in my test the pushing task required not only learning a new way of opening the box but also understanding that a detour is necessary to obtain the reward. Several subjects exposed to the three-way box opening problem again after 1 year had elapsed, reached the learning criterion faster than they had done in the initial tests.

In the case of the double cylinder task, the subjects confirmed their capacity to master complex manipulations. All were able to perform the simultaneous handling of the cord and the thread in the second step.

The use of a mirror for complex manipulations has not, to my knowledge, been tested before with mouse lemurs. Seven of eight subjects tested learned efficiently to catch an object (a mealworm suspended by a thread) that was not directly visible. However, it does not follow that gray mouse lemurs used the reversed image of their hands to coordinate their movements as has been demonstrated in chimpanzees (Menzel et al. 1985), African (Anderson 1986), Japanese (Itakura 1987), and South American monkeys (Heschl and Burkart 2006). The device used in my study did not control sufficiently for spatial habituation bias. Consequently, it is possible that the mouse lemurs showed simple associative learning rather than "mirror-guided reaching" (Anderson 1986), even if all the subjects clearly took time to look around inside the device before starting each manipulation. On the other hand, results with the round box task indicate that mouse lemurs can adapt their response rapidly to new conditions, which require a change of manipulative strategy (such as a different way to turn the lid).

As for the visual and spatial reversal tasks conducted by Cooper (1974; 1980), the mouse lemurs' learning curve (Fig. 37.4c) demonstrates that they improved their scores markedly from the second reversal test. This ability is considered one of the cognitive features, which differentiate prosimians from rats, and allies them with other primates (Rumbaugh and Pate 1984), and may be due to an improvement in attention and memory processes.

Tasks were solved differently by different individuals. Videotaped observations allow me to distinguish several types of learning:

1. During the training phase, accidental handling led the subject to find the solution to a problem, e.g., incidentally half-opening the round box by bumping the lid or jumping on to it.
2. When the training phase was too long, the response was shaped by the experimenter, e.g., by half-opening the drawer or the lid of a box that animals failed to pull or raise in the allotted time. In most cases (except for one mirror test), this led to successful learning.
3. During the training phases, some animals responded incorrectly for several trials but suddenly found the solution to a problem (e.g., when confronted with the three-way opening box or with the double-cylinder task). After this, they rapidly reached the learning criterion. This type of learning complies with Weisberg's (1995) definition of insight. Its occurrence in gray mouse lemurs implies that, as with other primates, they do not solve problems simply by trial and error but by mental representation of the environment linking prior experience and present cues to the goal of the task.
4. Lastly, I investigated social learning in three subjects that had difficulty solving one kind of problem. If I introduced a conspecific who had mastered the task into the cage, the cage inhabitants reached the learning criterion when retested alone. I conclude that, like other primates (Hauser et al. 1999), mouse lemurs can learn manipulations by imitation.

In terms of object manipulation, gray mouse lemurs are rapid, flexible, and persevering learners (up to 10 min without distraction) and capable of executing complex tasks.

An aptitude for learning is present in very young subjects. In addition, learning seems to be well memorized. All of this suggests that prosimians have cognitive capacities close to those of simian primates, especially New World monkeys (Ohta et al. 1984; Picq 2000; Santos et al. 2005b), as well as Old World monkeys (Rumbaugh and Pate 1984; Santos et al. 2005a). The capacity of *Microcebus murinus* to respond to new situations is, along with its many physiological and social adaptations (Schilling 2000), an important factor in its evolutionary success in Madagascar.

References

Anderson JR (1986) Mirror-mediated finding of hidden food by monkeys (*Macaca tonkeana* and *Macaca fascicularis)*. J Comp Psychol 100:237–242

Anderson JR, Fornasieri I, Ludes E, Roeder JJ (1992) Social processes and innovative behaviour in changing groups of *Lemur fulvus*. Behav Proc 27:101–112

Cooper HM (1974) Learning set in *Lemur macaco*. In: Martin RD, Doyle GA, Walker AC (eds) Prosimian biology. Duckworth, London, pp 293–300

Cooper HM (1980) Ecological correlates of visual learning in nocturnal prosimians. In: Charles-Dominique P, Cooper HM, Hladik A, Pages E, Pariente GF, Petter-Rousseaux A, Petter J-J, Schilling A (eds) Nocturnal malagasy primates. Academic, New York, pp 191–203

Cunningham CL, Anderson JR, Mootnick AR (2006) Object manipulation to obtain a food reward in hoolock gibbons, *Bunopithecus hoolock*. Anim Behav 71:621–629

Hauser MD, Kralik J, Botto-Manhan C (1999) Problem solving and functional design features: experiments on cotton-top tamarins, *Saguinus oedipus oedipus*. Anim Behav 57:565–582

Heschl A, Burkart J (2006) A new mark test for mirror self-recognition in non-human primates. Primates 47:187–198

Itakura S (1987) Mirror guided behaviour in Japanese monkeys (*Macaca fuscata fuscata*). Primates 28:149–161

Joly M, Zimmermann E (2007) First evidence for relocation of stationary food resources during foraging in a strepsirhine primate (*Microcebus murinus*). Am J Primatol 69:1045–1052

Menzel EW Jr, Savage-Rumbaugh ES, Lawson J (1985) Chimpanzee (*Pan troglodytes*) spatial problem solving with the use of mirrors and televised equivalents of mirrors. J Comp Psychol 99:211–217

Ohta H, Ishida H, Matano S (1984) Learning set formation in ring-tailed lemurs (*Lemur catta*). Folia Primatol 43:53–58

Parker CE (1974) Behavioral diversity in ten species of non-human primates. J Comp Physiol Psychol 87:930–937

Perret M (1992) Environmental and social determinants of sexual function in the male lesser mouse lemur (*Microcebus murinus*). Folia Primatol 59:1–25

Picq JL (2000) La cognition chez le microcèbe murin et les autres lémuriens. In: Primatologie, vol 3. ADRSC, Marseille, pp 173–207

Rumbaugh DM, Pate JL (1984) The evolution of cognition in primates: a comparative perspective. In: Roitblatt HL, Bever TG, Terrace HS (eds) Animal cognition. Lawrence Erlbaum Associates, Hillsdale, NJ, pp 569–587

Santos LR, Barnes JL, Mahajan N (2005a) Expectations about numerical events in four lemur species (*Eulemur fulvus, Eulemur mongoz, Lemur catta* and *Varecia rubra*). Anim Cogn 8:253–262

Santos LR, Mahajan N, Barnes JL (2005b) How prosimian primates represent tools: experiments with two lemur species (*Eulemur fulvus* and *Lemur catta*). J Comp Psychol 119:394–403

Santos LR, Pearson HM, Spaepen GM, Tsao F, Hauser MD (2006) Probing the limits of tool competences: experiments with two non-tool-using species (*Cercopithecus aethiops* and *Saguinus oedipus*). Anim Cogn 9:94–109

Schilling A (2000) Organes des sens et communication chez le microcèbe. In: Primatologie, vol 3. ADRSC, Marseille, pp 85–143

Schilling A, Richard JP, Servière J (2001) Effect of aging on circadian activity in gray mouse lemurs. Int J Primatol 22:25–42

Torigoe T (1985) Comparison of object manipulation among 74 species of non-human primates. Primates 26:182–194

Vauclair J (1996) Tool use and spatial and temporal representations. In: Vauclair J (ed) Animal cognition. An introduction to modern comparative psychology. Harvard University Press, Cambridge, MA, pp 53–82

Weisberg RW (1995) Prolegomena to theories of insight in problem solving: a taxonomy of problems. In: Sternberg RW, Davidson JE (eds) The nature of insight. MIT Press, Cambridge, MA, pp 157–196

Part VII
Conservation of Prosimians

Chapter 38
Status, Distribution, and Conservation of Slender Lorises in India

Honnavalli N. Kumara, Mewa Singh, Mohammed Irfan-Ullah, and Shanthala Kumar

Abstract Two recognized subspecies of slender loris, *Loris lydekkerianus lydekkerianus* and *L. l. malabaricus*, are endemic to Peninsular India. *L. l. lydekkerianus* has been reported from the drier forests of the Eastern Ghats south of the Godavari River, while *L. l. malabaricus* has been found in the wet forests of the Western Ghats south of the river Tapti. On the basis on confirmed sightings of individuals, we present a review of current understanding of the distribution and conservation status of India's endemic slender loris subspecies. A possible third subspecies occupies a patchy distribution along the eastern foothills of the southern Western Ghats. To facilitate conservation planning, we modeled potential distributions for each recognized subspecies.

H.N. Kumara (✉)
Sálim Ali Centre for Ornithology and Natural History,
Anaikatty P. O., Coimbatore 641 108, Tamil Nadu, India

National Institute of Advanced Studies, Bengaluru, Karnataka, India
e-mail: honnavallik@gmail.com

M. Singh
Bio-Psychology Laboratory, Department of Psychology, University of Mysore,
Mysore 570 005, Karnataka, India
e-mail: msingh@psychology.uni-mysore.ac.in; mewasinghltm@gmail.com

M. Irfan-Ullah
Ecoinformatics Centre, Ashoka Trust for Research in Ecology and the Environment (ATREE),
659, 5th-A Main Road, Hebbal, Bengaluru, Karnataka 560 024, India

RMSI Pvt. Ltd, A-7, Sector-16, Noida, UP 201301, India
e-mail: irfan26@gmail.com

S. Kumar
Riverstone Ruby, Flat No. 107, Vallalar Nagar, Vadavalli, Coimbatore 641041,
Tamil Nadu, India
e-mail: shaanyk@gmail.com

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_38,

Resume Deux sous-espèces reconnues de loris, *Loris lydekkerianus lydekkerianus* et *L. l. malabaricus*, sont endémiques de la Péninsule indienne. *L. l. lydekkerianus* a été signalé dans les forêts sèches des Ghâts orientaux, au sud du fleuve Godâvarî, alors que *L. l. malabaricus* a été trouvé dans les forêts humides des Ghâts occidentaux, au sud du fleuve Tapti. En nous fondant sur les observations directes, nous synthétisons l'information disponible concernant la distribution géographique et le statut de conservation des deux sous-espèces endémiques de loris indiens. Une possible troisième sous-espèce, à distribution discontinue, est rencontrée au pied des collines du sud des Ghâts occidentaux . Pour faciliter les plans de conservation, nous avons modélisé la distribution potentielle des sous-espèces reconnues.

Introduction

In the taxonomic scheme commonly employed, slender lorises (Lorisidae) comprise two known species, *Loris tardigradus* Linnaeus 1758 and *Loris lydekkerianus* Cabrera 1908, and six subspecies endemic to southern Peninsular India and Sri Lanka. Four subspecies (*L. lydekkerianus nordicus*, *L. l. grandis*, *L. tardigradus tardigradus*, and *L. t. nycticeboides*) have been reported from Sri Lanka (Chaps. 9 and 10) and two (*L. l. lydekkerianus* and *L. l. malabaricus*) from India (Hill 1953; Groves 2001). *L. l. lydekkerianus* occurs in the drier forests of the Eastern Ghats south of the Godavari River, and *L. l. malabaricus* inhabits the wet forests of the Western Ghats south of the river Tapti (Groves 2001). Schulze and Meier (1995) undertook the first comprehensive attempt to map the distribution of slender loris subspecies based on records dating back almost 100 years.

During the past century, however, habitat loss and hunting have had a major impact on the distribution and status of slender lorises. Although the specimens collected over this period were sourced from several different areas, the continued presence of slender lorises in all of these sites had not been confirmed through recent field work. New surveys, based on confirmed sightings of individuals, were started around Dindigul in Tamil Nadu by Singh et al. (1999), and later extended to Indira Gandhi Wildlife Sanctuary (IGWS) in Tamil Nadu (Kumar et al. 2002), southern Andhra Pradesh (Singh et al. 2000), and Karnataka (Kumara et al. 2006; Kumara 2007). On the basis of these studies, we present a comprehensive review of current understanding of the distribution and conservation status of India's endemic slender loris subspecies. We also model potential distributions for each recognized subspecies to facilitate conservation planning.

Methods

Geographic Area

The Indian Peninsula has two major hill systems, the Western Ghats and the Eastern Ghats. The Western Ghats run parallel to the west coast of south-western India from 21°N to 8°N (Pascal 1988) (Fig. 38.1), passing through six states. Being close to the

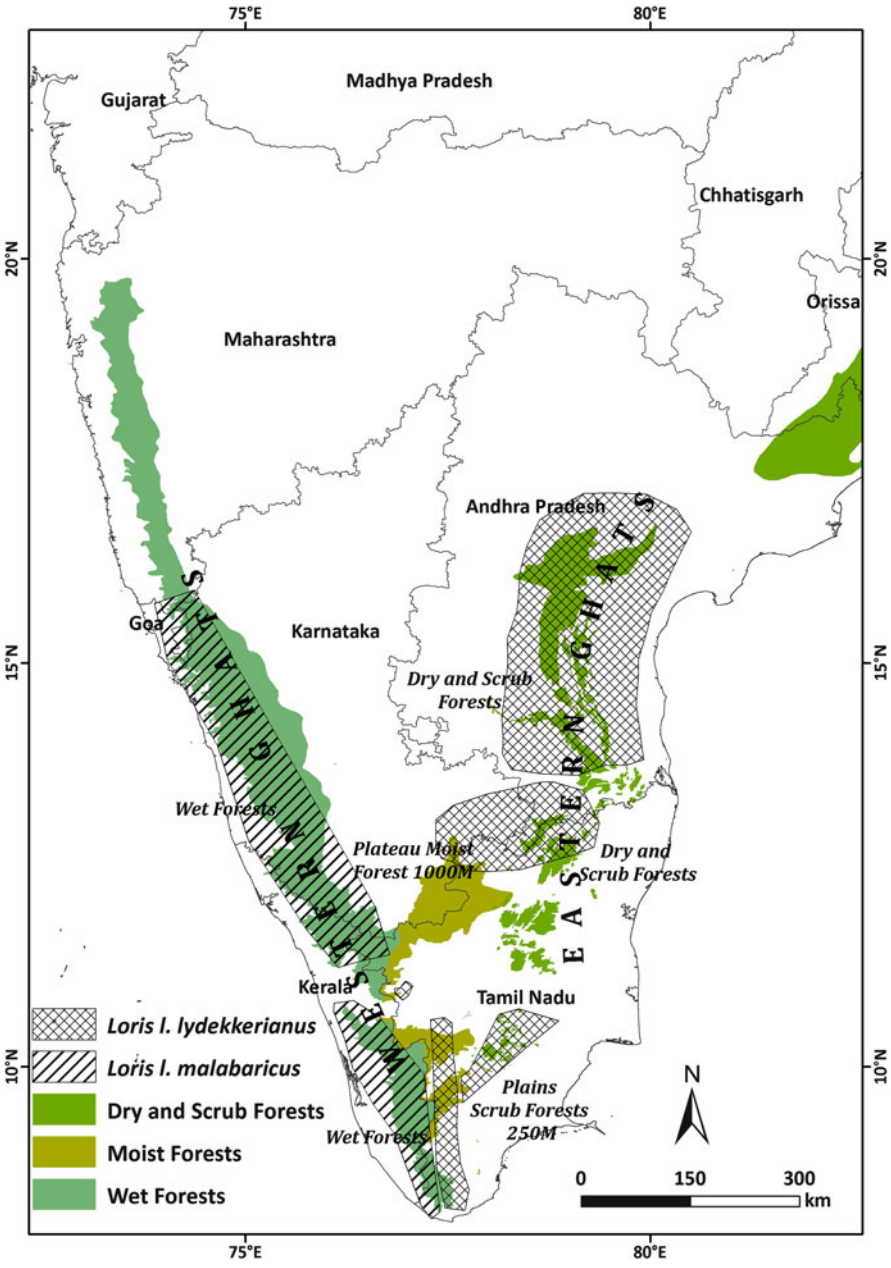


Fig. 38.1 Map of South India showing the Western and Eastern Ghats hill systems and ranges of recognized subspecies

Arabian Sea, these ranges receive heavy south-westerly monsoons. The western slopes and ridges are covered with primary rainforests, while the eastern slopes, being in rain shadow, support dry forests. The Ghats, with a length of ~1,600 km from north to south and an east–west extent of 30–80 km, are a mosaic of habitat types. On the basis of biogeographic parameters, Ramesh (2001) classified the ecological zones of the Western Ghats as Wet Evergreen Forests, Dry Evergreen Climax Forests, and Deciduous Climax Forests. The rainfall varies between 3,000 and 6,000 mm on the western slopes of the hill system.

The Eastern Ghats are a series of discontinuous hills running north-east to south-west, parallel to the coast of the Bay of Bengal. They cover an area of ~75,000 km^2, from the Mahanadi River in the north to the Vaigai River 1,750 km to the south, passing through Tamil Nadu, Andhra Pradesh, and Orissa with small areas in the southern part of Karnataka. The region falls within the tropical monsoon climatic distribution, receiving rainfall from both the south-west monsoon and the north-east retreating monsoon. In the northern part the rainfall ranges from 1,200 to 1,600 mm, whereas it is lower in the central and southern parts (600 and 1,000 mm, respectively), and the climate is semiarid, except in the hilly peaks. The mean temperature in January ranges from 20 °C to 25 °C, reaching a maximum of 41 °C with an increasing trend from north to south. The vegetation in the Eastern Ghats includes moist forests in the high hills but mainly dry deciduous and scrub forests across the hill system.

Slender lorises occur in both these hill systems and are distributed across six Indian states: Maharashtra, Goa, Karnataka, Kerala, Tamil Nadu, and Andhra Pradesh (see Fig. 38.1). Previous surveys, however, were restricted to a few regions in south India that included the plateaus of Dindigul, Deccan, parts of the central and southern Western Ghats, and the Eastern Ghats. Our surveys since 1999, therefore, add significantly to our information on the distribution of India's slender lorises.

Identification of Subspecies

Morphological characteristics like body size, coat color, and shape of circumocular patches distinguish the Mysore slender loris from the Malabar slender loris (Groves 2001). The Malabar slender loris is reddish brown with large circumocular patches, while the Mysore slender loris is a relatively larger animal (about 260 g vs. 180 g for *L. l. malabaricus*) and grayish-brown with narrow circumocular patches (Kumara et al. 2006).

Abundance Surveys

Surveys of slender lorises are available from Kalakkad-Mundanthurai Tiger Reserve (KMTR) in Tamil Nadu (Kar-Gupta, unpublished data), Dindigul in Tamil Nadu and southern Andhra Pradesh (Singh et al. 1999, 2000), IGWS in Tamil Nadu

(Kumar et al. 2002), and Karnataka (Kumara et al. 2006; Kumara 2007) (Fig. 38.1). The goal of these surveys was to cover large spatial areas documenting slender loris abundance.

Mapping entire distributions by ground surveys was beyond the capability of our research team, and we found the method to be biased toward easily accessible or well-sampled regions. Since systematic surveys had produced a good number of sight records for the loris subspecies, we used an alternative method to reconstruct their potential distributions, combining occurrence records with climatic and environmental parameters (see Kumara et al. 2009) to build ecological niche models (hereafter ENM; Peterson and Kluza 2003; Peterson et al. 2003; Peterson 2005).

Results

Vegetation Types Occupied by the Slender Loris Subspecies and Population Status

Recognized subspecies were observed in all study sites except KMTR and IGWS. *L. l. malabaricus* were sighted in the forests of western Karnataka, whereas *L. l. lydekkerianus* were observed in Dindigul, southern Andhra Pradesh, and south-east Karnataka (Table 38.1, Fig. 38.1). *L. l. lydekkerianus* occurred in various habitats except deciduous forests lacking undergrowth and degraded scrub forests, whereas *L. l. malabaricus* were found in all available forest types. Slender lorises found in the rain shadow areas of the Western Ghats, in mixed deciduous forests, riverine forests with thick vegetation, and plantations on the eastern slopes of the KMTR and IGWS, appear to represent a hitherto unrecognized subspecies. While they have pale coats like the Mysore subspecies, they are much smaller in body size and have circumocular patches that differ from those of both the Mysore and Malabar subspecies.

In total, 785 lorises have been sighted during surveys to date, including 501 *L. l. lydekkerianus*, 119 *L. l. malabaricus*, and 165 individuals of the unidentified subspecies (Table 38.1). The *L. l. lydekkerianus* encounter rate varied substantially (0.13–1.10 animals/km) among different forest patches within the same region, with the highest encounter rate reported from Dindigul (Singh et al. 1999, 2000; Kumara et al. 2006). The *L. l. malabaricus* encounter rate was between 0.21 and 0.27 animals/km across all surveys.

Distribution Patterns of Recognized Slender Loris Subspecies

The vegetation of western Karnataka is made up chiefly of the wet forests of the Western Ghats. The subspecies confirmed from this region, *L. l. malabaricus* (Fig. 38.1), is predominantly found in the wet forests of the western slopes, extending

Table 38.1 Details of areas surveyed to assess current ranges of slender loris populations in Peninsular India

State	Region	Vegetation types supporting lorises[a]	Vegetation type without lorises[a]	Subspecies of slender loris recorded	Effort (km walked/ motored)	No. loris sighted	Abundance (animals/km)
Tamil Nadu	Dindigul[b]	MD, AS, SST, CVR	–	*L. l. lydekkerianus*	280.0	313	1.10
	Indira Gandhi Wildlife Sanctuary[c]	MD, RTU, PL, AS	MOD, EG, MS, DEG, CP	?	818.0	37	0.04
	Kalakkad-Mundanthurai Tiger Reserve[d]	MD, RTU, PL	EG	?	146.4	128	0.90
Andhra Pradesh	Southern Andhra Pradesh[e]	MD, DSU, AS, SST, RTU, CVR	–	*L. l. lydekkerianus*	734.0	98	0.13
Karnataka	Western Karnataka[f]	MOD, EG, MS, DEG, CP	–	*L. l. malabaricus*	293.0	63	0.21
	Western Karnataka (three Protected Areas)[g]	MOD, EG, MS, DEG, CP	–	*L. l. malabaricus*	203.0	56	0.27
	South-east Karnataka[f]	MD, AS, SST, RTU, CVR	DSU, DOS	*L. l. lydekkerianus*	255.0	90	0.35

[a]MD, Mixed deciduous; DSU, Deciduous forest with sparse undergrowth; AS, *Acacia* spp. dominated scrub forest; SST, Scrub forest with sparse trees; DOS, Degraded open scrub; PL, Plantation; RTU, Riverine forest with thick undergrowth; CVR, Cultivated land, villages and roadside trees; MOD, Moist deciduous; EG, Evergreen forest; MS, Montane scrub; DEG, Degraded evergreen forest; CP, Cardamom plantation

[b]Singh et al. (1999)

[c]Kumar et al. (2002)

[d]Kar-Gupta (unpublished data)

[e]Singh et al. (2000)

[f]Kumara et al. (2006)

[g]Kumara (2007)

into moist deciduous forests on the eastern side of the Western Ghats. No evidence exists, however, of their presence in the Mangrove forests of the west coast. The forests of Dindigul, southern Andhra Pradesh, and south-east Karnataka support the dry forests of the Eastern Ghats, occupied primarily by *L. l. lydekkerianus*. The potential distributions of these taxa were modeled using ENM.

Our results indicated that, in terms of environmental characteristics, the distribution of *L. l. lydekkerianus* may include large geographical tracts of drier forest patches and human-dominated landscapes spread across the rain shadow area of Peninsular India, while that of *L. l. malabaricus* is restricted to a relatively narrow geographic range and shows no overlap with *L. l. lydekkerianus* (Fig. 38.2). *L. l. malabaricus* is apparently confined to the western side of the Western Ghats—a region dominated by wetter climate, receiving summer (June–September) rainfall through south-west monsoons, while *L. l. lydekkerianus* prefers the drier habitats of the subcontinent's rain shadow. The hitherto unrecognized subspecies appears to occupy a patchy distribution along the eastern foothills of the southern Western Ghats—a region characterized by intermediate climate and precipitation, receiving winter rains from the retreating north-east monsoons, and an average annual rainfall of ~1,500 mm.

Discussion

According to our analysis, the two recognized slender loris subspecies in southern India occupy very different habitat types and show very different patterns of abundance. The hills of the Eastern Ghats include discontinuous and patchy forests surrounded by human-dominated landscapes with varying levels of disturbance (Jayakumar et al. 2002), and *L. l. lydekkerianus* abundance varied widely between forest patches within the region, possibly in response to the degree of disturbance. Slender lorises cannot leap between trees and find it hard to climb trunks of large girth; hence, they prefer scrubby forests with continuous, thin-branched pathways for easy movement (see Chaps. 9 and 10 for similar observations of slender lorises in Sri Lanka). *L. l. lydekkerianus* abundance also varied widely between regions (Kumara et al. 2006; Singh et al. 2000) and was particularly high in certain small forest patches in south-east Karnataka and southern Andhra Pradesh. By contrast, *L. l. malabaricus* consistently showed low abundance across its distribution, which could include continuous forests along the western side of the Western Ghats (Kumara 2007).

The two subspecies are separated by large geographic areas in both the northern and middle regions of their distribution ranges; in mid-range, they are separated by approximately 200 km of the deciduous forests of the southern plateau from Kanakapura to the Coorg hills. In the south, the subspecies' ranges approach each other more closely, separated by ~50 km. The extent of the *L. l. malabaricus* range on the eastern slopes of the Western Ghats, however, still remains to be confirmed taxonomically.

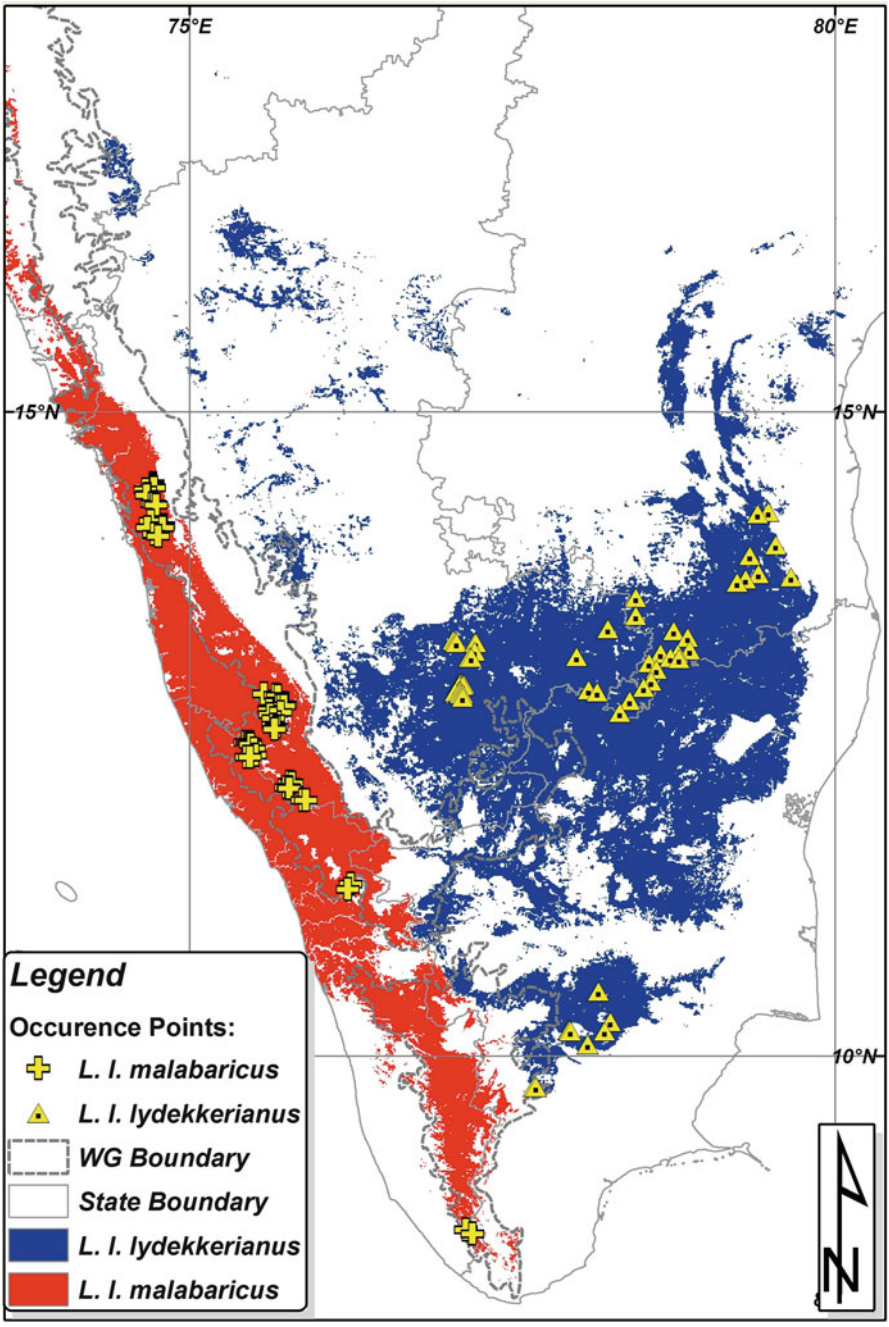


Fig. 38.2 Map showing modeled potential distributions of slender loris subspecies in Peninsular India

The potential subspecies distributions predicted by ENM accord well with their observed distributions. This allows us to develop a model-based framework for future sampling and for planning conservation strategies against the growing threat of landscape change and habitat loss linked to increasing urbanization. Our survey results suggest that the morphologically distinct subspecies are adapted to different environmental regimes, and this was supported by the potential niches derived by our ENM. We recommend a systematic molecular study of the subspecies be undertaken at the population level to establish the genetic status of the different morphotypes.

During the course of the surveys, a previously unrecognized morphotype was identified from the eastern slopes of the KMTR and IGWS. This habitat is more similar to that of *L. l. lydekkerianus*, but the population's status needs further investigation with respect to morphological, ecological, and genetic differentiation.

Conclusion

Slender loris distribution has clearly undergone substantial changes in the past century, particularly in the case of *L. l. lydekkerianus*, which currently occupies a very large range and encounters varying degrees of anthropogenic disturbance. The rapidly changing, human-dominated landscape poses the major threat to loris survival through range reduction and fragmentation, as reported in south-east Karnataka (Kumara et al. 2006). Studies like ours can help to predict the most vulnerable parts of the species' range and to identify previously unknown morphological variation and potential environmental adaptation among slender lorises.

Ackowledgments We thank the forest departments of Karnataka, Tamil Nadu, and Andhra Pradesh for research permits and the organizers of the South Africa Prosimians 2007 meeting for sponsorship to attend the conference. We thank R. Sasi for helping in the preparation of map. We thank the editors for their support in improving the chapter.

References

Groves CP (2001) Primate taxonomy. Smithsonian Institution Press, Washington, DC

Hill WCO (1953) Primates: comparative anatomy and taxonomy, vol 1, Strepsirhini. Edinburgh University Press, Edinburgh

Jayakumar S, Arockiasamy DI, Britto SJ (2002) Conserving forests in the Eastern Ghats through remote sensing and GIS: a case study in Kolli hills. Curr Sci 82:1259–1267

Kumar MA, Singh M, Srivastava S, Udhayan A, Kumara HN, Sharma AK (2002) Distribution and management of wild mammals in Indira Gandhi Wildlife Sanctuary, Tamil Nadu, India. J Bombay Nat Hist Soc 99:184–210

Kumara HN (2007) Impact of local hunting on abundance of large mammals in three protected areas of the Western Ghats, Karnataka. Final technical report, Rufford Maurice Laing Foundation, UK. National Institute of Advanced Studies, Bangalore

Kumara HN, Singh M, Kumar S (2006) Distribution, habitat correlates and conservation of slender loris (*Loris lydekkerianus*) in Karnataka. India Int J Primatol 27:941–969

Kumara HN, Irfan-Ullah M, Kumar S (2009) Mapping potential distributions of slender loris subspecies in peninsular India. Endanger Species Res 7:29–38

Pascal JP (1988) Wet evergreen forests of the Western Ghats of India: ecology, structure, floristic composition and succession. Institut français de Pondicherry, Pondicherry, India

Peterson AT (2005) Kansas gap analysis: the importance of validating distributional models before using them. Southwest Nat 50:230–236

Peterson AT, Kluza DA (2003) New distributional modelling approaches for gap analysis. Anim Conserv 6:47–54

Peterson A, Papes M, Kluza D (2003) Predicting the potential invasive distributions of four alien plant species in North America. Weed Sci 51:863–868

Ramesh BR (2001) Patterns of vegetation, biodiversity and endemism in the Western Ghats. In: Memoir, vol 47. Geological Society of India, pp 973–981

Schulze H, Meier B (1995) The subspecies of Loris tardigradus and their conservation status: a review. In: Alterman L, Doyle GA, Izard MK (eds) Creatures of the dark: the nocturnal prosimians. Plenum, New York, pp 193–210

Singh M, Kumar MA, Kumara HN, Mohnot SM (2000) Distribution and conservation of slender lorises (*Loris tardigradus lydekkerianus*) in southern Andhra Pradesh, South India. Int J Primatol 21:721–730

Singh M, Lindburg DG, Udhayan A, Kumar MA, Kumara HN (1999) Status survey of slender loris (*Loris tardigradus lydekkerianus*) in Dindigul, Tamil Nadu, India. Oryx 33:31–37

Chapter 39
Berenty Reserve: Past, Present, and Future

Hajarimanitra Rambeloarivony and Alison Jolly

Abstract The Berenty Reserve is part of a 400-ha forest fragment bordered by the Mandrare River, sisal plantations and pasture lands. It was founded in 1936 by the de Heaulme family in negotiation with local Tandroy clans, and the forest has been preserved through political changes for over 75 years. Exotic trees have been planted on the western side, and the forest is infiltrated by trails which facilitate assault by invasive plants, particularly sisal and *Cissus quadrangularis*. Pressure is aggravated by high lemur density, especially introduced hybrid brown lemurs *Eulemur rufifrons*×*E. collaris*, which are displacing native *Lemur catta.* Alopecia of *Lemur catta* is directly linked to ingestion of the exotic plant *Leucaena leucocephala*. Successive forest managers have attempted to resolve these problems. Predicted scenarios of global warming and a lower water table will exacerbate both biological and social stress.

Resume La Réserve de Berenty fait partie d'un fragment de forêt de 400 ha bordé par le fleuve Mandrare, des plantations de sisals et des prés. Elle fut fondée en 1936 par la famille de Heaulme, en négociation avec les clans Tandroy, et a été préservée, malgré les changements politiques successifs, pendant plus de 75 ans. Des arbres exotiques sont plantés sur la partie ouest, et la forêt est parcourue par des sentiers qui facilitent l'invasion de plantes introduites, en particulier le sisal et *Cissus quadrangularis*. La pression est aggravée par la densité élevée de lémuriens, surtout de

H. Rambeloarivony (✉)
Ecole Nomale Supérieure, Université d'Antananarivo, Antananarivo 101, Madagascar

Department of Zoology and Entomology, University of Fort Hare,
Private Bag X1314, Alice 5700, South Africa
e-mail: haja.kely2010@gmail.com

A. Jolly
Department of Biology and Environmental Science,
University of Sussex, School of Life Sciences,
Falmer, Brighton, United Kingdom
e-mail: ajolly@sussex.ac.uk

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_39,

Eulemur rufifrons x *E. collaris*, hybrides introduits qui déplacent les *Lemur catta* indigènes. L'alopécie de *Lemur catta* est directement liée à l'ingestion d'une autre plante introduite, *Leucaena leucocephala*. Les gérants de la réserve qui se sont succédés ont tenté de résoudre ces problèmes. On peut prédire que le réchauffement climatique et l'abaissement de la nappe phréatique aggraveront le stress biologique et social.

Introduction: The Berenty Forest

The Berenty Reserve contains an isolated forest fragment, cradled between an ancient and a modern riverbed in a semi-arid area. "This forest is so beautiful" said the de Heaulme family on their arrival in 1936, "that no-one must ever cut it down." The de Heaulmes negotiated its preservation with local Tandroy clans and have maintained it through the drastic political changes of the past 75 years (Jolly 2004).

The gallery forest is dominated by tamarind trees ("kily," *Tamarindus indica*) and emergent acacias ("benono," *Acacia rovumae*). In drier areas, closed forest gives way to open scrub and a narrow tongue of climax spiny forest (Fig. 39.1).

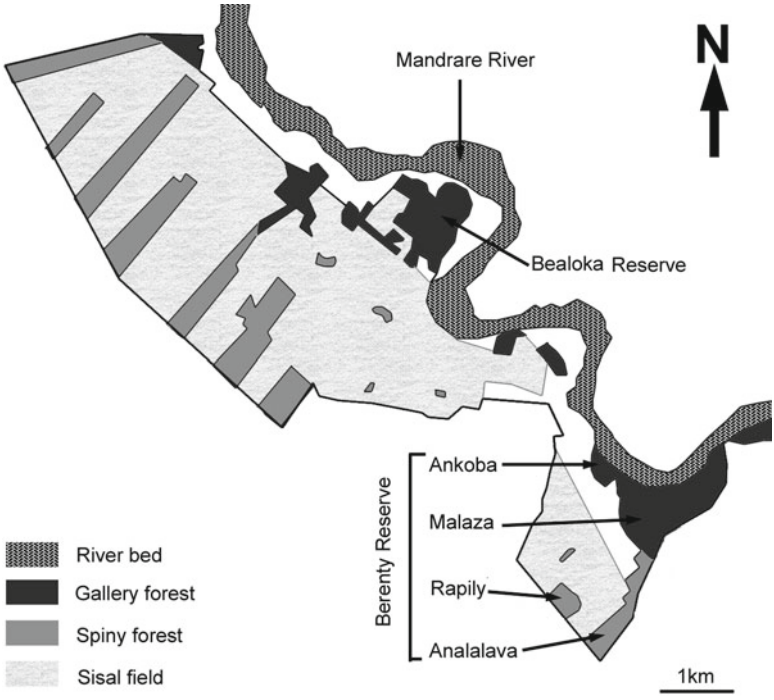


Fig. 39.1 The reserve complex on Berenty Estate, and the surrounding area

Berenty is home to six lemur species: sifakas (*Propithecus verreauxi*), ring-tails ("maky," *Lemur catta*), introduced brown lemurs ("gidro," *Eulemur rufifrons* × *E. collaris*), sportive lemurs ("pondiky," *Lepilemur leucopus*), and two mouse lemurs ("hataka," *Microcebus murinus* and *M. griseorufus*). They share the forest with flying foxes ("fanihy," *Pteropus rufus*), 99 recorded bird species, and reptiles including the rare burrowing snake *Pseudoxyrhophus kely* (Jolly et al. 2006).

Being so small, Berenty should not be a major issue for conservation; however, it supports the largest of four patches of gallery forest left on the Mandrare River. The other three are Bealoka (100 ha), also on the de Heaulme estate, and two sacred forests near Ifotaka. Berenty and Bealoka are thus relics of the richest forest type of southern Madagascar and well worth the conservation effort.

Berenty's History

Traditionally, the Berenty forest provided housing, fuel, fodder, medicine, cosmetics, pasture for livestock, and starchy tubers for use during times of food shortage. All lemurs were "fady" (taboo) to local Tandroy. In 1936, Henry de Heaulme founded the 6,000 ha Berenty Estate, cutting spiny forest and planting sisal (*Agave sisalis*) for its high-quality fiber. Five years earlier the Androy region had suffered the worst famine of the twentieth century following destruction of the prickly pear ("raketa," *Opuntia macracantha*) by cochineal scale insects (Middleton 1999). Local clans made their agreement with de Heaulmes in the hope that never again would they suffer so many deaths through starvation. From its founding, Berenty Estate involved cross-cultural politics, local experiences of life and death, and two Mexican desert species, the prickly pear and sisal, which became the foundations of two overlapping local economies.

One thousand hectares of Berenty Estate remain as forest reserves. Flowering and fruit trees—superenriched lemur habitat (Rasamimanana and Rafidinarivo 1993) —were planted among the plantation houses. Tourism began in the early 1980s, initially as a desperate political gamble to save the forest (Russell, cited in Jolly 2004). Berenty now hosts up to 10,000 tourists, a dozen scientists, and half a dozen TV teams annually.

Sheila O'Connor compared the Berenty and Bealoka Reserves in 1983–1984. On her recommendation, grazing was prohibited in Bealoka (O'Connor 1987). Helen Crowley was appointed forest manager in 1992–1993. She cleared invasive species, especially *Cissus quadrangularis*, cut new small trails, and summarized previous and current research; her report gives fundamental background on the reserve (Crowley 1995). In 1992–1993, Maxim Allorge raised an experimental plot of tamarind trees at Beaoloka and extended the spiny forest botanical gardens in 1993. Hajarimanitra Rambeloarivony was appointed forest manager from 2006 to 2008, and succeeded by Sahoby Marin Raharison from 2009 to 2010. Currently, the de Heaulme family manages the reserve.

Threats to Berenty's Future

The Problem of Isolation

For long-term conservation, an isolated small forest is not viable. The nearest gallery forest is Bealoka reserve, 5 km away. Most land between the two reserves belongs to the de Heaulme family, but some parcels still belong to Tandroy people (Fig. 39.1). Bealoka lacks many of Berenty's invasive species, with no brown lemurs and few *Cissus*. Although a long-term project linking the two reserves is desirable, Berenty's problems must be resolved first.

A second possibility is extension of the reserves into the convex bends of the flood plain of the Mandrare River. However, these are also prime areas for local crops. Turning land over to forest would require compensation for the people who currently use these areas.

Analalava, the south-western extremity of Berenty Reserve, is only 800 m from the spiny forest Rapily Reserve; attempts to connect these tracts by a corridor are underway. Rapily in turn connects through locally used forest patches to windbreaks of spiny forest that extend the length of the De Heaulme property to Anjapolo, 20 km west of Berenty.

Experiments in reforesting the gallery forest have been undertaken. Allorge showed that young tamarinds must be planted in semi-shade and watered throughout their first two dry seasons. The 1993 seedlings have now reached 5–7 m in height. Spiny forest can be extended by planting cut *Alluaudia* branches about 1 m in length. This technique has long been known to local Tandroy as a means of fortifying villages, or more recently, of replanting for timber beside the main road. The *Alluaudia* branches' survival, however, depends on a good rainy season following planting.

Fragmentation by Trails

Fragmentation speeds invasive plant dissemination and leads to desiccation of the forest. There is no remedy except to avoid making new trails. However, there is a major difference between the pre-1950 roads and the new, small footpaths dating from the 1990s, which were made without cutting trees and left the canopy intact. The large roads are sunny with noticeably higher temperatures than the surrounding forest; however, they can serve as firebreaks and access roads in case of fire, which may be crucial in the future.

Invasive Plants

There are two principal invasive plant species in Berenty: *Cissus quadrangularis* and *Agave sisalana*. *Cissus* is a succulent vine which stifles host trees and may

Fig. 39.2 Stacking *Cissus* pulled from trees in the scrub zone of Berenty Reserve

eventually break the host by its sheer weight. A team of 12 men remove *Cissus* by hand (Fig. 39.2), with the debris carried off by tractors. We began with an experimental zone 20 m × 100 m to evaluate the clearing method used, the damage caused by *Cissus*, the damage resulting from removal, and the possibility of forest regeneration. The method was effective, but even small pieces of *Cissus* left on the ground may take root and regrow in the rainy season; the experimental plot thus needs continual monitoring to check the rate of regrowth and need for weeding. A control plot in the same area provides comparative data.

Sisal was originally planted as fencing to prevent intrusion by cattle. It is now invasive, especially in the spiny forest, where it prevents regeneration of native trees. The spiny forest area of the reserve is very small (14 ha), and the 4 ha invaded by sisal constitutes a substantial portion of it. Rudimentary mechanical methods are also used to cut down sisal and drag it away. In bare spaces, we replant native spiny forest trees, particularly *Alluaudia*.

Rapid Growth of the Brown Lemur Population

The *Eulemur* population has increased exponentially following the introduction of 8 animals in 1974, to 341 in 1993, and 624 in the 2007 census (Pinkus 2004; Chap. 40). Brown lemurs are serial opportunists; they concentrate on the two or three best foods in the forest at any given time, then shift in space and diet—in other words, a taxon poised to provoke the tragedy of the commons (Hardin 1968; Overdoff 1996; Pinkus 2004; Pinkus et al. 2006). Sussman's (1974) early work in Antseranananomby estimated a density of 1,000 *E. rufifrons* per km^2 so the end is not in sight.

Arguably, the provision of water first to the gallery forest in the 1980s and then the scrub in the early 1990s has facilitated their spread into habitats more suitable for *Lemur catta.* We stopped water provision in 2007, and results of this measure are not yet known. There is no political, and perhaps no ethical, possibility of culling a lemur population. In the future, other measures may need to be considered, e.g., contraception.

Alopecia from Leucaena leucocephala

Studies up to 2006 strongly suggested that the mimosine content of *Leucaena leucocephala* was the main cause of alopecia in *Lemur catta* (Crawford et al. 2006; Chaps. 41 and 42). In 2006–2007 almost all of the *Leucaena* in the main forest was removed, again by hand, cutting, and digging out roots. After the *Leucaena* clearance, ring-tailed lemur fur condition in the main part of Berenty improved dramatically. By 2010, alopecia had all but disappeared from the reserve.

Future Prospects

Managers and researchers continue to investigate the impact of eradicating invasive plants and stopping water provisioning and to record *Lemur catta* fur condition. A plant nursery has been set up to fill gaps in the forest. Besides this, research continues to be encouraged, especially to census numbers and condition of all three diurnal lemur species: *Propithecus verreauxi, Lemur catta,* and the *Eulemur* hybrids. However, many problems are beyond the scope of management in a small reserve.

In the memory of M. Jean de Heaulme, the Mandrare River used to run 1 m deep, even in the dry season. Now, it is a meander within its wide bed, ankle deep during most Septembers. In drought years, the flow is a meter or more below the surface sand, and people dig pits to gather water for themselves and their herds. Virtually no gallery forest remains below the headwaters. The forests of Androy lose 3.9 % coverage per year—higher than all but one other region in Madagascar; the national average was estimated by Conservation International (2007) at 1.3 % loss per year. Overgrazing greatly decreases the absorptive capacity of Tandroy pasturelands (Heurtebize personal communication). In short, the water table of Berenty is likely to become progressively lower and less reliable.

In a climate as erratic as that of southern Madagascar, we cannot be certain whether the current situation reflects anthropogenic climate change. However, since 2000 there have been four drought years. In the apparently "wet" years of 2006 and 2007, the rains did not actually begin until December, 2 months after the normal planting season for crops. Rain fell largely during cyclones in the growing season of January–March, flooding and destroying many fields. In the forest this led to a dearth of tamarind fruit during 2006 and its complete failure during 2007, removing the diurnal lemurs' staple food during the birth season, and one of the people's fall-back

foods during scarcity. These effects accord with the predictions of climate modelers. Agrarian economies like that of southern Madagascar will be on the battle-line if the world's climate becomes more harsh and variable.

The next generations of the de Heaulme family continue to live in Madagascar and to profit from ecotourism at Berenty. The family has maintained the reserve and weathered past political upheavals (Jolly 2004), and this may well continue into the future—but only as long as the local people, who are increasingly pressured by climate change and their own population growth, are willing to welcome the richest segment of the world's tourists among them. Management at Berenty is not just a question of technical skill. In the longer term, Berenty's survival is a question of social commitment and wisdom.

References

Conservation International (2007) Madagascar FCC Map revised. Conservation International, Antananarivo

Crawford GC, Andriafaneva L-E, Blumenfeld-Jones K, Calaba G, Clarke J, Gray L, Ichino S, Jolly A, Koyama N, Mertl-Millhollen A, Ostpak S, Pride RE, Rasamimanana H, Simmen B, Soma T, Tarnaud L, Tew A, Williams G (2006) Bald lemur syndrome and the miracle tree: alopecia associated with *Leucaena leucocephala* at Berenty Reserve, Madagascar. In: Jolly A, Koyama N, Rasamimanana HR, Sussman RW (eds) Ringtailed lemur biology: *Lemur catta* in Madagascar. Springer, New York, pp 332–342

Crowley HM (1995) Berenty Reserve management plan. Wildlife Preservation Trust International, Philadelphia, PA

Hardin G (1968) The tragedy of the commons. Science 162:1243–1248

Jolly A (2004) Lords and lemurs: mad scientists, kings with spears, and the survival of diversity in Madagascar. Houghton Mifflin, Boston, MA

Jolly A, Koyama N, Rasamimanana H, Crowley H, Williams G (2006) Berenty Reserve: a research site in southern Madagascar. In: Jolly A, Sussman RW, Koyama N, Rasamimanana H (eds) Ringtailed lemur biology. Springer, New York, NY, pp 32–42

Middleton K (1999) Who killed 'Malagasy Cactus'? Science, environment and colonialism in southern Madagascar (1924–1930). J S Afr Stud 25:215–248

O'Connor SM (1987) The effect of human impact on vegetation and the consequences to primates in two riverine forests, southern Madagascar. Unpublished PhD Thesis, Cambridge University, Cambridge

Overdoff DJ (1996) Ecological correlates to activity and habitat use of two prosimian primates: *Eulemur rubriventer* and *Eulemur fulvus rufus* in Madagascar. Am J Primatol 40:327–342

Pinkus S (2004) Impact of an introduced population of *Eulemur fulvus* on a native population of *Lemur catta* at Berenty Reserve, Southern Madagascar. Unpublished MSc Dissertation, University of British Columbia, Vancouver

Pinkus S, Smith JNM, Jolly A (2006) Feeding competition between introduced *Eulemur fulvus* and native *Lemur catta* during the birth season at Berenty Reserve, southern Madagascar. In: Jolly A, Sussman RW, Koyama N, Rasamimanana H (eds) Ringtailed lemur biology. Springer, New York, pp 119–140

Rasamimanana HR, Rafidinarivo E (1993) Feeding behavior of *Lemur catta* females in relation to their physiological state. In: Kappeler PM, Ganzhorn JU (eds) Lemur social systems and their ecological basis. Plenum, New York, pp 123–134

Sussman RW (1974) Ecological distinctions in sympatric species of *Lemur*. In: Martin RD, Doyle GA, Walker AC (eds) Prosimian biology. Duckworth, London, pp 75–108

Chapter 40
Berenty Reserve: Interactions Among the Diurnal Lemur Species and the Gallery Forest

Hantanirina Rasamimanana, Josia Razafindramanana, Anne S. Mertl-Millhollen, Kathryn Blumenfeld-Jones, Sahoby Marin Raharison, Donald Raymond Tsaramanana, Voahirana Razoliharisoa, and Laurent Tarnaud

Abstract The gallery forest of Berenty Reserve contains two native diurnal lemurs, the ring-tailed lemur, *Lemur catta* and Verreaux's sifaka, *Propithecus verreauxi*, as well as introduced hybrid brown lemurs *Eulemur rufifrons*×*E. collaris*. Feeding data indicate that competitive mutualism, an indirect interaction, may be occurring among these three species: *L. catta* and *P. verreauxi* apparently prevent *Eulemur* from accessing certain foods, although brown lemurs are dominant and compete directly with the ring-tailed lemurs for tamarind fruits. Indeed, brown lemurs eat the fruits while still green and deplete the abundance of ripe fruit later available to the ring-tailed lemurs. This behavior may reduce recruitment of tamarind seedlings. In contrast, ring-tailed lemurs benefit the gallery forest by dispersing the few ripe tamarind seeds available.

H. Rasamimanana (✉) • S.M. Raharison • D.R. Tsaramanana • V. Razoliharisoa
École Nomale Supérieure, Université d'Antananarivo, Antananarivo 101, Madagascar
e-mail: rasamitovo@gmail.com; sahobymarin@yahoo.fr; rhevhydonald@yahoo.fr; sifaka9@yahoo.fr

J. Razafindramanana
Nocturnal Primate Research Group, Department of Anthropology, School of Social Science and Law, Oxford Brookes University, Oxford OX3 0BP, UK
e-mail: r_josia@hotmail.com

A.S. Mertl-Millhollen
Department of Anthropology, University of Oregon, Eugene, OR 97401, USA
e-mail: hplam_1998@yahoo.com

K. Blumenfeld-Jones
School of Human Evolution and Social Change, Arizona State University, Tempe, AZ, USA
e-mail: corbeau@linuxmail.org

L. Tarnaud
Unité scientifique 104 du Muséum "Eco-anthropologie et ethnobiologie," Muséum National d'Histoire Naturelle, 75231, Paris Cedex 05, France
e-mail: laurent.tarnaud@free.fr

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_40,

Resume La forêt-galerie de la Réserve de Berenty abrite deux lémuriens indigènes, le Maki, *Lemur catta*, et le sifaka, *Propithecus verreauxi.* Une troisième espèce a été introduite, le lémur brun hybride *Eulemur rufifrons* x *E. collaris*. Les données de régime alimentaire indiquent qu'un mutualisme compétitif, une interaction indirecte, pourrait se produire entre ces trois espèces: *Lemur catta* et *Propithecus verreauxi* empêchent apparemment *Eulemur* d'accéder à certaines ressources, bien que les lémurs bruns soient dominants et soient en compétition directe avec les makis pour les fruits de tamarins. En effet, les lémurs bruns consomment ces fruits encore verts, réduisant d'autant la disponibilité de fruits mûrs aux lémurs à la queue annelée. Ce comportement pourrait aussi avoir un impact négatif sur la régénération des tamariniers. Les makis sont des disperseurs efficaces des graines qui restent disponibles et ont un impact positif sur la forêt galerie.

Introduction

Berenty Reserve has a fragment of gallery forest (Chap. 39) that supports two diurnal lemur species, the ring-tailed lemur, *Lemur catta* and Verreaux's sifaka, *Propithecus verreauxi*. Tamarind trees, *Tamarindus indica*, dominate the forest (Budnitz and Dainis 1975) and are the keystone food resource for ring-tailed lemurs (Sauther 1998). For unknown reasons, the closed canopy forest near the river is declining (Blumenfeld-Jones et al. 2006). Tamarind trees are disproportionately affected and have low recruitment rates. The diurnal lemur fauna has also changed as a result of the 1975 introduction of a few brown lemurs, *Eulemur rufifrons* and *E. collaris* (Pinkus et al. 2006), which hybridized, and now number over 600 individuals (Chap. 39).

Our study had three phases. We began by studying the dietary diversity of Berenty's three diurnal lemur taxa. Secondly, we investigated the presence of direct interspecific competition between brown and ring-tailed lemurs and its potential consequences for tamarind seedling recruitment. Finally, we evaluated whether ring-tailed lemurs facilitate or inhibit tamarind seedling recruitment.

Methods

Dietary Diversity

Between November 2004 and January 2005, we followed two troops of each diurnal lemur taxon from 5:30 to 18:30 h, for a total of 429 h. Daily activities, particularly feeding behaviors, of the troops were recorded using 5-min scan sampling (Altmann 1974). The plant species consumed were identified either in the forest or by botanists in the Laboratory of Eco-anthropology and Ethno-biology, Muséum National d'Histoire Naturelle de Paris; the botany laboratory at Tsimbazaza Zoo; or the Missouri Botanical Garden laboratory in Antananarivo.

Direct Interspecific Competition

From October to December 2004 (wet season) and from August to September 2005 (late dry season), we conducted a study to estimate the pressure of the introduced brown lemurs on tamarind trees and to assess the impact of brown lemurs on the feeding behavior of the native ring-tailed lemurs. We collected data using scan sampling of 12 tamarind trees for a total of 192 h. We recorded each lemur species eating in the focal tamarind tree, noting their feeding times and durations, and the tamarind parts they ate. We also followed a brown lemur troop of 14 individuals for 12 h/day, using instantaneous scan sampling for a total of 336 h. Behavioral scan samples were collected every 5 min and included troop activities, type of food consumed (plant species and parts), and location. In interspecific encounters, we scored interactions between individuals according to four categories (0) no perceptible aggression, (1) threat with no movement or contact, (2) threat accompanied by movement from the aggressor, and (3) threat involving contact. We counted tamarind trees with DBH > 50 cm occurring within the home ranges of the focal troops and assessed food availability by recording phenology data from the species consumed and the tamarind trees censused.

Tamarind Seed Dispersal

Only 3 % of existing Berenty tamarind seedlings and saplings grow directly under the tamarind canopy, and laboratory data indicate that tamarind roots, leaves, bark, and seeds produce allopathic chemicals that inhibit growth (Blumenfeld-Jones et al. 2006). To enhance survival, tamarind seeds must disperse away from the mature trees. Sauther (in Simmen et al. 2006) discovered that tamarind seeds found in ring-tailed lemur feces are viable. However, because the lemurs spend most of their time resting, feeding, and sleeping in tamarind trees (Mertl-Millhollen et al. 2003), we predicted that they would generally deposit seeds under those trees, and therefore not enhance tamarind regeneration.

From 30 September to 6 November 2006, we observed two ring-tailed lemur troops for 10 days each, from 6:00 to18:00 h. We collected behavioral scan samples every 5 min, recording time, location, and activity plus food species and plant part eaten. We measured all tamarind trees in their ranges and visually assessed fruit abundance in the canopies (Chapman et al. 1992). When the lemurs defecated, we recorded whether the feces fell under tamarind canopy and whether there were any tamarind seedlings or saplings within a 2-m radius.

We calculated probable gut passage times and dispersal distances for seeds based on daily records of when lemurs ate tamarind fruit and when they defecated (Dew 2003). Captive lemur food passage rates averaged either 4.75 h (Cabre-Vert and Feistner 1995) or 2.4 h (Overdorff and Rasmussen 1995). Because leaves slow the processing time for digestion (Traveset and Verdú 2002) and lemurs fed upon leaves of various species for 65 % of the feeding scans, we assumed a minimal processing

time of 3 h. We calculated the distance traveled by the lemurs between the locations of fruit consumption and defecation to estimate dispersal distances.

Results

Dietary Diversity

Overall, 60 plant species were exploited by at least one of the three lemur taxa, and the lemurs focused 0.18–19 % of their feeding time on any given plant species (Fig. 40.1). Each lemur species fed on many plants not eaten by the other two, and only five to six plant species were shared between species. The two native lemur species consumed a greater number of plant species than did the introduced brown lemurs (43, 31, and 20 species used by *Propithecus verreauxi*, *Lemur catta,* and *Eulemur*, respectively).

Direct Interspecific Competition

Of the three diurnal lemur taxa inhabiting the reserve, brown lemurs are the greatest users of tamarind trees; 50 % of the sampled trees were exploited by brown lemurs for 80 % of the observation time. Ring-tailed lemurs exploited less than 30 % of the sampled tamarind trees and spent 35 % of the observation time on these trees. *Tamarindus indica* unripe fruit dominated the brown lemurs' diet during the late dry season (40 %). Brown lemurs were the greatest consumers of buds, new leaves, and green fruit of tamarind trees (Wilcoxon, $z=0.2$; $N=5$; $x=3$; $P=0.05$). Because brown lemurs ate the tamarind fruit when green, they depleted the abundance of ripe fruit later available to the ring-tailed lemurs: 72 % of the unripe fruits available within the home range of the focal troop were eaten by brown lemurs.

During interspecific encounters, brown lemurs dominated ring-tailed lemurs. Interspecific food competition was expressed through aggressive conflict. The brown lemurs entered tamarind patches occupied by ring-tailed lemur troops 24 times in 28 encounters; we seldom saw a ring-tailed troop enter tamarind patches already occupied by brown lemurs. Brown lemur intrusions had an average conflict level of 2.

Each ring-tailed lemur troop's range overlapped with those of several brown lemur troops. During the wet season, we counted four troops of brown lemurs ranging within the territory of one ring-tailed lemur troop. This number was tripled in the late dry season when unripe tamarind fruits were available in the area. This could explain the high competition for unripe tamarind fruit between brown and ring-tailed lemurs: because there was low tamarind fruit productivity in the rest of the reserve, the brown lemur troops moved to areas where they could find resources, especially unripe tamarind fruit.

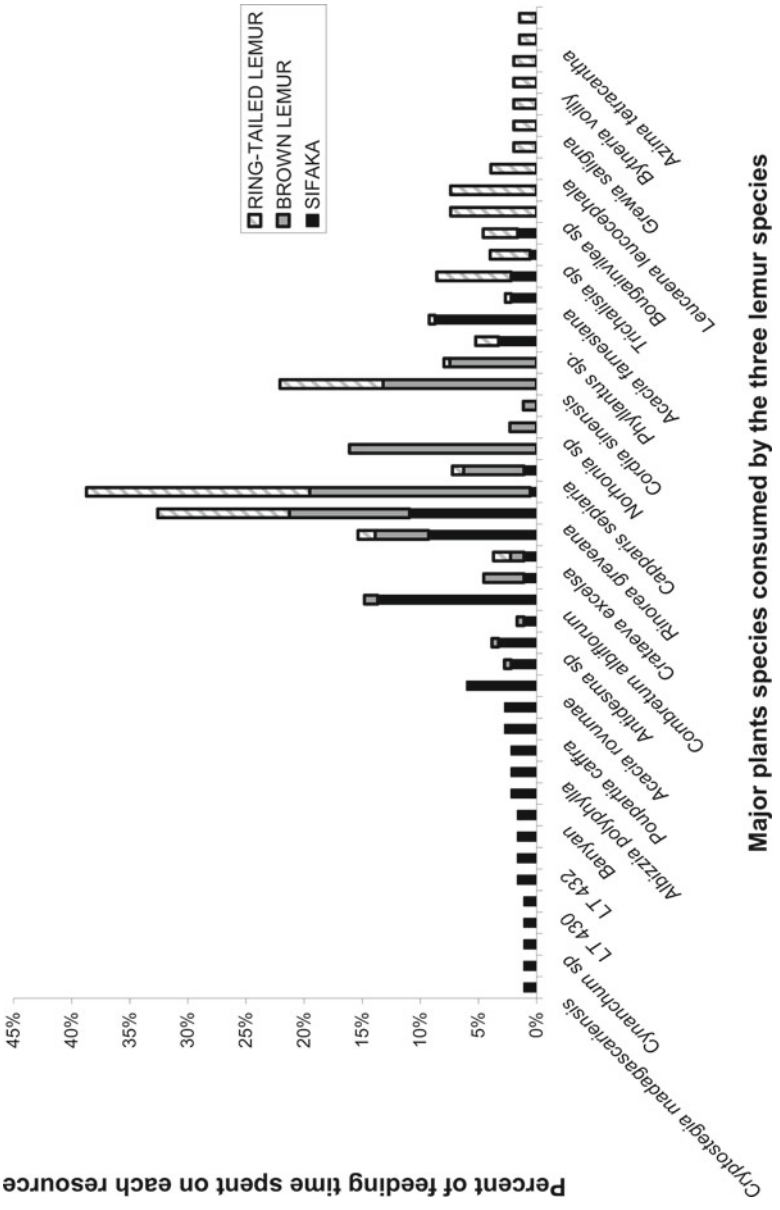


Fig. 40.1 Percentage time spent by each lemur species feeding on food plant species in Berenty

Tamarind Seed Dispersal

One ring-tailed lemur troop home range was 6.5 ha, containing 117 tamarinds of DBH >25 cm and 7.5 % of the potential ripe fruit abundance. The other was 10.1 ha, containing 187 tamarinds with 3 % fruit abundance. Overall, 55 % of their feeding was on tamarinds: 41 % on leaves and leaf buds and 59 % on fruit. Within the home ranges we found a total of 271 tamarind seedlings: 35 under tamarind tree canopy and 236 away from it.

Ninety-five percent of the fruit feeding observed occurred between 6:00 and 11:00 h and 15:00 and 18:00 h, while 87 % of the defecations occurred before 8:00 h and after 14:00 h. For both troops, the longest seed dispersal distance corresponded to the greatest width of the troops' ranges (300 m and 486 m, respectively). Mean daily travel distances were 241 ± 62 m and 363 ± 61 m, respectively.

Within a 2-m radius of where the feces fell, we found 128 seedlings away from the tamarind canopy and only 5 under tamarind canopy. Of our recorded 417 defecations, 58 % were deposited away from tamarind canopy (Mertl-Millhollen et al. 2011).

Discussion

The introduced brown lemurs at Berenty share resources to a significant degree with ring-tailed lemurs, and interspecific competition, particularly for unripe *Tamarindus indica* fruits, could have a negative impact on the long-term viability of the indigenous lemur populations. This is exacerbated by the fact that brown lemurs generally dominate ring tails in territorial confrontations. However, the native lemur species have substantially broader diets than the brown lemurs. Brown lemurs, as opportunistic foragers, are known to have a smaller dietary range than other diurnal lemurs, even when they do not experience interspecific competition, as on Mayotte Island where no other lemur species occur (Tarnaud 2004). But the less diverse diet of Berenty's introduced lemurs may also be indicative of indirect competition, or "competitive mutualism" (Pianka 1981), which posits that two species with partially overlapping diets can prevent a third species from gaining access to certain resources. Thus, the native diurnal lemurs may be depleting the resources that could potentially be used by brown lemurs. On the other hand, the wider dietary diversity observed in ring-tailed lemurs may be a consequence of direct competition between brown lemurs and ring tails. Indeed, Simmen et al. (2003) showed that the dietary overlap of the species is high, but ring-tailed lemurs might be more efficient at coping with fibrous plant materials than *Eulemur*. In either case, such ecological processes may serve to limit the rate of brown lemur increase or decline of the indigenous species.

There is a possibility that more habitat could open up in future for the ring tails, who could then shift their range away from the closed canopy forest near the river (Mertl-Millhollen et al. 2006; Razafindramanana 2011), which contains the largest brown lemur population (Razafindramanana 2005). An open forest along an ancient river bed appears to be developing increased canopy cover and could provide new feeding areas with less harassment from brown lemurs.

Contrary to our expectation that lemurs would generally disperse tamarind seeds under the canopy where they would encounter allopathic chemicals retarding their growth, our focal ring-tailed lemur troops were highly effective seed dispersers, distributing over 50 % of the seeds away from the canopy of mature tamarind trees. The *Eulemur* hybrids are also likely to disperse tamarind seeds, and this is the subject of ongoing study. Not all of the indigenous lemurs are so beneficial to the forest. Verreaux's sifakas are known to be primarily seed predators. None of the nocturnal taxa (*Lepilemur* and *Microcebus*), however, are known to swallow such large seeds (Ganzhorn et al. 1999).

Our combined study suggests that the native and introduced lemurs of Berenty are able to share resources because of indirect interactions like competitive mutualism. Despite the decline of the gallery forest near the river and the behavioral and feeding dominance shown by the introduced brown lemurs, the overall population size of the native lemur species in Berenty has not decreased (Jolly et al. 2006; Razafindramanana 2011). The complexity of these interspecific interactions, the dietary flexibility of the indigenous lemur species, and the possibility of new areas of habitat, augur well for the future coexistence of these taxa (Razafindramanana 2011).

Conclusions

Our study indicates that the influences and impacts of Berenty's introduced brown lemurs on the area's indigenous inhabitants are more complex and less destructive than previously thought. Despite their dominance in territorial disputes over feeding areas and their fondness for unripe tamarind seeds, brown lemurs eat only a fraction of the plant species consumed by the other lemur species present in the reserve. Either the two diurnal species, *Lemur catta* and *Propithecus verreauxi*, deny the brown lemurs access to many food resources through competitive mutualism, or they themselves are being driven to broaden their diets by the feeding behavior of brown lemurs. In either case, the species appear to be developing ways of sharing Berenty's food resources, an interpretation borne out by the observation that ring-tailed lemur populations are not in decline. *Eulemur* may also, as in the case of *L. catta*, assist tamarind recruitment by dispersing seeds away from the mature forest.

Acknowledgments We thank the de Heaulme family for preserving Berenty and permitting us to do the research. The studies were funded in part by the Wildlife Preservation Trust International, the Museum National d'Histoire Naturelle, the Fyssen Foundation, and the Committee for Research and Exploration, National Geographic Society.

References

Altmann J (1974) Observational study of behaviour sampling methods. Behaviour 49:227–265

Blumenfeld-Jones K, Randriamboavonjy TM, Williams G, Mertl-Millhollen AS, Pinkus S, Rasamimanana H (2006) Tamarind recruitment and long-term stability in the gallery forest at Berenty, Madagascar. In: Jolly A, Sussman RW, Koyama N, Rasamimanana H (eds) Ringtailed lemur biology. Springer, New York, pp 69–85

Budnitz N, Dainis K (1975) *Lemur catta*: ecology and behavior. In: Tattersall I, Sussman RW (eds) Lemur biology. Plenum, New York, pp 219–235

Cabre-Vert N, Feistner ATC (1995) Comparative gut passage time in captive lemurs. Dodo J Wildl Preserv Trust 31:76–81

Chapman CA, Chapman LJ, Wangham R, Hunt K, Gebo D, Gardner L (1992) Estimators of fruit abundance of tropical trees. Biotropica 24(4):527–531

Dew JL (2003) Feeding ecology and seed dispersal. In: Setchell JM, Curtis DJ (eds) Field and laboratory methods in primatology: a practical guide. Cambridge University Press, Cambridge, pp 174–183

Ganzhorn JU, Fietz J, Rakotovao E, Schwab D, Zinner D (1999) Lemurs and the regeneration of dry deciduous forest in Madagascar. Conserv Biol 13:794–804

Jolly A, Rasamimanana H, Braun M, Dubovick T, Mills C, Williams G (2006) Territory as bet-hedging: *Lemur catta* in a rich forest and an erratic climate. In: Jolly A, Sussman RW, Koyama N, Rasamimanana H (eds) Ringtailed lemur biology. Springer, New York, pp 187–207

Mertl-Millhollen AS, Blumenfeld-Jones KC, Raharison SM, Tsaramanana DR, Rasamimanana H (2011) Tamarind tree seed dispersal by ring-tailed lemurs. Primates 52:391–396

Mertl-Millhollen AS, Moret ES, Felantsoa D, Rasamimanana H, Blumenfeld-Jones KC, Jolly A (2003) Ring-tailed lemur home ranges correlate with food abundance and nutritional content at a time of environmental stress. Int J Primatol 24:969–985

Mertl-Millhollen AS, Rambeloarivony H, Miles W, Kaiser VA, Gray L, Dorn LT, Williams G, Rasamimanana H (2006) The influence of tamarind tree quality and quantity on *Lemur catta* behavior. In: Jolly A, Sussman RW, Koyama N, Rasamimanana H (eds) Ringtailed lemur biology. Springer, New York, pp 102–118

Overdorff DJ, Rasmussen MA (1995) Determinants of nighttime activity in 'diurnal' lemurid primates. In: Alterman L, Doyle GA, Izard MK (eds) Creatures of the dark: the nocturnal prosimians. Plenum, New York, pp 61–74

Pianka ER (1981) Competition and niche theory. In: May RM (ed) Theoretical ecology. Blackwell, Oxford, pp 167–196

Pinkus S, Smith JNM, Jolly A (2006) Feeding competition between introduced *Eulemur fulvus* and native *Lemur catta* during the birth season at Berenty Reserve, southern Madagascar. In: Jolly A, Sussman RW, Koyama N, Rasamimanana H (eds) Ringtailed lemur biology. Springer, New York, pp 119–140

Razafindramanana J (2005) Impacts de l'introduction des lémurs bruns hybrides sur la productivité des Tamariniers dans la Reserve de Berenty – Sud de Madagascar. Mémoire de fin d'étude CAPEN ENS

Razafindramanana J (2011) Behavioural ecology of sympatric lemur species *Lemur catta* and *Eulemur* sp. in forest fragments, South-eastern Madagascar. Unpublished PhD thesis, Oxford Brookes University, Oxford

Sauther ML (1998) Interplay of phenology and reproduction in ring-tailed lemurs: implications for ring-tailed lemur conservation. Folia Primatol 69(S1):309–320

Simmen B, Hladik A, Ramasiarisoa P (2003) Food intake and dietary overlap in native *Lemur catta* and *Propithecus verreauxi* and introduced *Eulemur fulvus* at Berenty, southern Madagascar. Int J Primatol 5:949–968

Simmen B, Sauther ML, Soma T, Rasamimanana H, Sussman RW, Jolly A, Tarnaud L, Hladik A (2006) Plant species fed on by *Lemur catta* in gallery forests of the southern domain of Madagascar. In: Jolly A, Sussman RW, Koyama N, Rasamimanana H (eds) Ringtailed lemur biology. Springer, New York, pp 55–68

Tarnaud L (2004) Ontogeny of feeding behaviour of *Eulemur fulvus* in the dry forest of Mayotte. Int J Primatol 25:803–824

Traveset A, Verdú M (2002) A meta-analysis of the effect of gut treatment on seed germination. In: Levy DJ, Silva WR, Galetti M (eds) Seed dispersal and frugivory: ecology, evolution and conservation. CABI Publishing, New York, pp 339–350

Chapter 41
Why Do Some Ring-Tailed Lemurs Feeding on *Leucaena* Not Suffer from Alopecia Syndrome?

Vonjy Nirina Andrianome, Hajarimanitra Rambeloarivony, and Hantanirina Rasamimanana

Abstract Alopecia (i.e. hair loss) in ring-tailed lemurs, or "bald lemur syndrome", appeared in Berenty Reserve in the 1990s. The consumption of the leaves of *Leucaena leucocephala*, an introduced tree rich in toxic mimosine, has been linked to hair loss. Here, we show that individuals respond differently to the toxin, and bad fur condition is also influenced by other factors, particularly dietary diversity and social stress.

Resume L'alopécie (i. e. perte de poils) chez *Lemur catta*, ou « syndrome des lémuriens chauves » est apparue dans la Réserve de Berenty au cours des années 1990. La consumation de feuilles de *Leucaena leucocephala*, un arbre qui contient une toxine appelée mimosine, conduit à une perte de poil. Ici nous montrons que les individus répondent différemment à cette toxine, la condition de la fourrure des animaux étant aussi influencée par d'autres facteurs tels que la diversité du régime et le stress social.

V.N. Andrianome
Département des Eaux et Forêts, Ecole Supérieure des Sciences Agronomiques, Université d'Antananarivo, Antananarivo, Madagascar
e-mail: vonjynirina@gmail.com

H. Rambeloarivony (✉)
Ecole Nomale Supérieure, Université d'Antananarivo, Antananarivo 101, Madagascar

Department of Zoology and Entomology, University of Fort Hare, Private Bag X1314, Alice 5700, South Africa
e-mail: haja.kely2010@gmail.com

H. Rasamimanana
Ecole Nomale Supérieure, Université d'Antananarivo, Antananarivo 101, Madagascar
e-mail: hantani1@yahoo.fr

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_41,

Introduction

Ring-tailed lemurs have been studied in Berenty Private Reserve since the 1960s. Alopecia in ring-tailed lemurs, or "bald lemur syndrome," first appeared in the area in the late 1990s (Jolly et al. 2006). The majority of individuals affected by alopecia live in the forest fragment dominated by introduced planted species (Crawford et al. 2006; Jolly et al. 2009a, b). The de Heaulme family, owners of Berenty Private Reserve, planted the exotic *Leucaena leucocephala* in the Ankoba forest because of its multiple uses (Crawford et al. 2006). *L. leucocephala* contains an alkaloid called mimosine, which can be degraded by some species but not by others. The toxin causes alopecia, weight loss, skin diseases, appetite loss, retarded growth, and cataracts in rabbits, sheep, and goats (Sriskandarajah and Komolong 1986; Malini et al. 1989) and inhibits the production of eggs and causes a delay in sexual maturation in poultry (Rahman and Dewan 1986; Tangengjaja and Sarmanu 1986; Ekpenyong 1989).

Crawford et al. (2004) proposed that "bald lemur syndrome" was either due to malnutrition or to a toxin. Because the majority of the individuals affected by the disease live in the *Leucaena* areas, this hypothesis found favor (Crawford et al. 2004, 2006; Soma 2006; Chap. 42). Here, we investigated the relationship between fur condition and the consumption of *Leucaena*, as well as other factors potentially influencing alopecia in Berenty's lemurs, namely dietary diversity and social relationships.

Methods

Research Site and Subjects

We conducted the study in Ankoba forest in the northern section of Berenty Private Reserve (25°0.29′S, 46°19.37′E, Madagascar) (Fig. 41.1). The site not only comprises 40 ha of mature secondary forest dominated by introduced plant species such as *Pithecellobium dulce* and *L. leucocephala* but also includes native plant species like *Rinorea greveana* and *Tamarindus indica*, the latter being a keystone food source for Berenty's ring-tailed lemurs (Mertl-Millhollen et al. 2006; Simmen et al. 2006).

We focused on 20 adult females belonging to 4 ring-tailed lemur groups living in the *Leucaena* affected area. Two groups (C2A with 5 females and T1A with 6 females) ranged in areas in which *Leucaena* had been removed but still showed some regrowth; the other two groups (River with 5 females and Standing Stone with 4 females) were in the area where *Leucaena* has not been removed. All females were observed over 8 months from April to November 2005. Data on aggression were only available for three (C2A, River, and Standing Stone) of the four groups. Only females were included in the study, because female ring-tailed lemurs are philopatric, while males often disperse.

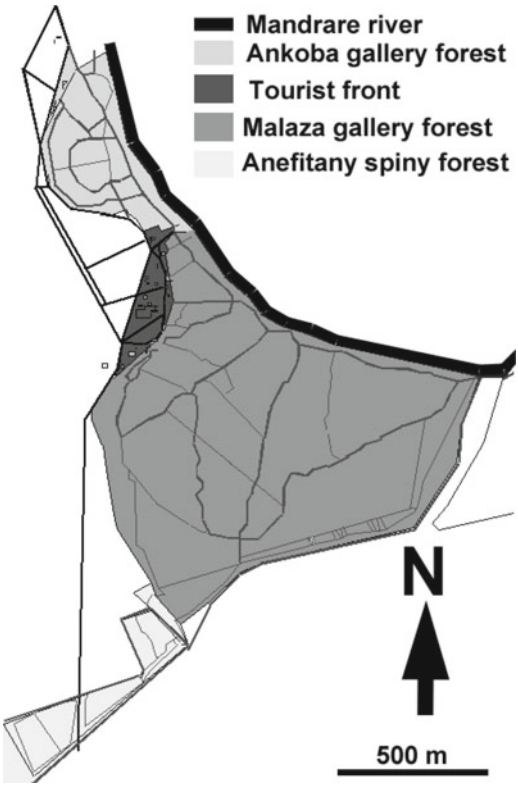


Fig. 41.1 Map of Berenty Private Reserve showing the location of Ankoba, the study site

Estimation of Fur Condition and Behavioral Observations

We used the criteria of Berg et al. (2009) for recording fur condition, ranging from 0 (perfectly fluffy) to 5 (half or more of body or tail hairless). Body and tail condition were measured separately and summed. For the analyses, we used the fur condition of the animals at the end of the study.

We collected behavioral data 4 days a week during the animals' active hours (06:00–12:00 and 14:00–18:00) using 15 min continuous focal sampling (Altmann 1974), for a total observation time of 1180 h. During observations we recorded all activities, including feeding behavior and social interactions.

Data Analysis

We defined "cultivated species" as all species that were planted for either agricultural or ornamental purposes and are not native to the region. Observation duration

differed between individuals, so all variables were controlled for observation time. The time spent feeding on *Leucaena* and the number of aggressive acts received were sorted and given values from 1 to 14 in accordance with increasing frequency. For each individual, the values for feeding on *Leucaena* and for aggressive acts received were added to compute an "index of constraint."

For data analysis we used Kendall's Tau correlation, as the data set had a large number of tied ranks (i.e. several animals showed the same index of fur condition). Partial correlation was used to investigate the relationship between cultivated species and fur condition while controlling for the effects of *Leucaena*. Semipartial correlation was used to control for the effect of time spent feeding on *Leucaena* or the effect of number of aggressive acts received while examining the link between *Leucaena* or aggression and fur condition.

Results

The index of fur condition was positively correlated with the time spent feeding on *Leucaena* ($r_t = 0.569$, $P < 0.01$, $N = 20$; Fig. 41.2), with the number of aggressive acts received ($r_t = 0.426$, $P < 0.05$, $N = 14$; Fig. 41.3), with the time spent feeding on cultivated species ($r_t = 0.569$, $P < 0.01$, $N = 20$), and with the number of cultivated species included in the diet ($r_t = 0.525$, $P < 0.01$, $N = 20$). In addition, time spent feeding on *Leucaena* correlated positively with the time spent feeding on cultivated species ($r_t = 0.832$, $P < 0.01$, $N = 20$) and with the number of introduced plant species included in the animals' diet ($r_t = 0.516$, $P < 0.01$, $N = 20$). However, when controlling for the effect of *Leucaena* on fur condition, partial correlation showed that neither the number of introduced plant species included in the diet ($r_t = 0.312$, $P = 0.194$, $N = 17$) nor the time animals spent feeding on them ($r_t = 0.312$, $P = 0.194$, $N = 17$) were significantly correlated with fur condition.

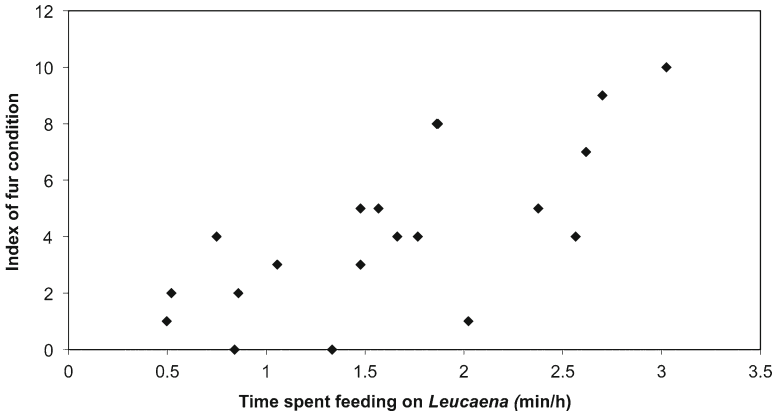


Fig. 41.2 Relationship between fur condition and the time spent feeding on *Leucaena*

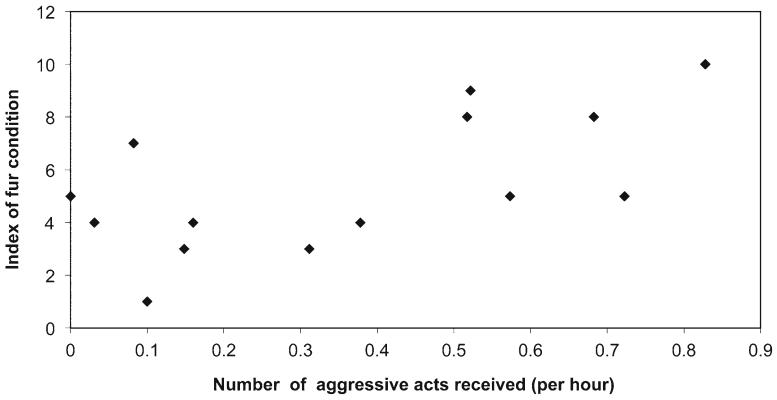


Fig. 41.3 Relationship between fur condition and number of aggressive acts received

On the other hand, semipartial correlation showed that both time spent feeding on *Leucaena* and aggressive acts received are significantly and positively correlated with fur condition, even when controlling for one (controlling the effects of the time spent feeding on *Leucaena*: $t=3.160$, $P<0.01$, $r=0.561$) or the other (controlling the effects of aggressive acts received: $t=2.867$, $P<0.05$, $r=0.509$) independent variable. Some individuals who consumed large amounts of *Leucaena*, however, remained in good condition, while others who consumed small amounts of *Leucaena* had bad hair loss. The "index of constraint" was positively correlated with the fur condition index ($r_t=0.639$, $P<0.01$, $N=14$), so individuals that received more aggressive acts and also ate more *Leucaena* had a higher fur condition index. This finding could explain, for example, the good fur condition of the dominant female in C2A (index of fur condition = 1) despite her high consumption of *Leucaena* (2.02 min/h, MIN = 1.06, MAX = 3.02), as she received only 0.1 aggressive acts per hour (MIN = 0, MAX = 0.83). On the other hand, a subordinate female in C2A had bad fur (index of fur condition = 5) even though she ate only a small amount of *Leucaena* (1.48 min/h) as she received a high number of aggressive acts (0.72/h).

Discussion

The mimosine present in *Leucaena* has been proposed as the cause of "bald lemur syndrome" in Berenty (Crawford et al. 2006; Jolly 2009a, b). Our results confirmed that, on average, ring-tailed lemurs ingesting more *Leucaena* lost more hair than others. However, certain females coped better with the toxin than others; Crawford et al. (unpublished data) found mimosine in only 15 of 29 individuals observed consuming the plant, which might be due to individual variation in the capacity for detoxification.

There was a superficial correlation between cultivated species and fur condition. However, after controlling for the effects of *Leucaena*, neither the time spent feeding on cultivated species nor the number of cultivated species included in the diet explained the fur condition of the animals. In the study area, the forest is dominated by introduced plant species, particularly *Azadirachta indica*, *L. leucocephala*, and *Pithecellobium dulce* (Jolly et al. 2006). *Lemur catta* fed on them heavily, maybe due to the rarity of keystone resources, in particular *Tamarindus indica* (Simmen et al. 2003; 2006; Soma 2006).

Furthermore, bald lemur syndrome appears to be influenced by social factors. Ring-tailed lemurs live in hierarchical groups (Jolly 2003), and in general, dominant females encounter less aggression than subordinates. Alopecia was positively correlated with the frequency of agonistic behaviors received. Furthermore, cortisol, the "stress hormone" is known to decrease hair growth (Pride 2003), so high levels of social stress may enhance baldness.

Finally, a synergistic effect between the toxin and social stress may explain individual variation in alopecia. While dominant females seemed to be more resistant to the toxin, individuals that were attacked more often had worse fur condition than others that spent similar amounts of time feeding on *Leucaena*. Not surprisingly, the worst fur condition (fur condition index of 10, a female in River group) was found in the individual most frequently targeted for aggressive acts, who also ate high quantities of *Leucaena*.

Acknowledgments We thank the de Heaulme family for permission to conduct research in Berenty Reserve, and A. Jolly and G. C. Crawford for providing background data on bald lemur syndrome and for supervising the research. For help and advice in the field we thank the Rakotomalala family and the Berenty Reserve staff and field researchers, especially W. Berg. We thank I. Porton and the Saint Louis Zoo staff who provided financial support for the study, and the Prosimians 2007 congress organizers, especially J. Masters and J. Ratsimbazafy.

References

Altmann J (1974) Observational study of behavior sampling methods. Behavior 49:227–265

Berg W, Jolly A, Rambeloarivony H, Andrianome V, Rasamimanana H (2009) A scoring system for coat and tail condition in ringtailed lemurs, *Lemur catta*. Am J Primatol 71:183–190

Crawford GC, Jolly A, Rasamimanana HR, Ostapak S. Investigation of *Leucaena leucocephala* toxicity in ring-tailed lemurs *(Lemur catta)* at Berenty Reserve, Madagascar. Report to National Geographic Committee for Research and Exploration Grant no. 8018-006 (Unpublished data)

Crawford GC, Ichino S, Jolly A, Koyama N, Ostpak S, Rafanomiazantsoa F, Rambeloarivony H, Rasamimanana HR, Simmen B, Soma T, Tew A, Andrianome VN, Andriafaneva LE, Clarke L (2004) *Leucaena leucocephala*: a probable cause of alopecia in ring-tailed lemurs (*Lemur catta*). Folia Primatol 75:159

Crawford GC, Andriafaneva L-E, Blumenfeld-Jones K, Calaba G, Clarke J, Gray L, Ichino S, Jolly A, Koyama N, Mertl-Millhollen A, Ostpak S, Pride RE, Rasamimanana HR, Simmen B, Soma T, Tarnaud L, Tew A, Williams G (2006) Bald lemur syndrome and the miracle tree: alopecia associated with *Leucaena leucocephala* at Berenty Reserve, Madagascar. In: Jolly A, Koyama N, Rasamimanana HR, Sussman RW (eds) Ringtailed lemur biology: *Lemur catta* in Madagascar. Springer, New York, pp 332–342

Ekpenyong TE (1989) Effect of *Leucaena* leaf meal in layer ration. Leucaena Res Rep 10:54
Jolly A (2003) *Lemur catta*, ring-tailed lemur, maki. In: Goodman SM, Benstead JP (eds) The natural history of Madagascar. University of Chicago Press, Chicago, pp 1329–1331
Jolly A (2009a) Coat condition of ringtailed lemurs, *Lemur catta*, at Berenty Reserve, Madagascar. I. Differences by age, sex, density and tourism, 1996–2006. Am J Primatol 71:191–198
Jolly A (2009b) Coat condition of ringtailed lemurs, *Lemur catta*, at Berenty Reserve, Madagascar. II. Coat and tail alopecia associated with *Leucaena leucocephala*, 2001–2006. Am J Primatol 71:199–205
Jolly A, Koyama N, Rasamimanana H, Crowley H, Williams G (2006) Berenty Reserve: a research site in southern Madagascar. In: Jolly A, Koyama N, Rasamimanana HR, Sussman RW (eds) Ringtailed lemur biology: *Lemur catta* in Madagascar. Springer, New York, pp 32–42
Malini BP, Gloridoss RG, Munne Gowda MK, Govindaiah MG (1989) Preliminary studies on the effects of feeding *Leucaena leucocephala* to rabbits. Leucaena Res Rep 10:31–32
Mertl-Millhollen AS, Rambeloarivony H, Miles W, Kaiser VA, Gray L, Dorn LT, Williams G, Rasamimanana H (2006) The influence of tamarind tree quality and quantity on *Lemur catta* behavior. In: Jolly A, Koyama N, Rasamimanana HR, Sussman RW (eds) Ringtailed lemur biology: *Lemur catta* in Madagascar. Springer, New York, pp 102–118
Pride RE (2003) The socio endocrinology of group size in *Lemur catta*. Ecology and evolutionary biology. Unpublished PhD thesis, Princeton University, Princeton, NJ
Rahman MH, Dewan ML (1986) Effects of *Leucaena leucocephala* seed meal on ducks. Leucaena Res Rep 7:24–25
Simmen B, Hladik A, Ramasiarisoa P (2003) Food intake and dietary overlap in native *Lemur catta* and *Propithecus verreauxi* and introduced *Eulemur fulvus* at Berenty, Southern Madagascar. Int J Primatol 24:949–968
Simmen B, Sauther ML, Soma T, Rasamimanana H, Sussman RW, Jolly A, Tarnaud L, Hladik A (2006) Plant species fed on by *Lemur catta* in gallery forests of the southern domain of Madagascar. In: Jolly A, Koyama N, Rasamimanana HR, Sussman RW (eds) Ringtailed lemur biology: *Lemur catta* in Madagascar. Springer, New York, pp 55–68
Soma T (2006) Tradition and novelty: *Lemur catta* feeding strategy on introduced tree species at Berenty Reserve. In: Jolly A, Koyama N, Rasamimanana HR, Sussman RW (eds) Ringtailed lemur biology: *Lemur catta* in Madagascar. Springer, New York, pp 141–159
Sriskandarajah N, Komolong M (1986) Mimosine tolerance of sheep and goats fed *Leucaena* in Papua New Guinea. Leucaena Res Rep 7:99–101
Tangengjaja B, Sarmanu (1986) Effect of *Leucaena* leaf meal and pure mimosine on sexual maturity of layers. Leucaena Res Rep 7:83–84

Chapter 42
The Impact of Alopecia Syndrome on Female Reproductive Parameters in Ring-Tailed Lemurs (*Lemur catta*) in Berenty Reserve, Madagascar

Shinichiro Ichino, Takayo Soma, and Naoki Koyama

Abstract Alopecia syndrome was identified in ring-tailed lemurs in the Berenty Reserve, southern Madagascar, in the late 1990s and spread extensively in 2001–2003. A ring-tailed lemur population inhabiting a 14.2-ha area has been studied with individual identifications since 1989. To understand the alopecia syndrome, we recorded the fur condition of all individuals (around 100 lemurs) in 2001, 2004, and 2005. The number and ratio of alopecic lemurs decreased over time from 19 lemurs (22%) in 2001 to 6 (6%) in 2004, to only 3 (3%) in 2005. Of the 19 alopecic lemurs in 2001, 15 were females and only 4 were males. They ranged in age from 2 to 15 years, with by far the highest occurrence of alopecia among young lemurs (2 years old: 55%; 3 years old: 50%; and 4 years old: 40%). Nine of the 19 animals (47%) recovered their fur condition over 3 years. The mortality rate of the alopecic females over the same period was 43%, similar to that of nonalopecic females (40%) as was their birth rate. Infant mortality was higher for alopecic mothers (57%) than for nonalopecic females (19%), although the difference was not significant.

Resume Le syndrome d'alopécie qui touche les lémurs cattas de la Réserve de Berenty, située au sud-est de Madagascar, a été identifié à la fin des années 90, et s'est répandu entre 2001 et 2003. Une population de lémurs cattas, occupant une zone d'étude de 14.2 ha, et dont les individus sont tous suivis individuellement est étudiée depuis 1989. Pour mieux comprendre le syndrome d'alopécie, nous avons

S. Ichino (✉)
Unit of Behavioral Ecology and Sociobiology, German Primate Center, Kellnerweg 4, D- 37077 Göttingen, Germany

Genome Diversity Section, Primate Research Institute, Kyoto University, Kanrin, Inuyama-city, Aichi 484-8506, Japan
e-mail: shinichiro.ichino@gmail.com

T. Soma • N. Koyama
The Center for African Area Studies, Kyoto University, 46 Shimoadachi-cho, Yoshida, Sakyo-ku, Kyoto 606-8501, Japan
e-mail: soma@jambo.africa.kyoto-u.ac.jp; mv2z67@bma.biglobe.ne.jp

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_42,

évalué la condition de la fourrure de tous les individus (environ 100 lémurs) en 2001, 2004 et 2005. Le nombre et la proportion de lémurs touchés par le syndrome d'alopécie a diminué, passant de 19 lémurs (22%) en 2001 à six (6%) en 2004, et seulement trois (3%) en 2005. Sur les 19 lémurs alopéciques observés en 2001, 15 étaient des femelles et seulement quatre des mâles. Les animaux atteints étaient âgés de deux à 15 ans, mais étaient bien plus souvent des jeunes (deux ans : 55% ; trois ans : 50% ; quatre ans : 40%). Neuf animaux sur 19 (47%) ont recouvré une bonne condition de fourrure en trois ans. L'alopécie n'a affecté ni le taux de mortalité des femelles (43% pour 40%), ni leur taux de natalité. La mortalité infantile des femelles alopéciques était plus élevée (57%) que celles des femelles non alopéciques (19%), bien que cette différence ne soit pas significative.

Introduction

Ring-tailed lemurs (*Lemur catta*) in Berenty Reserve, south-eastern Madagascar, have been studied since the 1960s (Jolly 1966, 2012; Jolly et al. 2002). Alopecia syndrome was identified in the population in the late 1990s and spread extensively between 2001 and 2003 (Crawford et al. 2006). The most severely afflicted animals lost most of their body fur.

Alopecia has been reported in many mammals including primates (chimpanzees in Gombe: Wallis and Lee 1999; gorillas in Buwndi National Park: Macfie 1996; Mudakikwa 2001; Kalema-Zikusoka et al. 2002) and is most commonly caused by mite infestations. Until the detection of alopecia, however, no evidence of infectious diseases had been found in the ring-tailed lemurs of Berenty. An introduced plant (*Leucaena leucocephala*) was targeted as a potential cause of the syndrome (Crawford et al. 2006), and several researchers focused their research accordingly (Jolly 2009b; Chaps. 39 and 41), although the causes and consequences of the syndrome remain obscure. A program to remove *Leucaena* trees from the tourist area began in late 2004, although lemurs continue to eat the leaves of some small trees remaining in the forest (Jolly et al. 2006; Chap. 39; Ichino personal observation).

We believe the causes and long-term consequences of the syndrome can best be understood through detailed information on individuals acquired over several years. Our group has been studying a population of known ring-tailed lemur individuals within a 14.2-ha area since 1989 (Koyama et al. 2001, 2002). To add to the knowledge base of alopecia in Berenty's ring-tailed lemurs, we contribute our observations and discuss the syndrome's impact on the population over several years.

Methods

Berenty is a 250-ha private reserve located in south-eastern Madagascar. Its semideciduous gallery forest is dominated by tamarind trees (*Tamarindus indica*), and the area is bounded by the Mandrare River and commercial sisal plantations (Jolly 2004; Jolly et al. 2006; Chap. 39).

Ring-tailed lemurs (*Lemur catta*) are diurnal animals that live in multimale, multifemale groups consisting of around 15 individuals. Approximately 100 individuals comprising seven troops were present in the area during our study. Ages and kin relationships were known for all individuals born after 1989 (Koyama et al. 2001, 2002). We monitored the population over three study periods, in which we recorded fur condition (1) April 2001 to January 2002, (2) September 2004, and (3) November 2005 to January 2006. The first two study periods predated the *Leucaena* eradication project.

Scoring fur condition without observer bias is difficult, although methods have been proposed (Berg et al. 2009; Jolly 2009a). We minimized bias by considering only those individuals with severe hair loss alopecic, corresponding to the "bald (body fur score 5)" and "sheared (body fur score 4)" criteria of Berg et al. (2009). These extreme conditions are unlikely to be overlooked by different observers. The fur condition of all individuals was recorded at least twice when the focal animals were on the ground, and scores were assigned by a single observer (Ichino).

Most of our data were collected between 2001 and 2002, when alopecia syndrome was most severe. Interannual comparisons included data for September 2001 and 2004 and November 2005. We compared mortality and birth rates of females, and infant mortality for alopecic and nonalopecic mothers using the data collected in 2001 and 2004. When estimating mortality, we considered only females because ring-tailed lemurs show female philopatry, and males sometimes emigrate to troops outside the study area (Jones 1983; Sussman 1992; Koyama et al. 2002).

Results

Characteristics of Alopecia Syndrome

During the 10-month study period in 2001–2002, the fur condition of the lemurs changed seasonally from relatively good in April 2001 (the end of rainy season; Fig. 42.1), becoming progressively worse through the dry season until September, when fruit was scarcest. Their fur condition was still bad in January 2002, the early rainy season (Fig. 42.2), when several lemurs were bald (Fig. 42.3). However, new fur growth appeared at that time. The animals' fur condition also changed from year to year. In 2001, 19 lemurs (21.6% of the population) were alopecic, but the proportion decreased to 6 lemurs (5.8%) in 2004, and only 3 (2.7%) in 2005.

Fur condition was variable among troops (Table 42.1). In 2001, alopecic lemurs were observed in four of seven study troops, especially Troop C1 (61.1%). Troops with alopecic lemurs occupied the area most visited by tourists comprising a number of bungalows surrounded by exotic plant species (Fig. 42.4). There was also a great deal of individual variation in fur condition, with alopecic females outnumbering alopecic males every year. In 2001, we recorded 14 females and only 5 males with severe hair loss; in 2004, this number dropped to four females and two males; and by 2005, we noted only two females and one male with alopecia. Because of the

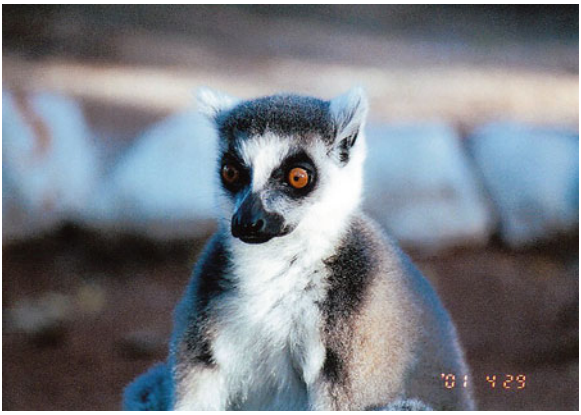


Fig. 42.1 A ring-tailed lemur (ME-8993♀) with good fur condition in April 2001 (photo by Ichino)

Fig. 42.2 The same ring-tailed lemur (ME-8993♀) with bad fur condition in January 2002 (photo by Ichino)

Fig. 42.3 A bald ring-tailed lemur (ME-8994♀) in January 2002 (photo by Ichino)

Table 42.1 The number and percentage of alopecic lemurs in each troop in September 2001 and 2004

	2001			2004		
	No. alopecic			No. alopecic		
Troop	Troop size	Lemurs	%	Troop size	Lemurs	%
C1	18	11	61.1	21	0	0.0
C2A	9	2	22.2	12	2	16.7
C2B	6	1	16.7	1	0	0.0
CX	11	0	0.0	9	0	0.0
T1A	13	0	0.0	16	1	6.3
T1B	13	5	38.5	11	2	18.2
T2	18	0	0.0	19	0	0.0
YF	–	–	–	14	1	7.1
Total	88	19	21.6	103	6	5.8

Note: Troop YF did not exist in September 2001 (see Ichino and Koyama 2006)

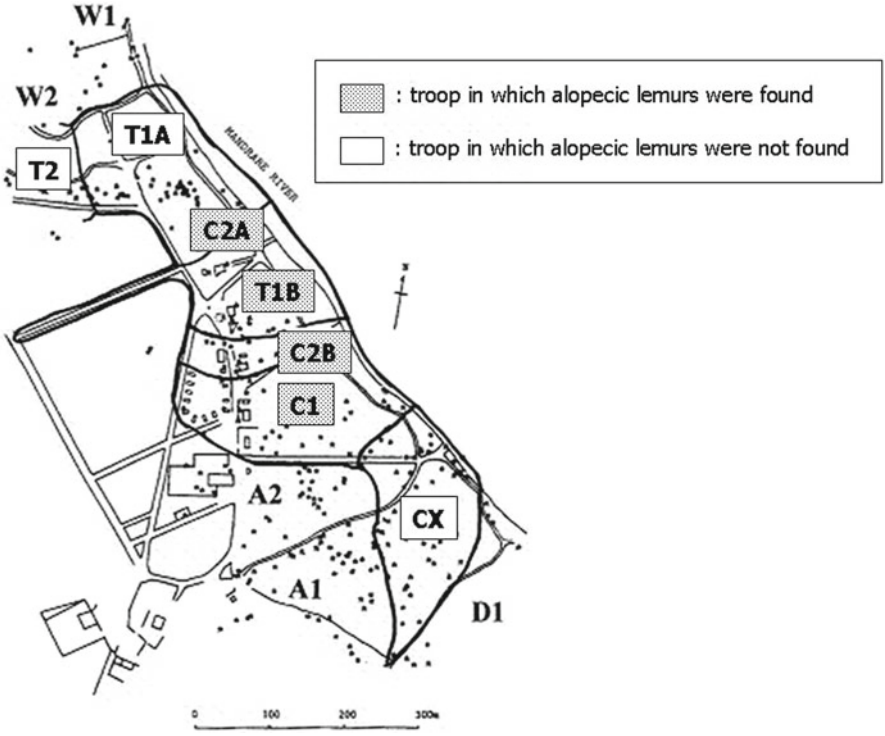


Fig. 42.4 Locations of the home ranges of seven study troops within the study area in 2001 (modified from Koyama et al. 2002)

limited sample size, the difference in the affliction of males and females was not significant ($\chi^2 = 3.18$, df = 1, Fisher's exact test, two-tailed $P = 0.12$).Variation was also age related. Alopecic lemurs ranged from 2 to 15 years in age, but no 1-year-old

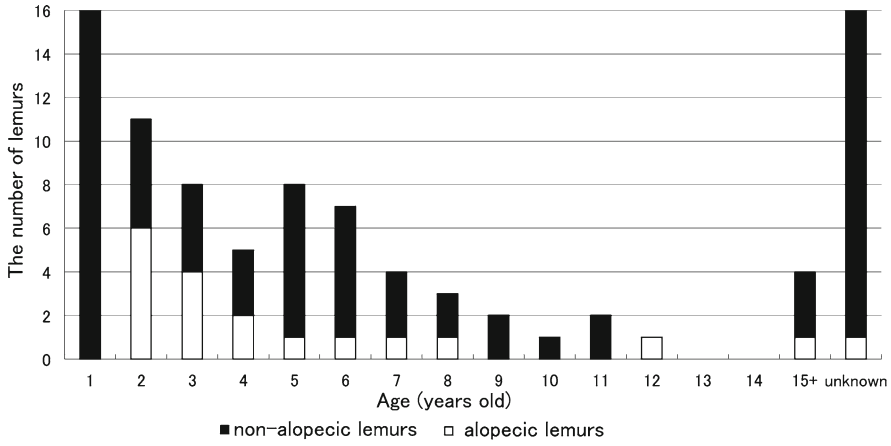


Fig. 42.5 Numbers of alopecic and nonalopecic lemurs in each age category in 2001

animals were affected. In 2001, the proportion of alopecic lemurs was the highest among younger animals (2–4 years old; Fig. 42.5): 54.5% ($n=11$) of 2 years old, 50% ($n=8$) of 3 years old, and 40% ($n=5$) of 4 years old were alopecic.

Comparison Between 2001 and 2004

The 19 alopecic lemurs recorded in 2001 experienced a variety of fates. By 2004, six (31.6%) had died, and two (10.5%) had disappeared from the study site, either through emigration or death outside the area. Only two lemurs (10.5%) were still alopecic. Nine animals (47.4%) were still alive and had recovered their fur condition; thus, alopecia syndrome was not necessarily fatal.

The mortality rate of alopecic females from 2001 to 2004 was 42.9% (6/14), not significantly different from that of nonalopecic females (40.0%, 10/25) ($\chi^2=0.03$, df = 1, Fisher's exact test, two-tailed $P=1$). However, this result might simply reflect the age composition of the population. Of 14 alopecic females, 9 were young (2–4 years old), and the remaining 5, 5 years or older. Among the young alopecic females, only two (22.2%) died within the 3-year period, while four of the five older females (80%) died during this time.

In 2001, the birth rate of the alopecic females was 77.8% (7/9), while that of nonalopecic females was 72.7% (16/22), and not significantly different ($\chi^2=0.09$, df = 1, Fisher's exact test, two-tailed $P=1$). These values are also similar to the annual birth rate over 10 years, from 1989 to 1998 (75.0%, range: 63.3–85.7%), in the same population (Koyama et al. 2001). Infant mortality among alopecic mothers was 57.1% (4/7), higher than that among nonalopecic mothers (18.8%, 3/16) as well

as the average 3-month infant mortality over 10 years in the same population (27.9%: Koyama et al. 2001). The difference between alopecic and nonalopecic mothers was not significant ($\chi^2 = 3.39$, df = 1, Fisher's exact test, two-tailed $P = 0.14$). Additionally, in September 2004 we witnessed a case where the infant of an alopecic female in Troop T1B had difficulty clinging to its mother and fell down. Ultimately the infant disappeared from the troop.

Discussion

We describe the age and sex profile of the ring-tailed lemurs afflicted with alopecia syndrome in Berenty Reserve, south-eastern Madagascar between 2001 and 2005; the troop distribution of the alopecic animals; and the consequences of the syndrome for female reproduction. The only clear disadvantage to female reproductive success is the difficulty infants experience in clinging to the mothers' scant fur, leading to higher infant mortality. Alopecia syndrome is not necessarily fatal to the sufferers themselves, and 47.4% of alopecic lemurs recovered their fur condition between 2001 and 2004, especially young individuals 2–4 years old. Birth rates were not statistically different between alopecic and nonalopecic females in 2001. Rambeloarivony (unpublished data) observed similar results in 2005. Thus, barring the effects of maternal hair loss on infant mortality, alopecia syndrome appears to be a relatively low risk disease for Berenty's ring-tailed lemurs.

However, our data also show that the effects of alopecia may be different for different age groups. Although we found no significant difference in mortality between alopecic and nonalopecic females, this may simply reflect the age composition of the alopecic group, which was biased toward young animals. Alopecia may indeed raise mortality for older animals. Fortunately, the present number of alopecic lemurs is far lower than in 2001–2003 and we can no longer examine our results statistically.

Causes of Alopecia Syndrome

Crawford et al. (2006) proposed three possible causes of alopecia syndrome (1) infectious disease, (2) malnutrition or stress associated with high population densities, and (3) the toxic effects of an introduced plant, *Leucaena leucocephala*. Our data provide insight into the cause by tracking the distribution of the syndrome over several years: it occurred only among troops frequenting the part of the forest that has been most transformed for human habitation by building tourist bungalows and planting exotic plant species (Fig. 42.4). This implies that anthropogenic changes to the forest are related to the occurrence of alopecia in Berenty's ring-tailed lemurs.

Alopecia syndrome among wild mammals is often caused by mite infestations, as seen in other wild primates (Wallis and Lee 1999; Macfie 1996; Kalema-Zikusoka

et al. 2002; Mudakikwa 2001). At Berenty, a species of tick [*Haemaphysalis* (*Rhipistoma*) *lemuris* Hoogstraal 1953] was found on the eyes and external auditory meatuses of ring-tailed lemurs (Takahata et al. 1998), but mange has not been reported among Berenty's mammals. The veterinary study by Crawford et al. (2006) found no evidence of commonly recognized diseases among the lemurs, and a parasitologist from the Koyama team could not find any mange-inducing ectoparasites on the skins of captured alopecic lemurs in 2001 (Hirai, personal communication). The fact that alopecic lemurs were observed in two different parts of the reserve (Crawford et al. 2006; Jolly 2009b) also argues against the infection hypothesis.

A second possible cause of alopecia is malnutrition or stress associated with high population densities or directly associated with tourism (Crawford et al. 2006). Within our study area, the population of ring-tailed lemurs has increased since 1989 (Koyama et al. 2001) as has an introduced population of hybrid brown lemurs (*Eulemur rufifrons*×*E. collaris*) (Jolly et al. 2002; Pinkus et al. 2006). Thus, competition within and between troops has been increasing over the last two decades. However, no evidence of malnutrition was found by Crawford et al. (2006).

In our study, alopecic lemurs were found in troops C1, C2A, C2B, and T1B (Table 42.1, Fig. 42.4). We did not observe alopecic lemurs in troop CX in 2001 or 2004 (Table 42.1). Within the range of CX, the availability of tamarind fruits, the most important food item in the dry season, was lower than that of other areas (Koyama et al. 2006). Soma (2006) reported that troop CX often entered the ranges of C1, C2A, and C2B and fed there, suggesting that food resources within the range of CX were less abundant than in the C1, C2A, and C2B ranges. Indeed, Soma (unpublished data) showed that CX females consumed lower quantities of food than C1 females. There is no evidence that food resources were scarce in 2001, and year-to-year changes in food availability do not explain the numbers of alopecic lemurs in our population. Thus, our data do not support the malnutrition hypothesis.

The third hypothesis is that toxin from a newly introduced tree species (*Leucaena leucocephala*) caused fur loss (Crawford et al. 2006). *Leucaena* contains mimosine, a nonprotein amino acid which disturbs cell division and causes feather/fur loss among some birds, ruminants, and fruit bats. Ring-tailed lemurs within the study area feed on leaves, flowers, and young seeds of *Leucaena* (Simmen et al. 2006; Soma 2006; Ichino unpublished data). Several researchers are studying the relations between *Leucaena* and alopecia at Berenty (Jolly 2009b; Chaps. 39 and 41). *Leucaena* trees were removed from our study area following this study (Chap. 39), although a few small trees remain in the forest (Ichino personal observation). In the intervening years (until November 2011), we have rarely observed severely alopecic ("bald" or "sheared") lemurs (Ichino and Soma, unpublished data). Our results are hence most consistent with the *Leucaena* hypothesis, but questions remain (1) Why did the number of severely alopecic lemurs decrease in the years preceding *Leucaena* removal? (2) Why were there more alopecic females than males? (3) Why was the proportion of alopecic lemurs higher among young lemurs? These questions urge research into the physiological mechanisms underlying alopecia as the surest means of controlling outbreaks of the syndrome.

Acknowledgments We thank M. Jean de Heaulme and his family for their hospitality at Berenty Reserve and permission to carry out this study; A. Randrianjafy and H. Andriamialison, former directors of the Botanical and Zoological Park of Tsimbazaza; and the government of the Republic of Madagascar for permission to conduct the research. We sincerely thank the Prosimian 2007 congress organizers, especially J. Masters and F. Génin for their kind help. Our work was supported by Grants in Aid for Scientific Research from the Ministry of Education, Culture, Sports, Science and Technology, Japan, to S. Kobayashi (no. 16252004) and to Y. Tahakata (no. 21405015), by the Canon Foundation in Europe, the Kyoto University Foundation, and the Young Researcher Overseas Visits Program for Vitalizing Brain Circulation of JSPS to S. Ichino.

References

Berg W, Jolly A, Rambeloarivony H, Andrianome V, Rasamimanana H (2009) A scoring system for coat and tail condition in ringtailed lemurs, *Lemur catta*. Am J Primatol 71:183–190

Crawford GC, Andriafaneva L-E, Blumenfeld-Jones K, Calaba G, Clarke L, Gray L, Ichino S, Jolly A, Koyama N, Mertl-Millhollen A, Ostpak S, Pride RE, Rasamimanana H, Simmen B, Soma T, Tarnaud L, Tew A, Williams G (2006) Bald lemur syndrome and the miracle tree: alopecia associated with *Leucaena leucocephala* at Berenty Reserve, Madagascar. In: Jolly A, Sussman RW, Koyama N, Rasamimanana H (eds) Ringtailed lemur biology. Springer, New York, pp 332–342

Ichino S, Koyama N (2006) Social changes in a wild population of ringtailed lemurs (*Lemur catta*) at Berenty, Madagascar. In: Jolly A, Sussman RW, Koyama N, Rasamimanana H (eds) Ringtailed lemur biology. Springer, New York, pp 234–244

Jolly A (1966) Lemur behavior. University of Chicago Press, Chicago

Jolly A (2004) Lords and lemurs: mad scientists, kings with spears, and the survival of diversity in Madagascar. Houghton Mifflin, Boston

Jolly A (2009a) Coat condition of ringtailed lemurs, *Lemur catta*, at Berenty Reserve, Madagascar. I. Differences by age, sex, density and tourism, 1996–2006. Am J Primatol 71:191–198

Jolly A (2009b) Coat condition of ringtailed lemurs, *Lemur catta*, at Berenty Reserve, Madagascar. II. Coat and tail alopecia associated with *Leucaena leucocepahala*, 2001–2006. Am J Primatol 71:199–205

Jolly A (2012) Berenty Reserve, Madagascar: a long time in a small space. In: Kappeler PM, Watts DP (eds) Long-term field studies of primates. Springer, Berlin, pp 21–44

Jolly A, Dobson A, Rasamimanana HM, Walker J, O'Connor S, Solberg M, Perel V (2002) Demography of *Lemur catta* at Berenty Reserve, Madagascar: effects of troop size, habitat and rainfall. Int J Primatol 23:327–353

Jolly A, Koyama N, Rasamimanana H, Crowley H, Williams G (2006) Berenty Reserve: a research site in southern Madagascar. In: Jolly A, Sussman RW, Koyama N, Rasamimanana H (eds) Ringtailed lemur biology. Springer, New York, pp 32–42

Jones KC (1983) Inter-troop transfer of *Lemur catta* males at Berenty, Madagascar. Folia Primatol 40:145–160

Kalema-Zikusoka G, Kock RA, Macfie EJ (2002) Scabies in free-ranging mountain gorillas (*Gorilla beringei beringei*) in Bwindi Impenetrable National Park, Uganda. Vet Rec 150:12–15

Koyama N, Nakamichi M, Ichino S, Takahata Y (2002) Population and social dynamics changes in ring-tailed lemur troops at Berenty, Madagascar between 1989–1999. Primates 43:291–314

Koyama N, Nakamichi M, Oda R, Miyamoto N, Ichino S, Takahata Y (2001) A ten-year summary of reproductive parameters for ring-tailed lemurs at Berenty, Madagascar. Primates 42:1–14

Koyama N, Soma T, Ichino S, Takahata Y (2006) Home ranges of ringtailed lemur troops and the density of large trees at Berenty Reserve, Madagascar. In: Jolly A, Sussman RW, Koyama N, Rasamimanana H (eds) Ringtailed lemur biology. Springer, New York, pp 86–101

Macfie L (1996) Case report on scabies infection in Bwindi gorillas. Gorilla J 13:19–20
Mudakikwa A (2001) An outbreak of mange hits the Bwindi gorillas. Gorilla J 22:24
Pinkus S, Smith JNM, Jolly A (2006) Feeding competition between introduced *Eulemur fulvus* and native *Lemur catta* during the birth season at Berenty Reserve, southern Madagascar. In: Jolly A, Sussman RW, Koyama N, Rasamimanana H (eds) Ringtailed lemur biology. Springer, New York, pp 119–140
Simmen B, Sauther ML, Soma T, Rasamimanana H, Sussman RW, Jolly A, Tarnaud L, Hladik A (2006) Plant species fed on by *Lemur catta* in gallery forests of the southern domain of Madagascar. In: Jolly A, Sussman RW, Koyama N, Rasamimanana H (eds) Ringtailed lemur biology. Springer, New York, pp 55–68
Soma T (2006) Tradition and novelty in feed species used by *Lemur catta* at Berenty Reserve: how did they develop their feeding strategy on introduced plant species? In: Jolly A, Sussman RW, Koyama N, Rasamimanana H (eds) Ringtailed lemur biology. Springer, New York, pp 141–159
Sussman RW (1992) Male life history and intergroup mobility among ringtailed lemurs (*Lemur catta*). Int J Primatol 13:395–413
Takahata Y, Kawamoto Y, Hirai H, Miyamoto N, Koyama N, Kitaoka S, Suzuki H (1998) Ticks found among the wild ringtailed lemurs at the Berenty Reserve, Madagascar. Afr Study Monogr 19:217–222
Wallis J, Lee DR (1999) Primate conservation: the prevention of disease transmission. Int J Primatol 20:803–826

Chapter 43
Conservation of Malagasy Prosimians: A View from the Great Red Island

Jonah H. Ratsimbazafy, Summer J. Arrigo-Nelson, Luke Dollar, Christopher M. Holmes, Mitchell T. Irwin, Steig E. Johnson, Nancy J. Stevens, and Patricia C. Wright

Abstract Madagascar is a global biodiversity hotspot, with high levels of endemism coupled with a high degree of anthropogenic disturbance. Lemurs are important in maintaining the island's ecosystems. We examine the primary and emerging threats to lemurs, present a brief history of the conservation efforts implemented to preserve Malagasy ecosystems, and discuss the future direction of and prospects for conservation in Madagascar.

Resume Madagascar est un point chaud de biodiversité globale, avec un niveau d'endémisme très élevé associé à un fort niveau d'anthropisation. Les lémuriens jouent un rôle important dans le maintien des écosystèmes de l'île. Nous examinons les menaces anciennes et nouvelles pesant sur les lémuriens, présentons un bref historique des mesures de conservation initiées sur les écosystèmes malgaches, et discutons les futures directions et les perspectives offertes pour la conservation à Madagascar.

J.H. Ratsimbazafy (✉)
Durrell Wildlife Conservation Trust, B.P. 8511, Lot II 49J, Ampasanimalo, 101 Antananarivo, Madagascar
e-mail: jonah.ratsimbazafy@durrell.org

S.J. Arrigo-Nelson
Department of Biological and Environmental Sciences, California University of Pennsylvania, 250 University Ave, Box 45, California, PA 15418, USA
e-mail: arrigonelson@calu.edu

L. Dollar
Department of Biology, Pfeiffer University, Post Office Box 960, 48380 US HWY 52N, Misenheimer, NC 28109, USA
e-mail: luke.dollar@pfeiffer.edu

C.M. Holmes
Wildlife Conservation Society, B.P. 8500, Soavimbahoaka, 101 Antananarivo, Madagascar
e-mail: cholmes@wcs.org

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1_43,

Introduction: Lemur Origins and Diversity

Madagascar is among the most important global biodiversity hotspots, combining high levels of endemism with imminent extinction threats (Myers et al. 2000). Lemurs represent a significant component of Madagascar's mammalian diversity and serve important roles in the island's ecosystems (Birkinshaw 1999; Ganzhorn et al. 1999). Madagascar's history, including its early separation from Gondwana (Masters et al. 2006; Samonds et al. 2012) and unique floral and faunal composition, provided conditions that led to an extensive adaptive radiation of strepsirhine primates across the island. Although the geographic origin and timing of their appearance is debated, most colonization hypotheses involve an African origin in the early Tertiary drawing support from either fossil evidence (Seiffert et al. 2003) or molecular data (Yoder 1996). While a dearth of fossils obscures much of lemur history (Stevens and Heesy 2006), during the last 2,000 years climate change and human colonization have contributed to waves of lemur extinctions (at least 17 species), with the larger taxa disappearing almost completely (Mittermeier et al. 2010). Currently, 99 lemur species are recognized (Mittermeier et al. 2010), a number that has grown from the 32 species recognized in the early 1990s (Chap. 2). This increase in species numbers is controversial (Tattersall 2007, Chap. 2) and mainly reflects the partitioning of existing taxa into new species on the basis of genetic divergence (Rasoloarison et al. 2000). Regardless of the precise number of extant species, it is clear that a substantial proportion of Madagascar's primate diversity faces an extinction crisis.

M.T. Irwin
Department of Anthropology, Northern Illinois University, DeKalb, IL 60115, USA
e-mail: varibolo@yahoo.com

S.E. Johnson
Department of Anthropology, University of Calgary, 2500 University Dr NW, Calgary, AB, T2N 1N4, Canada
e-mail: steig.johnson@ucalgary.ca

N.J. Stevens
Department of Biomedical Sciences, Heritage College of Osteopathic Medicine, Center for Ecology and Evolutionary Studies, Ohio University, 228 Irvine Hall, Athens, OH 45701, USA
e-mail: stevensn@ohio.edu

P.C. Wright
Department of Anthropology, Stony Brook University, Stony Brook, New York, 11794 NY, USA
e-mail: patricia.wright@stonybrook.edu

Threats to Lemur Survival

Primary Threats

Habitat loss is rated the highest threat to lemur species (CBSG 2002), with Madagascar having experienced a 90% reduction in its original forest cover (Green and Sussman 1990; Du Puy and Moat 1998; Harper et al. 2007). Deforestation produces habitat fragmentation and edge effects (Lehman et al. 2006), effectively reducing the extent and connectivity of lemur habitats. Traditional slash-and-burn agriculture and the clearing of pastureland with fire are long established causes of forest loss (Gade 1996; Godfrey and Irwin 2007). Selective harvesting for construction materials, crafts, fuel wood, and commercial hardwoods further degrades forests (Patel 2007; Mittermeier et al. 2010) and reduces key lemur resources (Arrigo-Nelson 2006; Irwin 2008). Mining, large-scale plantations, and other new economic projects are also driving habitat loss (Vincelette et al. 2003; Mittermeier et al. 2010). Despite traditional taboos and national laws, hunting for food, the pet trade, medicinal resources, and pest control continues to deplete lemur populations (Mittermeier et al. 2010), and the extent of lemur hunting is probably unsustainable (Golden 2009).

Emerging Threats

Madagascar is prone to extreme seasonality and high interannual variability, including recurrent cyclones (Jury 1993; Dewar and Richard 2007), and short-term declines in lemur populations have been recorded following storms and droughts (Gould et al. 1999; Ratsimbazafy et al. 2002; Johnson et al. 2011). Although Malagasy ecosystems probably evolved under similar climatic conditions (Wright 1999; de Gouverain and Silander 2003), habitat disturbance and projected climate change may combine to exacerbate existing threats (Chap. 39). The frequency of cyclones and droughts may increase with global warming (Emanuel 2005; Ingram and Dawson 2005; Elsner et al. 2008) and fragmented forests may be less resilient to these stochastic events (Catterall et al. 2008). In addition, anticipated increases in fragmentation and the isolation of remaining forests due to climate change (Hannah et al. 2008) may further hinder lemur dispersal among suitable habitats, and rising sea levels threaten to decimate littoral forests containing locally endemic species (Consiglio et al. 2006). In fact, climatic impacts are already observable in southeastern Madagascar, where changes in phenology and food supply are associated with declining lemur populations (Wright 2006).

As the human population grows and forest fragmentation increases, conservationists must also consider cross-species disease transmission. Although no outbreaks have been documented to date, potential pathogens include toxoplasmosis, arboviruses, and herpesviruses (Junge and Sauther 2006).

History of Conservation Practices in Madagascar

Various approaches have been adopted over time to combat the threats to Madagascar's flora and fauna: primary among these is area-based conservation. The first substantial roots of Madagascar's protected area network lie in ten "Réserves Naturelles Intégrales" (RNI) covering 560,181 ha, gazetted in 1927 under the French colonial regime (Andriamampianina 1987). These areas followed a "preservationist" philosophy and were exclusionary: scientists were allowed to enter but local people were prohibited from using the reserves in any way. Three decades later, two new kinds of protected areas were established: "Réserves Spéciales" (RS) in 1956 and "Parcs Nationaux" (PN) in 1958 (Andriamampianina 1987). These areas dominated during the remainder of the twentieth century, gradually giving way to the Integrated Conservation and Development Projects (ICDPs) of the 1990s. These ICDPs featured a more "conservationist" philosophy and essentially followed the "Yellowstone" model (Marcus and Kull 1999). People were still physically excluded from the core areas, but an effort was made to ensure that local populations were included in the planning process and benefited from tourism revenues and/or development projects to offset the cost of their exclusion (Wright and Andriamihaja 2002).

In 1989 the Malagasy government developed Africa's first National Environmental Action Plan (NEAP), arguably the most ambitious and comprehensive African environmental program to date. It was implemented in three phases over 15 years (Razafindralambo and Gaylord 2006). The first phase (1991–1997) aimed to create an official environmental policy with a regulatory and institutional framework that would foster ownership of the environmental agenda by the country rather than by donors. This period saw significant growth of the protected area system with the establishment of several new protected areas, visits from unprecedented numbers of tourists, and the creation of the parastatal ANGAP ("Association Nationale pour la Gestion des Aires Protégées") charged with balancing conservation with research, education, ecotourism, and community development (Randrianandianina et al. 2003). With the creation of ANGAP came the formalization of a revenue distribution mechanism, with 50% of tourist revenue returning to local communities for development projects and improved land stewardship. The 1990s also saw a shift toward local enfranchisement with GELOSE legislation ("Gestion Locale Sécurisée"), which allowed local community organizations to apply for rights to manage local resources (Bertrand 1999). GELOSE and the revised GCF legislation ("Gestion Contractualisée des Fôrets de l'État") represented a clear shift away from the "Yellowstone" model, with communities clustered around parks, toward a "landscape" model, in which humans and wildlife overlap in a single managed landscape.

The second phase of the NEAP (1997–2003) consolidated first phase programs by putting national institutions more firmly into leadership positions. During this period, the government created COAP ("Code des Aires Protégées de Madagascar"), which streamlined guidelines for protected area creation.

The final phase (2003–2008) aimed to mainstream environmental thinking more broadly into macroeconomic management and sector programs, including mechanisms for sustainable financing (Razafindralambo and Gaylord 2006). During this

phase, the government launched a new era in Malagasy conservation. In 2003, President Marc Ravalomanana announced the "Durban Vision", pledging to increase Madagascar's protected area network from 1.8 to 6.0 million hectares (10% of the country's surface area; Randrianandianina et al. 2003) through a new system of protected areas—SAPM ("Système des Aires Protégées de Madagascar"). Under the direction of the Ministry of Environment, Forests and Tourism, SAPM's goals were even broader than those of ANGAP: conservation of Madagascar's biodiversity and cultural heritage, maintenance of ecological services, and the promotion of sustainable use of natural resources to reduce poverty and promote development (SAPM 2006). The SAPM mandate also included protected areas with less strict protection, not seen before in Madagascar: IUCN Categories 5 ("Protected Landscape") and 6 ("Managed Resource Protection Area"). The potential creation of "protected areas principally managed for the goal of sustainable use of natural ecosystems" (Category 6; SAPM 2006) raises the concern that some species could face extirpation if the economic value of forest resources is given higher priority than wildlife protection. Thus, despite the evolution of conservation in Madagascar, the fundamental conflict remains: biodiversity maintains a significant standing value (i.e., its value if preserved) but has a more easily perceived and rapidly available economic value if exploited.

Future Directions for Conservation in Madagascar

Conservation actions and initiatives in Madagascar have been shifting to address emerging threats, while at the same time increasing support for local people. In twenty-first century Madagascar, the fate of biodiversity is dependent not only on the resilience of the ecological systems but also equally on the system by which resources are managed. With an annual population growth rate of 2.8% and 44.7% of the population 14 years of age or younger (DESA 2001), the island's natural resources are facing unprecedented threats. Against this backdrop, the Malagasy government developed an integrative model promoting biodiversity conservation and sustainable resource use through improved community land stewardship linked to improved living standards. To this end, the government launched its "Madagascar Naturally" vision in 2005, recognizing the central role that a healthy environment plays in the social, economic, and spiritual well-being of the Malagasy people, and the Madagascar Action Plan in 2007, comprising a set of strategies for sustainable development with a commitment to "cherish the environment."

Creating incentives to ensure community investment in a system that has, until fairly recently, excluded them is critical to the success of conservation in Madagascar. In the absence of fair reimbursement, there is risk that disenfranchised members of the communities will persist in, or even exacerbate, destructive resource use. To accommodate the seemingly competing interests of conservation and sustainable resource use, Madagascar adopted several best practices including (1) protected area limits, internal zoning and resource use rules, defined in public consultation at local levels; (2) detailed forest inventories to inform strict management rules for

forest resource extraction; and (3) community-based ecological monitoring of biodiversity indicators as well as human disturbance. Underlying these practices is the identification of sustainable financing mechanisms for protected areas, and clear and direct returns to local communities engaged in contracted forest resource management in border forests of protected areas. The government began to promote equitable sustainable financing mechanisms at the project level through programs such as that in the Makira Forest Protected Area, which assures that 50% of revenue from the sale of sequestered forest carbon credits returns to local communities to support a variety of activities including community-based ecological monitoring (Holmes et al. 2008).

The 2009 Political Crisis, a Serious Setback for Conservation

The political crisis in Madagascar initiated in 2009 has had a substantial, negative impact on Madagascar's conservation efforts. During this period, opposition to the administration of President Ravalomanana manifested in regime change backed by the armed forces. Opposition leader Andry Rajoelina assumed the role of head of state in the transitional government, Haute Autorité de la Transition (HAT). As the HAT was established through military intervention and without democratic elections, it was not recognized by many international governments and organizations. International agencies have largely suspended financial support to environmental programs, and illegal logging and export of tropical hardwood species has dramatically increased along with the deterioration of government regulation of these activities (Innes 2010). Strong local and regional economic interests have been displaced by even stronger transnational economic forces. The resulting rapid and extreme ecosystem degradation, coupled with a substantial increase in bushmeat hunting (Golden 2009), is precipitating a survival crisis for many lemur species. Increasing numbers of immigrants have flooded villages in eastern Madagascar in search of gold, with gold mining now occurring in Ranomafana National Park (Wright, personal observation). Studies conducted by the NGO *Madagasikara Voakajy* show that traditions that once protected lemurs have broken down (Jenkins et al. 2011). The increase in human–wildlife contact in degraded forests could enhance the risk of disease emergence and spread, potentially with global consequences (Barrett and Ratsimbazafy 2009).

At first glance, the future looks dire for lemurs, and the state of Madagascar's natural areas is precarious. Yet despite these daunting challenges, we find cause for optimism in the many conservation NGOs that persist in their efforts. Perhaps more importantly, local communities with whom we have worked for several years still hold out hope, if benefits of conservation can be realized locally; the empowerment of local communities may be Madagascar's only chance of preserving its endangered species, especially in remote areas where government control is weak.

There is also increasing cooperation among conservation practitioners: 2009 saw the creation of the *Alliance Voahary Gasy*, a civil society composed of Malagasy

Conservation associations/NGOs aimed at defending good governance and protecting Madagascar's resources against corruption and illegal trade. Such groups advance the following goals (1) implementation of a criminal justice court in Madagascar to prosecute traffickers/environmental delinquents; (2) implementation of community policing at a local level in places with weaker governmental control; (3) sustained efforts to combat corruption; and (4) expansion of ecotourism organized by and with benefits for local communities.

Conclusions

With lemurs facing so many threats, many populations may be lost before they are studied. Mittermeier et al. (2010) underscored the lack of information for many Malagasy primates, noting that ~40% of lemur species are classified by the IUCN as data deficient. What is the outlook for extant lemurs? Can we avoid a continuation of the Holocene extinctions?

Over the past century, conservation philosophy has moved from complete exclusion of local people, to compensation of local people, to their inclusion within protected landscapes and formalization of their rights to use natural resources. This shift was necessary both ethically and practically, and there is evidence of its success before the recent political crisis: national deforestation rates declined from 0.83% to 0.53% annually from 2000 to 2005, with considerably lower rates (0.12%) inside protected areas (CI/IRG/USAID data).

However, the balance between people and nature in new protected areas is still unstable and exacerbated by the ongoing political crisis. The long-term success of new conservation approaches will depend on how genuinely local communities are engaged, how effectively management plans protect biodiversity, and whether activities on the ground match those prescribed in the plans. In the future, conservationists in Madagascar are likely to be less concerned with destruction outside protected areas and more concerned with resource extraction (both legal and illegal) within them. This is the trade-off of the massive expansion of protected areas: even if virtually all forests in Madagascar are included in some protection regime (as is intended), at least some of these areas must generate tangible economic development for local communities and the nation as a whole.

References

Andriamampianina J (1987) Status des parcs et réserves de Madagascar. In: Mittermeier RA, Rakotovao LH, Randrianasolo V, Sterling EJ, Devitre D (eds) Priorités en Matière de Conservation des Espèces à Madagascar. IUCN, Gland, Switzerland, pp 27–30

Arrigo-Nelson SJ (2006) The impact of habitat disturbance on the feeding ecology of the Milne-Edwards' Sifaka (*Propithecus edwardsi*) in Ranomafana National Park, Madagascar. Unpublished PhD thesis, State University of New York at Stony Brook, Stony Brook, NY

Barrett MA, Ratsimbazafy JH (2009) Luxury bushmeat trade threatens lemur conservation. Nature 46:470

Bertrand A (1999) La gestion contractuelle, pluraliste et subsidiaire des ressources renouvelable à Madagascar. Afr Stud Q 3(2):75–81

Birkinshaw CR (1999) The importance of the black lemur (*Eulemur macaco*) for seed dispersal in Lokobe Forest, Nosy Be. In: Rakotosamimanana B, Rasamimanana H, Ganzhorn JU, Goodman SM (eds) New directions in lemur studies. Springer, New York, pp 189–199

Catterall CP, McKenna S, Kanowski J, Piper SD (2008) Do cyclones and forest fragmentation have synergistic effects? A before-after study of rainforest vegetation structure at multiple sites. Austral Ecol 33:471–484

CBSG (Conservation Breeding Specialist Group) (2002) Evaluation et Plans de Gestion pour la Conservation (CAMP) de la Faune de Madagascar: Lemuriens, Autres Mammifères, Reptiles et Amphibiens, Poissons d'eau douce: Rapport du Groupe Lemuriens. Mantasoa, Madagascar

Consiglio T, Schatz GE, McPherson G, Lowry PP II, Rabenantoandro J, Rogers ZS, Rabevohitra R, Rabehevitra D (2006) Deforestation and plant diversity of Madagascar's littoral forests. Conserv Biol 20:1523–1739

De Gouverain RC, Silander JA (2003) Do tropical storm regimes influence the structure of tropical lowland rain forests? Biotropica 35:166–180

DESA (Department of Economic and Social Affairs): Population Division (2001) World population ageing: 1950–2050. United Nations, New York. http://www.un.org/esa/population/publications/worldageing19502050

Dewar RE, Richard AF (2007) Evolution in the hypervariable environment of Madagascar. Proc Natl Acad Sci USA 104:13723–13727

Du Puy DJ, Moat JF (1998) Vegetation mapping and classification in Madagascar (using GIS): implications and recommendations for the conservation of biodiversity. In: Huxley CR, Lock JM, Cutler DF (eds) Chorology, taxonomy and ecology of the floras of Africa and Madagascar. Royal Botanic Gardens, Kew, pp 97–117

Elsner JB, Kossin JP, Jagger TH (2008) The increasing intensity of the strongest tropical cyclones. Nature 455:92–95

Emanuel K (2005) Increasing destructiveness of tropical cyclones over the past 30 years. Nature 436:686–688

Gade DW (1996) Deforestation and its effects in highland Madagascar. Mt Res Dev 16:101–116

Ganzhorn JU, Fietz J, Rakotovao E, Schwab D, Zinner D (1999) Lemurs and the regeneration of dry deciduous forest in Madagascar. Conserv Biol 13:794–804

Godfrey LR, Irwin MT (2007) The evolution of extinction risk: past and present anthropogenic impacts on the primate communities of Madagascar. Folia Primatol 78:405–419

Golden CD (2009) Bushmeat hunting and use in the Makira Forest, north-eastern Madagascar: a conservation and livelihoods issue. Oryx 43:386–392

Gould L, Sussman RW, Sauther ML (1999) Natural disasters and primate populations: the effects of a 2-year drought on a naturally occurring population of ring-tailed lemurs (*Lemur catta*) in southwestern Madagascar. Int J Primatol 20:69–84

Green GM, Sussman RW (1990) Deforestation history of the eastern rain forests of Madagascar from satellite images. Science 248:212–215

Hannah L, Dave R, Lowry PP, Andelman S, Andrianarisata M, Andriamaro L, Cameron A, Hijmans R, Kremen C, MacKinnon J, Randrianasolo HH, Andriambololonera S, Razafimpahanana A, Randriamahazo H, Randrianarisoa J, Razafinjatovo P, Raxworthy C, Schatz GE, Tadross M, Wilme L (2008) Climate change adaptation for conservation in Madagascar. Biol Lett 4:590–594

Harper GJ, Steininger MK, Tucker CJ, Juhn D, Hawkins F (2007) Fifty years of deforestation and forest fragmentation in Madagascar. Environ Conserv 34:325–333

Holmes CM, Ingram JC, Meyers D, Crowley H, Victurine R (2008) Forest carbon financing for biodiversity conservation, climate change mitigation and improved livelihoods: the Makira Forest Protected Area, Madagascar. Translinks, USAID

Ingram JC, Dawson TP (2005) Climate change impacts and vegetation response on the island of Madagascar. Philos Trans R Soc Lond A 363:55–59

Innes JL (2010) Madagascar rosewood, illegal logging and the tropical timber trade. Madag Conserv Dev 10:6–10

Irwin MT (2008) Feeding ecology of *Propithecus diadema* in forest fragments and continuous forest. Int J Primatol 29:95–115

Jenkins RKB, Keane A, Rakotoarivelo AR, Rakotomboavoanjy V, Randrianandrianina FH, Razafimanahaka HJ, Ralaiarimalala SR, Jones JPG (2011) Analysis of patterns of bushmeat consumption reveals extensive exploitation of protected in eastern Madagascar. PLoS One 6(12):e27570

Johnson SE, Ingraldi C, Ralainasolo FR, Andriamaharoa HE, Ludovic R, Birkinshaw CR, Wright PC, Ratsimbazafy JH (2011) Gray-headed lemur (*Eulemur cinereiceps*) abundance and forest structure dynamics at Manombo, Madagascar. Biotropica 43:371–379

Junge RE, Sauther ML (2006) Overview on the health and disease ecology of wild lemurs: conservation implications. In: Gould L, Sauther ML (eds) Lemurs: ecology and adaptation. Springer, New York, pp 423–440

Jury MR (1993) A preliminary study of climatological associations and characteristics of tropical cyclones in the SW Indian Ocean. Meteorol Atmos Phys 51:101–115

Lehman SM, Rajaonson A, Day S (2006) Edge effects and their influence on lemur density and distribution in southeast Madagascar. Am J Phys Anthropol 129:232–241

Marcus RR, Kull C (1999) Setting the stage: the politics of Madagascar's environmental efforts. Afr Stud Q 3(2):1–8

Masters JC, de Wit MJ, Asher RJ (2006) Reconciling the origins of Africa India and Madagascar with vertebrate dispersal scenarios. Folia Primatol 77:399–418

Mittermeier RA, Louis EE Jr, Richardson M, Schwitzer C, Langrand O, Rylands AB, Hawkins F, Rajaobelina S, Ratsimbazafy J, Rasoloarison R, Roos C, Kappeler PM, Mackinnon J, Nash S (2010) Lemurs of Madagascar, 3rd edn. Conservation International, Washington, DC

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Patel ER (2007) Logging of rare rosewood and palisandre (*Dalbergia* spp.) within Marojejy National Park, Madagascar. Madag Conserv Dev 2:11–16

Randrianandianina BN, Andriamahaly LR, Harisoa RM, Nicoll ME (2003) The role of protected areas in the management of the island's biodiversity. In: Goodman SM, Benstead JP (eds) The natural history of Madagascar. University of Chicago Press, Chicago, pp 1423–1432

Rasoloarison RM, Goodman SM, Ganzhorn JU (2000) Taxonomic revision of mouse lemurs (*Microcebus*) in the western portions of Madagascar. Int J Primatol 21:963–1019

Ratsimbazafy JH, Ramarosandratana HV, Zaonarivelo RJ (2002) How do black-and-white ruffed lemurs still survive in a highly disturbed habitat? Lemur News 7:7–10

Razafindralambo G, Gaylord L (2006) Part 3: Examples of MfDR in sector programs and projects. In: Madagascar: National Environment Action Plan, pp 75–82. Government report

Samonds KE, Godfrey LR, Ali JR, Goodman SM, Vences M, Sutherland MR, Irwin MT, Krause DW (2012) Spatial and temporal arrival patterns of Madagascar's vertebrate fauna explained by distance, ocean currents, and ancestor type. Proc Natl Acad Sci USA 109:5352–5357

SAPM (2006) Système des Aires Protégées de Madagascar: Orientations Générales Sur les Categories et les Types de Gouvernance des Aires Protégées. Unpublished Report

Seiffert ER, Simons EL, Attia Y (2003) Fossil evidence for an ancient divergence of lorises and galagos. Nature 422:421–424

Stevens NJ, Heesy CP (2006) Malagasy primate origins: fossils, phylogenies and biogeographic reconstructions. Folia Primatol 77:419–433

Tattersall I (2007) Madagascar's lemurs: cryptic diversity or taxonomic inflation? Evol Anthropol 16:12–23

Vincelette M, Randrihasipara L, Ramanamanjato JB, Lowry PP, Ganzhorn JU (2003) Mining and environmental conservation: the case of QIT Madagascar minerals in the southeast. In: Goodman SM, Benstead JP (eds) The natural history of Madagascar. University of Chicago Press, Chicago, pp 1535–1537

Wright PC (1999) Lemur traits and Madagascar ecology: coping with an island environment. Yearb Phys Anthropol 42:31–72

Wright PC (2006) Considering climate change effects in lemur ecology and conservation. In: Gould L, Sauther ML (eds) Lemurs: ecology and adaptation. Springer, New York, pp 385–401

Wright PC, Andriamihaja BA (2002) Making a rain forest national park work in Madagascar: Ranomafana National Park and its long-term research commitment. In: Terborgh J, van Schaik C, Rao M, Davenport L (eds) Making parks work: strategies for preserving tropical nature. Island Press, Washington, DC, pp 112–136

Yoder AD (1996) The use of phylogeny for reconstructing lemuriform biogeography. In: Lourenço WR (ed) Biogeographie de Madagascar. Editions de l'ORSTOM, Paris, pp 245–258

Index

J. Masters et al. (eds.), *Leaping Ahead: Advances in Prosimian Biology*, Developments in Primatology: Progress and Prospects, DOI 10.1007/978-1-4614-4511-1,