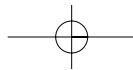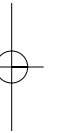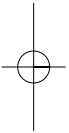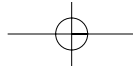# PART TWO

The Primates

3

The Lorisiform Primates of Asia and Mainland Africa
## Diversity Shrouded in Darkness
Anna Nekaris and Simon Bearder

INTRODUCTION

The primates known as galagos (or bushbabies), pottos (angwantibos and pottos), and lorises could easily vie for the position of "least known of all the primates." Despite the fact that the suborder Lorisiformes contains some of the most specialized primates, with a minimum of 34 species now recognized, some irresistible urge seems to possess the authors of textbooks to summarize what is known of this group in a hasty postscript to a chapter on their close cousins, the lemurs. One reason for this is that, unlike most lemurs, different taxa of lorisiforms can look very similar to each other (*cryptic* species), and for a long time they were misclassified as a few species and assumed to have little variation in genetics, behavior, and ecology. It is now known that superficial similarities are partly the result of extensive convergence due to the demands of nocturnal and arboreal niches and partly because members of each species recognize each other by more subtle visual, vocal, and olfactory signals. In this chapter, we intend to show that the nocturnal strepsirhines of Asia and Africa are a diverse group of primates and represent an untapped resource for the aspiring field biologist. One-sentence synopses, steeped in the literature of the 1960s, branding this enigmatic group as no more than acrobatic leapers and slow creepers (e.g., MacDonald 2001) seem to have hindered interest in their study in the wild, even though early biologists recognized great variability within this group (e.g., Gray 1863). The lorisiforms display a multitude of social systems, life histories, and locomotor strategies, a diversity evident despite the fact that only a handful of species have been studied in detail.

The lorisiform primates are widely dispersed in Africa (excluding Madagascar), southern Asia, and Southeast Asia. The relatively few long-term field studies that have been published on the galagos, pottos, and lorises are summarized in Table 3.1. Detailed behavior and ecological data are available for only 16 species, fewer than half of those currently recognized. In some cases where researchers have set out to study behavior, their projects were confounded by the discovery of too many new species (e.g., Honess 1996, Ambrose 1999). Instead, these studies have led to extensive useful descriptions of the presence/absence of species across a large geographical range, with morphological data gathered from trapping regimes (Oates and Jewell 1967; Honess 1996; Ambrose 1999; Perkin 2000, 2001a,b, 2002; Perkin et al. in press). Furthermore, despite advances in radio tracking, only nine species have been studied with this technology (Table 3.1) and only two studies have been able to take advantage of recent advances in molecular ecology (Pullen 2000, Pimley 2002). Clearly, an enormous avenue for research exists within this group.

Even what might appear to be the most fundamental questions regarding the evolutionary relationships among this group are far from resolved (Rasmussen and Nekaris 1998). For example, no consensus has yet been reached as to whether the pottos and lorises form a monophyletic clade to the exclusion of the galagos or if they form one of the most spectacular examples of parallel evolution among primates (Yoder et al. 2001b, Roos et al. 2004). Recent fossil discoveries have added new vigor to debates regarding the origins of the lorisiforms. Some authors contend that they may be among the most ancient of the living primates, with origins extending back to the Eocene (Seiffert et al. 2003, Martin 2003). Others propose an Asian origin for the Malagasy strepsirhines, with the deepest evolutionary relationships existing between the lemurs and lorises (Martin 2000, 2003; Tavare et al. 2002); yet another contrary view is that the lemurs are most closely related to the galagos (Charles-Dominique and Martin 1970, Roos et al. 2004). New molecular data have opened up questions about the genetic relationships between species. Mitochondrial deoxyribonucleic acid (DNA) analysis, for example, indicates that the galagos are not a single group of close relatives that have undergone recent speciation but can be divided into four deeply rooted clades which diverged over 30 million years ago (Bayes 1998). Further details of evolutionary relationships among galagos have been explored using comparisons of red blood cell enzymes (Masters et al. 1994,
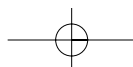
Table 3.1   Taxonomy and Conservation Status

LATIN NAME	COMMON NAME	HABITAT	DISTRIBUTION	POPULATION DENSITY[1]	IUCN RED LIST STATUS[2]
Galaginae					
Galagoides demidovii	Demidoff's dwarf	Understory/forest edge	Bioko, Cameroon, Gabon, Ivory Coast, Nigeria, Uganda	0.16/hr and 50–80/km²	Not listed
G. thomasi	Thomas's dwarf	Forest/mid- to high canopy	Bioko, Cameroon, Gabon, Ivory Coast, Nigeria, Uganda	0.46–2.0/hr and 50–80/km²	Not listed
G. orinus	Mountain dwarf	Submontane–montane forest/ mid- to high canopy	Tanzania	0.4/hr, 2.7–5.4/hr	Endangered
G. zanzibaricus (*udzungwensis*)	Zanzibar lesser	Secondary forest/mid- to high canopy	Tanzania	12.0/hr	Endangered
G. rondoensis	Rondo dwarf	Cloud coastal forest/understory	Tanzania	3–6/hr, 3–10/hr	Endangered
G. sp. nov. 3	Ukinga or Rungwe dwarf	Montane forest	Tanzania		Critically endangered
G. cocos	Kenya coastal	Coastal forest/middle story	Kenya, Tanzania	170–180/km²	Not listed
G. granti	Mozambique lesser	Coastal forest/middle story	Tanzania		Data deficient, unknown trend
G. nyasae	Malawi lesser	Woodland	Malawi		Not listed
G. sp. nov. 1	Kalwe lesser	Forest/middle story	Malawi		Not listed
G. sp. nov. 2	Mt. Thyolo lesser	Montane forest	Malawi		Not listed
Galago moholi (*senegalensis*)	Senegal lesser	Miombo, acacia woodland to forest/all strata	Cameroon, Kenya, Tanzania, Uganda	0.03–0.67/hr	Not listed
G. gallarum	Somali lesser	Acacia woodland, thicket/all strata	Kenya	1.0/hr	Low risk, trend unknown
G. moholi	Southern lesser	Acacia woodland/all strata	Botswana, Malawi, Namibia, South Africa, Tanzania		Not listed
G. matschiei	Spectacled	Forest/all strata	Uganda		Low risk, trend unknown
Euoticus elegantulus	Southern needle-clawed	Forest/mid- to high canopy	Cameroon, Gabon	15–20/km²	Low risk, trend unknown
E. pallidus	Northern needle-clawed	Forest/mid- to high canopy	Bioko, Cameroon	0.25/hr	Low risk, trend unknown
Sciurocheirus alleni	Allen's squirrel	Forest, forest edge/mid- to understory	Bioko, Cameroon	15/km²	Not listed
S. gabonensis	Gabon squirrel	Forest/mid- to understory	Cameroon, Gabon	15–20/km²	Low risk, trend unknown
Sciurocheirus sp. nov.	Makande squirrel	Forest/mid- to understory	Gabon		Not listed
Otolemur garnettii	Garnett's (small-eared) greater	Forest, farmland plantation/ mid- to high canopy	Kenya, Tanzania		Not listed
O. crassicaudatus	Thick-tailed greater	Woodland and forest edge/ mid- to high canopy	Malawi, South Africa, Tanzania, Zimbabwe		Not listed
O. monteiri	Silver greater	Woodland/unknown	Kenya		Not listed
Otolemur sp. nov.	Mwera (pygmy) greater	Woodland, farmland, plantation/mid- to high canopy	Tanzania		Not listed
Perodicticinae					
Perodicticus potto potto	Western potto	Secondary colonizing or flooded primary forest	Guinea, Guinea Bissau, Nigeria	?	Data deficient/not listed
P. p. edwardsi	Milne-Edwards or central potto	Swamp, lowland, mid-altitude montane rain forest	Nigeria, Zaire, Central African Republic	8–10/km², 4.7/km²	Data deficient/not listed
P. p. juju	S. Nigerian potto	Forest edge	Guinea Coast of Nigeria	?	Data deficient/not listed
P. p. faustus		Riverine forest	Congo Basin	?	Data deficient/not listed
P. p. ibeanus	Bosman's or eastern potto	Semimoist deciduous forest	Zaire, Burundi, Rwanda	0.04–0.26/hr and 1.8–17.7/km²	Data deficient/not listed
Arctocebus aureus	Golden angwantibo	Tree fall zones, forest edge, understory	Gabon	2/km²	Low risk, trends unknown
A. calabarensis	Calabar angwantibo	Tree fall zones, forest edge, understory	Cameroon, Gabon, Congo	0.7/km²	Low risk, trends unknown

Table 3.1 (*cont'd*)

LATIN NAME	COMMON NAME	HABITAT	DISTRIBUTION	POPULATION DENSITY[1]	IUCN RED LIST STATUS[2]
Lorisinae					
Loris lydekkerianus lydekkerianus	Mysore slender loris	Dry forest, acacia scrub jungle	South India	0.13–3.6/km² or 28/km²	Near threatened
L. l. malabaricus	Malabar slender loris	Rain forests, coastal forests	South India	?	Near threatened
L. l. nordicus	Northern Ceylon gray slender loris	Low-country dry zone, scrub forest, grassland	Sri Lanka	0.33–50/km²	Endangered
L. l. grandis	Highland Ceylon slender loris	Montane forest mixed with patana grassland	Sri Lanka	0.11–3.3/km²	Endangered
L. tardigradus tardigradus	Western Ceylon red slender loris	Lowland rain forest, intermonsoon forest	Sri Lanka	0.86–13/km²	Endangered
L. t. nycticeboides	Horton Plains slender loris	Montane rain and mist forests	Sri Lanka	0.08–0.16/km²	Critically endangered
Nycticebus bengalensis	Bengal slow loris	Bamboo forest mixed with hardwood trees, farmbush, mangrove swamps	Burma, Cambodia, China, India, Laos, Thailand, Vietnam	?	Data deficient, unknown trend
N. coucang	Greater slow loris	Tropical rain forest with continuous canopy	Sumatra, peninsular Malaysia, Thailand	?	Not listed
N. javanicus	Javan slow loris	Unknown	Indonesian Java	?	Data deficient, unknown trend
N. menagensis	Bornean slow loris	Unknown	Brunei, Indonesia, Malaysia	?	Not listed
N. pygmaeus	Pygmy slow loris	Bamboo forest mixed with hardwood trees, forest edge, dense scrub	Cambodia, China, Laos, Vietnam	8 seen during several night walks	Vulnerable, trend decreasing

[1] Because different survey methods were employed, some population densities are per kilometer squared, some are per kilometer, and some are a rate of animal encounters per hour.
[2] IUCN, World Conservation Union.

Masters and Brothers 2002) and highly repeated DNA sequences (Crovella et al. 1994, DelPero et al. 2000), which led to a new appreciation of the age and extent of their divergence. Finally, the Asian lorises have long been regarded as essential to understanding questions regarding the evolution of primate characteristics due to their having the greatest degree of orbital convergence of all primates (Cartmill 1972, Ross 1996). Only recently has the ecological significance of their visual adaptations been tested in the field (Nekaris in press, Bearder et al. in press).

With such a potential for discovery within this group, we hope that this summary of what is now known about lorisiform behavior and ecology will stimulate a new era of research. Our chapter contains more gaps than it provides answers, but these indicate a new direction for research on the strepsirhine primates in light of long-term field studies and surveys. Such research is urgently needed to help ensure their future protection.

TAXONOMY AND DISTRIBUTION

The Lorisiforms

Lorisiformes along with Lemuriformes of Madagascar comprise the infraorder Strepsirhini (Martin 1990). Although sometimes also classified as Prosimii along with the tarsiers, the strepsirhine primates are linked by a number of unique morphological traits, making them a monophyletic group to the exclusion of tarsiers, monkeys, and apes (Haplorhini). These traits include a moist nose, unfused mandibular symphasis and frontal bone, reduced upper incisors, a sloping talofibular facet (groove between the ankle and one of the lower limb bones), and a single grooming claw on the second digit of each hind foot. Living strepsirhines are further united by the possession of a *toothcomb*—a forward-pointing dental structure comprised of the lower incisors and canines used for both dietary and grooming purposes (Fleagle 1999).

Nocturnal primate taxonomy in general has gone through intense revision in the last few years (e.g., Nietsch and Kopp 1998, Yoder et al. 2001a, Pastorini et al. 2003). However, while the revision of lemur and tarsier taxonomy and the subsequent re-evaluation of their conservation status seem to have been accepted readily by the scientific community, the discovery of enormous taxonomic diversity among lorisiform primates has met with the same skepticism as acknowledgment of the diverse behavior within this group. We emphasize this point because even recent textbooks have updated their lemur and tarsier taxonomy to the exclusion of the galagos, pottos, and lorises (e.g., Dunbar and Barrett 2000, Falk 2000, MacDonald 2001, Boyd and Silk 2003).

Members of the infraorder Lorisiformes are currently con-servatively classified as one superfamily (Lorisoidea) and one family (Lorisidae), comprising three distinctive subfamilies (Galaginae, Perodicticinae, and Lorisinae) (Rasmussen and Nekaris 1998, Grubb et al. 2003) (Table 3.2). The galagos and pottos are restricted to Africa and range in size from 55 to 2,000 g. The lorises are found in Asia and range in size from 85 to 1,850 g (Table 3.3).

The Galagines

Before 1979, the accepted taxonomy of the Galaginae was monogeneric (*Galago*) and contained only six species (Petter and Petter-Rousseaux 1979). This classification is still reported in a number of prominent texts, despite several published revisions expanding the number of species to 11 (Olson 1979, Nash et al. 1989), 17 (Bearder et al. 1995), and 25 (Bearder et al. 2003). This extraordinary diversity of galagos makes them comparable to the guenon group (see Chapter 15) in having one of the widest distributions and abundance of species found in Africa. For the galagos we adopt the most recent classification by Grubb et al. (2003; but see also Groves 2001) and divide the taxa into five genera (Table 3.2). Bioacoustic studies, using Paterson's (1985) mate recognition concept of species, have been at the forefront of this taxonomic revision (Masters 1988, 1991, 1998; Honess 1996; Bearder 1999; Ambrose 2003). This classification is also supported by behavioral studies (e.g., Harcourt and Bearder 1989); genetic research (Bayes 1998, Roos 2003); examination of hand, foot, and sexual organ morphology; and comparisons of hair scale structure (Dixson 1989, 1995, 1998; Anderson 1998, 2000, 2001; Anderson et al. 2000). In this chapter, we have carefully gone through previous studies, updating the taxonomy for each of them in the tables and text. This is extremely important as these animals are indeed distinct species but aspects of life history and morphology of even the best studied taxa are often reported, even in the more recent literature, under the wrong name (e.g., *Galago moholi*, which was formerly known as *G. senegalensis*).

Galagos are distributed across the whole of Africa south of the Sahara, with the exception of southern regions of South Africa. They occupy a very wide range of habitats, from near-desert conditions in Somalia and northern Kenya through subtropical savannahs, woodlands, riverine, and montane forests to dense tropical rain forests. Up to four species can occur in sympatry with each other, as well as with up to two pottos. One country, Tanzania, currently boasts 13 species of galagos within its borders and one species; *Otolemur garnettii* has been found in association with any of 14 other galago species in different parts of its geographic range. With huge tracts of rain forest yet to be surveyed for these nocturnal primates and considering their secretive habits and relatively cryptic characteristics, it will not be astonishing if further research adds to the complexity of this emerging picture.

Perodicticines and Lorisines

Similar diversity is now being uncovered in the Perodicticinae in Africa and the Lorisinae in Asia, each of which was once thought to comprise two monospecific genera, one gracile and the other robust (Yoder et al. 2001a). Despite being less vocal than the galagos, vocalizations have again yielded important taxonomic information, as have differences in behavior, morphology, facial markings, and genetic data (Coultas 2002, Nekaris and Jayewardene 2003, Roos 2003). It is almost without doubt that most of the currently recognized subspecies within these two subfamilies will be elevated to species level; for this reason, we report data regarding the pottos and lorises at the subspecific level.

In Africa, the gracile forms are now recognized as two species, the golden angwantibo (*Arctocebus aureus*) and the Calabar angwantibo (*A. calabarensis*), both confined to the rain forests of central Africa. The taxonomy of the robust forms, the pottos, is being reevaluated but currently consists of one species with five subspecies. Following Kingdon (1997), these are *Perodicticus potto potto* in West Africa, *P. p. juju* in Nigeria, *P. p. edwardsi* in Cameroon and Gabon, *P. p. faustus* in the Congo Basin, and *P. p. ibeanus* in the Eastern Democratic Republic of Congo, Uganda, and western Kenya. Schwartz (1996) recognizes another genus of potto, *Pseudopotto martini*, differing from *Perodicticus* in having relatively long upper first premolars, a reduced third molar, and a relatively longer tail. Other researchers doubt this taxon, suggesting the differences fall within the range of variation of *Perodicticus* (Sarmiento 1998); tar-geted searches in the wild have failed to yield any evidence of this putative genus (Pimley 2002).

Groves (2001) recognizes two gracile lorisines in south Asia, although we follow the subspecific classification of Osman Hill (1953). The red slender loris, the smallest of the lorisines, resides only in the lowland (*Loris tardigradus tardigradus*) and montane (*L. t. nycticeboides*) rain forests of Sri Lanka. Two subspecies of the larger gray slender loris also are found on this island: the northern Ceylonese slender loris (*L. lydekkerianus nordicus*) and the highland slender loris (*L. l. grandis*) (Nekaris and Jayewardene 2004). Southern India harbors an additional two slender loris taxa (Roonwal and Mohnot 1977, Schulze and Meier 1995a). The Malabar slender loris (*L. l. malabaricus*) is distributed in the wet southwest, including the Western Ghats, whereas the largest of all slender loris taxa, the Mysore slender loris (*L. l. lydekkerianus*), is distributed in the dry scrub forests of the southeast, including the Eastern Ghats.

The taxonomy of the robust Asian form, *Nycticebus*, is currently undergoing extensive revision, with some auth-orities recognizing three species based on morphology (e.g., Groves 1998, 2001) and others recognizing five species based on genetic analyses (Roos 2003). Here, we follow the taxonomy suggested by Roos (2003). The Bengal or northern slow loris (*Nycticebus bengalensis*) has the largest geographic range, including Burma, Cambodia, southern

Table 3.2 Long-Term Behavioral Studies of Lorisoid Primates; Data in Other Tables Are Drawn from These Studies Unless Otherwise Specified

TAXA	COUNTRY	STUDY SITE(S)	STUDY LENGTH (MONTHS)	RADIO TRACKING	REFERENCES
Galaginae					
Galagoides demidovii	Gabon	Makokou	42	Yes	Charles-Dominique 1972, 1977a
G. thomasi	Gabon	Makokou	42	–	Charles-Dominique 1977a
G. cocos	Kenya	Gedi Ruins National Monument	20	Yes	Harcourt and Nash 1986a,b; Nash 1986, 1993
G. cocos	Kenya	Diani	22	Yes	Harcourt 1984, 1986a; Harcourt and Nash 1986a,b; Harcourt and Bearder 1989
G. rondoensis	Tanzania	Litipo, Rondo, Ziwani	20	No	Honess 1996, Honess and Bearder 1996
G. zanzibaricus (*udzungwensis*)	Tanzania	Matundu	20	No	Honess 1996, Honess and Bearder 1996
G. granti	Tanzania	Rondo, Mtopwa	20	No	Honess 1996, Honess and Bearder 1996
G. orinus	Tanzania	Amani	20	No	Honess 1996, Honess and Bearder 1996
Galago moholi	S. Africa	Mosdene	24, 12, 11	Yes	Bearder 1969, 1987; Harcourt 1980; Bearder and Martin 1980a,b; Bearder and Doyle 1974; Charles-Dominique and Bearder 1979; Crompton 1980; Harcourt and Bearder 1989
G. moholi	S. Africa	Nylsvley Nature Reserve	18	Yes	Pullen 2000, Pullen et al. 2000
Euoticus elegantulus	Gabon	Makokou	42	No	Charles-Dominique 1977a
Sciurocheirus gabonensis	Gabon	Makokou	42	Yes	Charles-Dominique 1977a,b
S. alleni cameronensis	Cameroon	WWF Mt. Kupe Forest Reserve, Bakossiland[1]	22	Yes	Pimley 2002, Pimley et al. 2002, in press
Otolemur garnettii	Kenya	Gedi Ruins National Monument	20	Yes	Nash 1986, Nash and Harcourt 1986
O. garnettii	Kenya	Diani	22	Yes	Harcourt 1984, Nash and Harcourt 1986
O. crassicaudatus	S. Africa, Zimbabwe, Kwazula	Transval, Umtali,Mtunzini	15	Yes	Bearder 1974, Bearder and Doyle 1974b
O. crassicaudatus umbrosus	S. Africa	Soutsanberg Range	16, 11	No	Clark 1978a,b, 1985; Crompton 1980, 1983, 1984
O. crassicaudatus	S. Africa	Louis Trichard	12	No	Harcourt 1980, 1986b
Perodicticinae					
Perodicticus potto edwardsi	Cameroon	WWF Mt. Kupe Forest Reserve, Bakossiland	22	Yes	Pimley 2002, Pimley et al. 2002
P. p. edwardsi	Gabon	Makokou	42	Yes	Charles-Dominique 1974a,b, 1977a
Arctocebus aureus	Gabon	Makokou	42	No	Charles-Dominique 1977a
Lorisinae					
Loris lydekkerianus lydekkerianus	India	Ayyalur Interface Forestry Division	11–21	No	Nekaris 2001, 2002, 2003a,b, 2004; Nekaris and Rasmussen 2003; Rhadakrishna 2001; Rhadakrishna and Singh 2002, 2004
L. l. nordicus	Sri Lanka	Several sites in the north	5	No	Nekaris and Jayewardene 2003, Nekaris 2003b
L. tardigradus tardigradus	Sri Lanka	Masmullah Forest Reserve; Bangamukande Estate	8	No	Nekaris 2003b, Nekaris et al. in press, Nekaris and Jayewardene 2003
Nycticebus coucang coucang	Malaysia	Manjung District, Perak	27.5	Yes	Wiens 1995, 2002; Wiens and Zitzmann 2003a,b
N. c. coucang	Malaysia	Pasoh Forest Reserve, Sungai Tekam Forestry Concession	16	Limited	Barrett 1984
N. pygmaeus	Vietnam	Cuc Phuong National Park	24	Yes	Streicher 2003, Streicher 2004

[1] WWF, World Wildlife Fund.

Table 3.3 Physical Characteristics: Body Weights of Wild Caught Individuals, Unless Otherwise Noted

TAXA	ADULT MALE (G)			ADULT FEMALE (G)			BOTH SEXES (G)		
	AVERAGE	RANGE	*N*	AVERAGE	RANGE	*N*	AVERAGE	RANGE	*N*
Galaginae									
Galagoides demidovii	60	52–72	17	55	45–68	16	57	45–72	33
G. thomasi	82	74–88	6	75	59–85	6	78	59–88	12
G. orinus							89.6	74–98	3
G. zanzibaricus							149		23
G. rondoensis	69.2	60–73	7	66.5		3	69.1		7
G. cocos	150	130–183	35	137	118–155		38		
G. granti							134		5
Galago moholi	360[1]	±72	9	266[1]	±47	10	202[1]		1
G. moholi	186.1	±16.3	20	162.8	±16.3	20	200	177–250	
G. matschiei							196–225	210	
Euoticus elegantulus							300	270–360	39
E. pallidus								182–210	
Sciurocheirus alleni cameronensis	280.5	265–307	3	258	246–355	10	288	258–319	4
S. alleni (Bioko)	429		1	446	395–502	5	443	395–502	6
S. gabonensis							260	188–340	17
Otolemur garnettii	690–1,060	846	14	805	604–985	11	842	604–1,060	25
O. crassicaudatus	1,510		9	1,258		8			
Perodicticinae									
Perodicticus potto potto							600		
P. p. edwardsi (Gabon)							1,100	850–1,600	33
P. p. edwardsi (Cameroon)	1,502	938–1,795	8	1,572	1,407–1,858	4	1,524	938–1,858	12
P. p. ibeanus	920		1	861	847–875	3			
Arctocebus aureus							210	150–270	30
A. calabarensis	318	315–320	2	298	270–325	9			
Lorisinae									
Loris lydekkerianus lydekkerianus	294.4	267–322	4	260	227–292	6	273	227–322	10
L. l. malabaricus[1]	222.14	180–275	6	189	168–210	2			
L. l. nordicus		228–285	4		238–287	5			
L. l. grandis	204.1		1	238.1		1			
Loris tardigradus tardigradus	162	153–172	2	118	103–148	3	137	103–172	5
L. t. nycticeboides	140		1	190		1	165	140–190	2
Nycticebus bengalensis	1,134		1	1,400		1		1,588–1,605	
N. coucang	737	±111	8	637	±61	11			
N. menagensis								265–300	3
N. pygmaeus	418 ± 98	367–578	70	422 ± 88	360–543	97			

[1] Captive.

China, northeast India, Laos, northern Thailand, and Vietnam. The greater slow loris (*N. coucang coucang*) is found in Indonesia, Malaysia, and Thailand. The Javan slow loris (*N. javanicus*) occurs only in Java. The Bornean slow loris (*N. menagensis*) is found in Brunei, Indonesia, and Malaysia. Finally, the pygmy or lesser slow loris (*N. pygmaeus*) is found in Cambodia, China, Laos, and Vietnam. Most authorities do not recognize *N. intermedius* but class it together with *N. pygmaeus*. A recent study by Streicher (2003, 2004) revealed that the characteristics that distinguished *N. intermedius* were in fact seasonal coat and body weight changes of *N. pygmaeus* (Fig. 3.1).

PHYLOGENETIC RELATIONSHIPS

The evolutionary history of the lorisiform primates has been the subject of a comprehensive review (Rasmussen and Nekaris 1998) and will be only briefly recapped here. Until recently, most evidence for lorisiform origins pointed back to the Miocene of East Africa. Intense debate characterizes the subfamilial designation of the three best-known early Miocene forms, *Mioeuoticus*, *Progalago*, and *Komba*. Both cranial and postcranial features have allied these genera with either lorisines or galagines (Le Gros Clark 1956, Walker 1969, Gebo 1986, McCrossin 1992). Other authors have

(A)

(B)

(C)

(D)

Figure 3.1 Photographs illustrating different genera within the Lorisidae: (A) *Loris tardigradus* tardigradus (K. A. I. Nekaris); (B) *Nycticebus pygmaeus* (U. Streicher); (C) *Galagoides rondoensis* (A. W. Perkin); (D) *Arctocebus calabarensis* (C. Wild);

Figure 3.1 (*cont'd*) (E) *Sciurocheirus* sp. (L. Ambrose); (F) *Perodicticus potto edwardsi* (E. R. Pimley); (G) *Otolemur crassicaudatus* (S. Bearder); (H) *Galago moholi* (S. Bearder).

suggested that basal lorisiforms may have demonstrated a combination of lorisine cranial characteristics and galagine postcranial adaptations (Rasmussen and Nekaris 1998). Two newly discovered fossils may resolve this debate, making lorisiform origins even earlier than previously thought. *Karanisia* and *Saharagalago*, based on analysis of dental characteristics, are putative early lorises and galagos, respectively, from late Eocene sites at the Fayum Depression in Egypt (Seiffert et al. 2003). True, unrefuted lorisines (*Nycticeboides simpsoni*) and galagines (*Galago howelli* and *G. sadimensis*) occur in the fossil record of the late Miocene of Pakistan and early Plio-Pleistocene of Ethiopia and Kenya.

Some authors have attempted to resolve the phylogenetic relationships of the lorisiforms with molecular and morphological evidence (Bayes 1998, Masters and Brothers 2002,

Roos et al. 2004). Although the standard practice is to consider the Lorisinae a monophyletic group to the exclusion of the Galaginae, most molecular and morphological studies cannot resolve the position of the African pottos (Rasmussen and Nekaris 1998). Behavioral evidence allies Asian slender lorises more closely with galagos than with pottos (Bearder et al. 2002, Pimley 2002). It is not implausible that the galagos, pottos, and lorises share a common ancestor and form three monophyletic groups (Yoder et al. 2001a). Rasmussen and Nekaris (1998) and Nekaris and Rasmussen (2003) suggest that the cause for the divergence of these groups may have been a deviation in foraging strategies, with the galagos specializing on evasive prey, resulting in an emphasis on hearing and leaping, and the pottos and lorises concentrating on toxic prey, with a subsequent reliance on olfaction and a reduced basal metabolic rate, coinciding with slow

Table 3.4   Diet and Activity Budgets of Wild Lorisiform Primates Based on Long-Term Studies

TAXON	Diet					Activity Budget				
	ANIMAL PREY (%)	FRUIT (%)	GUM (%)	NECTAR (%)	OTHER (%)	REST (%)	TRAVEL (%)	FORAGE (%)	SOCIAL (%)	OTHER (%)
Galaginae										
Galagoides demidovii/thomasi[1]	70	19	10						25	
G. cocos	70	30	0	0						
G. moholi	52	0	48	0		4.5	25	63.9	5.9–18	0.6
Euoticus elegantulus	20	5	75	0					24	
Sciurocheirus gabonensis	25	73	0	2					14	
S. alleni cameronensis	55	55	0	0					0.6–30.5	
Otolemur garnettii	50	50	0	0		9.4	52.3	21	14.5	2.8
O. crassicaudatus	5	33	62	0					20	
Perodicticinae										
Perodicticus potto edwardsi	40	50			10				4	
P. p. edwardsi	11	67	22						0.2–44	
Arctocebus aureus	87	13							3	
Lorisinae										
Loris lydekkerianus lydekkerianus	96	1.2	2.8			36.4	35.6	26	23	2
L. l. nordicus	95	5				20.8	75.5 (includes forage)		49.5	3.7
L. tardigradus tardigradus	100.5					19.1	80 (includes forage)		43.7	0.9
Nycticebus coucang coucang	2.5	22.5	43.3	31.7		5.4	70.6	21	3	
N. c. coucang	29	71								
N. pygmaeus	33	–	63		4					

[1] During his study, Charles-Dominique did not recognize *G. thomasi* as a distinct species and, thus, all data were "lumped."

locomotion and life history. Further studies will surely elucidate these evolutionary relationships.

ECOLOGY AND BEHAVIOR

Diet

Only seven studies have focused in detail on the diet of lorisiforms, with one of these (Charles-Dominique 1977a) gaining most of its data from the analysis of stomach contents (Table 3.4). A number of brief studies provide us with preliminary knowledge of particular food preferences (e.g., Happold and Happold 1992, Tan and Drake 2001, A. W. Perkin, personal communication; A. B. Rylands, R. A. Mittermeier, and B. R. Konstant, unpublished report). Both direct observations and stomach content analysis have their limitations, but what is clear is that dietary choice among the lorisiforms is varied, including gum-eating specialists, highly frugivorous taxa, and some that are among the most faunivorous of all the primates.

Galagos are extremely varied in their diet, but all species appear to consume at least some gum; the ability to consume and digest gum may be a fundamental adaptation of this group (Bearder and Martin 1980a; Harcourt 1980, 1984; Nash 1989; Nash and Whitten 1998). Apart from this, the smaller-bodied taxa (e.g., *Galagoides demidovii*, *G.*

thomasi, G. rondoensis) rely more on insects, medium-sized taxa (e.g., *Galago moholi, Euoticus elegantulus*) add more exudates to their dietary repertoire, and the largest of the galagos (e.g., *Sciurocheirus* sp., *Otolemur* sp.) increase their intake of fruit. Non-toxic orthopterans and beetles comprise the invertebrate portion of galago diets (Bearder and Doyle 1974b, Harcourt and Nash 1986a), and the fruits eaten by galagines are in general sweet and soft (Charles-Dominique 1977a). Preliminary observations of a yet unnamed taxon in south-eastern Tanzania indicate yet another feeding behavior, that of consuming floral nectar, suggesting an important role by this primate in pollination, not unlike that of the Malagasy *Eulemur mongoz* or the greater slow loris *N. coucang* (see below) (A. W. Perkin, personal communication; A. B. Rylands, R. A. Mittermeier, and B. R. Konstant, unpublished report).

Galagos have adapted to their varied diet through a variety of morphological and behavioral adaptations. All galagos are capable of localizing animal prey with the help of their particularly large and independently mobile ears and frequently use this sense to detect prey items that are out of sight. They also search for insects visually and find sources of gum using their keen sense of smell (Bearder 1969, Charles-Dominique 1977a, Hladik 1979, Pariente 1979). As with all strepsirhines, insects are grabbed in the hands in a stereotyped fashion involving control of the whole hand

as the individual fingers cannot be moved independently (Martin 1990). The toothcomb plays an important role in scraping gum from trees, and gum can be cleaned from between the teeth using a serrated cartilaginous sublingual, a second type of tongue located underneath the main tongue that is notched at the tip like a saw. Gum is processed in an elongated cecum containing microorganisms capable of digesting the complex polymerized sugars. *Euoticus* spp., which eat mainly gum, have additional specializations in the form of enlarged canines and premolars for exposing sources of gum and *keeled* (pointed) nails, allowing the animals to cling to large tree trunks and reach exudates that would otherwise be inaccessible (Osman Hill 1953, Charles-Dominique 1977a, Ambrose 1999). Galagos living in seasonal environments in South Africa may rely almost completely on carbohydrate-rich gum in the cold winters and reduce their activity accordingly (Bearder and Martin 1980a). Squirrel galagos (*Sciurocheirus* spp.), which usually feed on fallen fruits, are reported to eat rapidly and even swallow fruits whole, allowing them to fill their stomachs within minutes and retreat to areas safer from potential predators (Charles-Dominique 1977a).

Only limited observations are available of potto feeding behavior (Jewell and Oates 1969, Charles-Dominique 1977a, Oates 1984, Pimley 2002). In general terms, pottos (*Perodicticus* spp.) are mainly frugivorous but supplement their diet with a considerable amount of gums and animal prey, including ants, slow-moving arthropods, birds, and bats. Pottos are possessed with somewhat more powerful jaws than galagos and are able to consume fruits and stationary animal prey, in particular caterpillars and noxious beetles. Dietary conditioning is exhibited by all the African strepsirhines, whereby a young animal learns to eat by snatching food from its parent and examining novel food items with a curious, head-cocking movement (Bearder 1969, Charles-Dominique 1977a). This developmental behavior may be particularly important for the angwantibos (*Arctocebus* spp.), which process irritant prey in a specific manner (e.g., removing the hairs from caterpillars) before they can be consumed without discomfort.

In a detailed study of sympatric galagos (*Galagoides demidovii*, *G. thomasi*, *Euo. elegantulus*, *Sciurocheirus gabonensis*) and pottos (*P. p. edwardsi*, *A. aureus*) in Gabon, Charles-Dominique (1974a, 1977a) revealed classic dietary partitioning between nocturnal primate species that ensured they avoided competition. Species that spent most time in the forest canopy concentrated mainly on insects (*Galagoides*), gums (*Euoticus*), or fruits (*Perodicticus*). Species that preferred the undergrowth subsisted on caterpillars (*Arctocebus*) or fallen fruits (*Sciurocheirus*). Some years later, it was discovered that the dwarf galagos in Gabon were in fact two different species that live together throughout the tropical forests of central Africa (*Galagoides demidovii* and *G. thomasi*) (Wickings et al. 1998). Both these species prefer insects, but not surprisingly, one moves mainly in the canopy (*G. thomasi*) and the other is restricted to the

undergrowth (*G. demidovii*), where it consumes fast-moving insects in contrast to the noxious forms eaten by angwantibos (*A. aureus*). Similar separations occur between sympatric species in other parts of Africa. For example, in the Rondo Forest of southeastern Tanzania, Garnett's galagos (*O. garnettii*) forage in the canopy, Grant's galagos (*Galagoides granti*) use the middle story, and Rondo dwarf galagos (*G. rondoensis*) remain approximately 1 m above the ground and feed almost exclusively on insects and grubs from the leaf litter (Honess 1996).

Detailed observations have been made on the diet of three slender loris taxa. *L. l. lydekkerianus* was the focus of a long-term study (Nekaris and Rasmussen 2003), whereas *L. l. nordicus* and *L. t. tardigradus* were the subjects of short-term studies (Petter and Hladik 1970, Nekaris 2002, Nekaris and Jayewardene 2003). These studies concur that slender lorises are among the most faunivorous of primates (very like tarsiers, see Chapter 5). They specialize on prey of small size classes and are highly tolerant of toxic prey such as ants and darkling beetles (Tenibrionidae). Prey items are consistently eaten head first, followed by the animal lapping at the innards. Those insects which emit irritant sprays are removed individually from the colony, taken several meters away, and consumed while the loris slobbers, closes its eyes tightly, and shakes its head, all combined to produce what can be aptly termed a "disgust face." Although gum comprised a portion of the diet of *L. l. lydekkerianus*, it was not seen to be consumed by other taxa. Consumption of plant material was minimal to nonexistent. Vertebrates, particularly geckos and lizards, were consumed by all three taxa but comprised a large portion of the diet of *L. t. tardigradus* (Nekaris and Rasmussen 2003, Nekaris and Jayewardene 2003).

According to Barrett (1984), the greater slow loris (*N. coucang coucang*) predominantly eats fruit, supplemented by insects. A more detailed study of this species in Malaysia was conducted via direct observation and fecal analysis (Wiens 2002, Wiens and Zitzmann 2003a). This population consumed mainly nectar, gum, and sap, with fruit and arthropods comprising only a small portion of the diet. Nectar from the flowers of the Bertram palm (*Eugeissona tristis*) comprised more observations than any other dietary item, with animals spending up to 30 min feeding from these nectaries (Wiens 2002, Wiens and Zitzmann 2003a). Preliminary results of pygmy lorises (*N. pygmaeus*) suggested that they too rely on nectar (particularly *Saraca dives*) and gum, visit the same sites often, and leave noticeable gouges in the tree trunks (Tan and Drake 2001, Streicher 2004). As for galagos, gum is probably an important component of the diet during cold Vietnamese winters (Streicher 2004). Consumption of insects, including ants and moths, is relatively common; and processing of these prey items mirrors that of slender lorises (Streicher 2004). *N. pygmaeus* and *N. bengalensis*, sympatric in many parts of their range, are known from preliminary observations to share feeding sites; nothing is known about how they partition their niches (Duckworth 1994).

ACTIVITY PATTERNS AND LOCOMOTION

Activity

Very few activity budgets for the lorisiforms have been reported in the literature, but those that have are summarized in Table 3.4. What is clear is that all the lorisiforms are nocturnal in their activity patterns, with no diurnal or cathemeral species. Animals are not precluded from being active in daylight, however, and may do so in order to change position for thermoregulatory purposes, to eat during periods of intense food scarcity, and to avoid predators (Bearder et al. in press). What is becoming clearer is that, at least in more open habitats, activity patterns change with the amount of light available. *G. moholi*, for example, increased its behavior and range of travel patterns during the light moon and during periods of twilight, while *L. l. lydekkerianus* maintained activity regardless of moon phase (Bearder et al. 2002). Galago species living in closed forest, on the other hand, do not appear to be influenced by changes in the level of moonlight (Nash 1986). It is clear that further studies of nocturnal primates must take account of the importance of moonlight.

Locomotor Behavior

As the feature that is most often used to characterize this infraorder of strepsirhines, locomotion is possibly the best-studied aspect of their behavior (Table 3.5), forming the basis for entire field studies (Crompton 1980, 1983, 1984) and for numerous captive studies (e.g., Dykyj 1980, Glassman and Wells 1984, Oxnard et al. 1990, Ishida et al. 1992, Demes et al. 1998). A complex suite of morphological traits linked to locomotion differentiates the galagos from the pottos and lorises (Charles-Dominique and Bearder 1979). All taxa of galagos have long tails and elongated tarsal bones and are characterized by intermembral indices <100, whereas pottos and lorises, to varying degrees, have reduced or lost their tails and have intermembral indices close to 100 (Martin 1990). As a result, galagos can cross gaps by hopping and leaping, while lorises and pottos do this by stretching. Similarly, galagos usually evade predators by swift locomotion, whereas lorises and pottos have developed a suite of morphological characteristics that allow them to remain still for prolonged periods and to provide camouflage and protection if attacked (Charles-Dominique 1977a, Bearder 1987, Nekaris 2001). For example, both pottos and lorises exhibit features that allow for prolonged grip with no fatigue, such as shortened second digits on the hands and feet, highly mobile ankles and wrists, and retia mirabilia of the proximal limb vessels (Rasmussen and Nekaris 1998). Retia mirabilia are arteries and veins in the arms and legs that subdivide extensively to form networks of intertwining vessels which act as storage units, allowing blood to flow freely. Thus, the exchange of oxygen and waste materials in the muscles continues even though there is no bodily movement.

Perodicticus also possesses a scapular shield, a structure produced by a combination of raised apophyseal cervical spines, some of which protrude above the skin in the form of tubercles, which are covered by thick skin and bristles of sensory hair, which also extend to a wider nuchal region. This structure is used to provide defense against predators and possibly other pottos (Charles-Dominique 1977a). Slow lorises have developed an even more elaborate defense mechanism, that of being toxic. Before biting prey items or predators, slow lorises combine a secretion from brachial sebaceous glands with their saliva in order to produce a numbing poison, which can send humans into anaphylactic shock (Alterman 1995, Fry and Fry 2003). It is rumored that they also use this solution to cover their parked infants, although this is yet to be verified by field data.

Although vertical clinging and leaping is considered the quintessential galago locomotor mode, it is used by most galagos only to negotiate gaps between trees. Only a few taxa, such as *Sciurocheirus* spp. and *Galagoides rondoensis*, use it as their stereotypic mode of locomotion (Charles-Dominique 1977a, Honess 1996, Perkin 2002, Pimley 2002). In fact, *Otolemur* spp. rarely uses this mode of locomotion, although capable of leaping and bipedal hopping (Crompton 1983, Harcourt and Nash 1986a). These larger galagos are surprisingly monkey-like in their locomotion and regularly move quadrupedally through the trees on relatively broad and horizontal supports. Many of the smaller galagos (*Galagoides*) maneuver through the networks of tiny branches by quadrupedal running, climbing, and agile jumping (Charles-Dominique 1972, Ambrose 1999). Several taxa can cross the ground by walking or running (e.g., *Otolemur crassicaudatus*) or bipedal hopping (e.g., *O. garnettii*, *G. moholi*, and *G. moholi*), whereas others are strictly arboreal (e.g., *Galagoides* spp. and *Euoticus* spp.).

The absence of active leaping and the use of *cantilevering* (bridging or extending the body) to move across arboreal gaps are the key features that distinguish perodicticine and lorisine locomotion from that of the galagines (Sellers 1996). Both pottos (*Arctocebus* spp., *Perodicticus* spp.) and lorises (*Loris* spp., *Nycticebus* spp.) use their long bodies and flexible limbs to stretch across gaps in the canopy and, based on their body weights, require a certain gauge of branch to sustain their weight during the crossing (Charles-Dominique 1974b, Nekaris 2001). Unlike galagos, which can charge through the trees changing directions, the "slowness" of loris and potto locomotion comes from testing branches and having to back up and move position in the canopy to find a suitable crossing point (Charles-Dominique 1977a, Nekaris 2001). However, this progression need not be slow-paced. Captive studies have shown that the slender loris (*L. l. malabaricus*) is capable of a locomotor mode called the "race walk" (Demes et al. 1998). Wild *L. tardigradus* and *N. pygmaeus* regularly quadrupedally run and even negotiate gaps with mini-leaps, rearing up on their hindlegs and hurtling their bodies over gaps of several inches (Duckworth 1994, Nekaris and Stevens 2005). Even

Table 3.5　Locomotion and Habitat Use

TAXON	CHARACTERISTIC LOCOMOTION	USE OF STRATA/SUPPORTS WHEN ACTIVE	SLEEPING SITES	SLEEPING ASSOCIATIONS	HABITAT TYPE OF STUDY SITE
Galagoides demidovii	Fast-moving: mainly quadrupedal	0–5 m in dense secondary undergrowth, <1 cm fine branches and liane curtains, occur on roadside	Spherical leaf nest or dense vegetation, few sites	2–10 female w/offspring; male often sleeps alone	Primary equatorial rain forest
G. cocos	Fast-moving: mainly hopping and quadrupedal running	Ground to canopy (0–13 m), prefers undergrowth	Tree hollows, few sites	male sleeps with one or 2 female w/offspring	Lowland dry forest on coral rag
G. rondoensis	Vertical clinging and leaping from thin stems	Low-diameter perches (<3 m), small vertical supports (3.0 cm)	Flat and leafy nests in high trees (5 m)	At least 3	Lowland evergreen and semievergreen forest
G. orinus	Quadrupedal running and walking	Canopy dwellers (20 m)	Nests of leaves and twigs set in lianes	At least 1–3	Natural montane evergreen forest
G. granti	Agile jumping, quadrupedal climbing and walking	Mid-strata (5–7.5 m), 8.0 cm diameter vertical supports	Tree holes	4–5 individuals	Lowland and coastal forest
G. zanzibaricus (*udzungwensis*)	Quadrupedal walking and running	Upper strata (10 m): thick secondary growth and vine tangles, small horizontal perches	Tree hollows or secondary growth tangles	Male & female pair and offspring	Natural lowland evergreen forest
Galago moholi	Active leaping, bipedal hopping	Ground to upper canopy, prefer lower strata (0–4 m), use small vertical supports	Flat leaf nest, tree hollow or branch fork in a thorn tree	1–8; males never together but with 2 or more female w/offspring	Acacia woodland savanna
G. moholi	Leaping and bipedal hopping	Ground to mid-canopy (1–4 m), can cross open ground	Tangled vegetation and tree holes at 1–2 m, human-made bee hives	At least 1–3	Savanna *Acacia* thorn scrub, *Cynometra* thicket, and open woodland
Euoticus elegantulus	Running, leaping, and climbing	Canopy (5–35 m), use large-caliber branches and vines	Branch fork in dense shelter of foliage	1–7	Primary equatorial rain forest
E. pallidus	Quadrupedal running and leaping	Prefer upper strata (4–12 m), use large horizontal supports	Branch fork in dense shelter of foliage	At least 1–4	Primary equatorial rain forest
Sciurocheirus gabonensis	Active leaping	Undergrowth (1–2 m), prefer vertical supports			Primary equatorial rain forest
Sciurocheirus sp. nov. (Makande Allen's Galago)	Vertical clinging and leaping	Lower–mid-canopy (0–5 m), vertical substrates <10 cm		1–4	Primary equatorial rain forest
S. alleni cameronensis	Vertical clinging and leaping	Ground to mid-canopy (0–5 m), 2–5 cm vertical supports	Tree holes and woody lianes at 1–4 m	At least 2–3	Secondary forest and farm bush
Otolemur garnettii	Quadrupedal running, leaping, and bipedal hopping	Mid- to upper canopy 50% of the time, horizontal substrates >5 cm	Tangled vegetation, hollows rarely, many sites	1–4, male and female w/offspring	Coastal forest
O. crassicaudatus	Monkey–like quadrupedal walking and running, some leaping, no hopping	Low strata of canopy	Tangled vegetation or flat leaf nest, few sites	1–4, male and female w/offspring	Riverine forest
Perodicticinae					
Perodicticus potto edwardsi (Cameroon)	Slow climbing	Canopy at 6–10 m on 2–5 cm oblique branches	Leafy part of canopy at 10–30 m	1–3 individuals with male & female pairs	Farm bush, disturbed and secondary forest
P. p. edwardsi (Gabon)	Slow climbing	Canopy at 5–30 m, level branches and lianes of 1–15 cm diameter	Dense tangles or clumps with branches or forks	1–3, usually male sleeps alone, female w/offspring	Farm bush, primary and secondary forest
Arctocebus calabarensis	Slow climbing	Small branches, twigs, climbers	Dense vegetation	1–2, adults sleep alone, female w/offspring	Forest edges and tree fall zone
A. aureus	Slow climbing	0–5 m in undergrowth, <5 cm branches and lianes, use ground often	Dense vegetation	1–2, adults sleep alone, female w/offspring	Forest edges and tree fall zone
Lorisinae					
Loris lydekkerianus lydekkerianus	Quadrupedal climbing, walking, and cantilevering	Understory (<5 m), prefer oblique branches (1–5 cm), cross open ground and roads	Vine tangles, dense branches, few sites	1–7, female w/offspring and 1 or femore male	Acacia scrub forest
L. l. nordicus	Quadrupedal climbing, walking, and cantilevering	Dense understory (<5 m), oblique branches (1–5 cm), cross open ground and roads	Vine tangles, dense branches, few sites	At least 1–6, female w/offspring and 1 or more male	Acacia scrub forest
L. tardigradus tardigradus	Quadrupedal climbing and running	Understory to canopy (0–15 m), prefer horizontal and vertical branches, and rely on vines	Vine tangles, dense branches, few sites	At least 1–4, female w/offspring and 1 male	Monsoon rain forest
Nycticebus coucang coucang	Slow climbing	Trunks, branches, and lianes <10 cm, mid- to upper canopy, will use understory in disturbed forest	Trees, palms, shrubs, lianes at 1.8–35 m; many sites	1–3, female w/offspring, sometimes 1 male	Primary forest, logged over forest, padang savanna
N. pygmaeus	Quadrupedal climbing and running	"Steady trails through vegetation;" come to ground if substrate is discontinuous	Dense scrub, or fairly exposed and high terminal branches	?	Forested limestone hills, plantation forest and scrub

Table 3.6   Range Size and Range Use Patterns for Wild Populations

TAXA	AVERAGE HOME RANGE (HA)	ADULT MALE (HA)	ADULT FEMALE (HA)	MALE OVERLAP	FEMALE OVERLAP	MALE & FEMALE OVERLAP	METHOD	INFERRED SOCIAL ORGANIZATION
Perodicticinae								
Perodicticus potto edwardsi (Pimley 2002)	28.4	30.6	31.5	P: 29%	P: 25%	P: 47%	Kernel	Semidispersed unimale/unifemale
P. p. edwardsi (Charles-Dominique 1977a)		17.8	7.5	A	Limited	P	mcp	Dispersed unimale, multiple female
Lorisinae								
Loris lydekkerianus lydekkerianus	2.5	3.6	1.59	P: 20%	P: 57%	P: 14%	mcp	Semidispersed multimale
L. l. nordicus				P	P	P		?
L. t. tardigradus				P	No data	P		?
Nycticebus coucang coucang (Wiens and Zitzmann 2003b)	2	0.8	2.1	No data	No data	P: 80.6%	mcp	Semidispersed unimale/unifemale
N. c. coucang (Wiens and Zitzmann 2003b)	6.4	7.35	4.8	No data	No data	P: 97.8%	mcp	Semidispersed unimale/unifemale
N. c. coucang (Wiens and Zitzmann 2003a)	18.1	22	10.4	No data	No data	P: 94.6%	mcp	Semidispersed unimale/unifemale
N. c. coucang (Barret 1984)			4.19	Rarely	P	P	mcp	?
N. pygmaeus	3.1							?
Galaginae								
Galagoides demidovii/thomasi		0.5–2.7	0.6–1.4	P	P	P	mcp	Dispersed multimale
G. cocos		2.2	1.8	P (slight)	P	P	mcp	Spatial monogamy
G. moholi		9.5–22.9	4.4–11.7	P	P	P	mcp	Dispersed multimale
Sciurocheirus gabonensis		30–50	8–16	A	P	P	mcp	Dispersed harem
S. alleni cameronensis		2.84	1.97	A	P: 58%	P: 31%	Kernel	Dispersed multimale
Otolemur garnettii		17	12	P: different age classes	P: different age classes	P: extensive overlap	mcp	Dispersed multimale

A, overlap absent; mcp, minimum convex polygon; p, overlap present.

P. p. edwardsi has been described to have a mini-leap, when it simply cannot negotiate a gap with any amount of stretch (Charles-Dominique 1977a).

Locomotion has been implicated as a factor affecting the ranging behavior of the lorisiforms, with galagos able to cross a larger home range and return to dispersed sleeping sites with greater regularity than the pottos and lorises (Charles-Dominique 1977a, 1977b; Oates 1984). Table 3.6 shows that, in fact, home ranges of similar-sized galagos and lorises are of comparable area. Despite initial suggestions that both pottos and lorises move as little as 10 m per night, studies conducted with all-night follows (Nekaris 2003a, Bearder et al. in press) and with radiotracking (Wiens and Zitzmann 2003b, Pimley et al. in press) have shown much more extensive ranging. For example, pottos (*P. p. edwardsi*) may move up to 6 km in one night, gray slender lorises (*L. lydekkerianus*) move several hundred meters, red slender lorises (*L. tardigradus*) travel up to 1 km per night, and greater slow lorises (*N. c. coucang*) travel up to 400 m per hour.

Habitat Use

As already noted when illustrating dietary partitioning, the lorisiforms also show a wide preference for use of both

substrates and strata in the forest (e.g., Crompton 1983, Honess 1996, Ambrose 1999, Nekaris 2001, Pimley 2002, Nekaris et al. in press). Substrate size selection is almost always related to the body weight of the animal, with smaller animals moving on smaller-gauged twigs, branches, and lianas and larger animals negotiating sturdier supports with greater girth. An exception is made by *Euoticus*, which makes more use of large vertical supports (Charles-Dominique 1977a). A number of species (e.g., *S. gabonensis*, *Galagoides demidovii*, *A. aureus*, *L. lydekkerianus*) thrive in the undergrowth and in tree fall zones, whereas others (*G. orinus*, *N. coucang*) prefer the canopy. This ecological division is what allows the African lorisiforms in particular to occur in sympatry in many places throughout their range (Charles-Dominique 1977a) and may influence the distribution of sympatric Asian lorises (Duckworth 1994).

SOCIAL ORGANIZATION

Because of the difficulty of nocturnal observation, especially of taxa living in dense tropical rain forest, direct observations of social behavior may be limited (Sterling et al. 2000). Observations of associations between conspecifics, especially at sleeping sites, contribute to our knowledge of the social

lives of lorisiforms; but for the most part, indirect obser-vation has been more fruitful. Therefore, studies of communi-cation and patterns of home range overlap have provided the bulk of our knowledge of social behavior, supplemented by a few studies using radio tracking.

Olfactory Communication

One of the most understudied areas of lorisiform social behavior is that of olfactory or chemical communication aided by an acute sense of smell and Jacobson's organ in the roof of the mouth, which senses liquid chemicals transferred from the moist nose (Schilling 1979, Martin 1990). Nocturnal lorisiforms communicate both with a number of specialized scent glands as well as with urine, which has also been shown to play an important role in enhancing an animal's grip during locomotion (Welker 1973, Harcourt 1981). The visual systems of nocturnal lorisiforms are highly sensitive and are supplemented by olfactory communication (Bearder et al. in press). The main advantage of olfactory communi-cation via scent gland and urine marking in general is that it conveys information that is indirect and deferred in time, with a result that individuals do not have to come together in order to communicate. Although its prevalence has never been questioned, the difficulty of studying olfactory behavior has led to few systematic studies. Captive studies of pygmy lorises (Fisher et al. 2003a,b), Senegal galagos (Nash 1993), and thick-tailed galagos (Clark 1978a,b, 1982a,b) have shown the ability of nocturnal primates not only to differentiate the state of sexual receptivity of conspecifics using scent but also to recognize specific individuals of different age and sex classes. In fact, Clark (1985) suggested that the ability for fine olfactory differentiation contributed to increased gregariousness among *O. crassicaudatus*. In the only sys-tematic study of olfactory behavior in free-ranging nocturnal lorisiformes, Charles-Dominique (1974b, 1977b) showed that, rather than using scent as trails, the sympatric taxa he studied scent-marked in specific areas, with clear signals serving for sexual attraction and avoidance.

Vocal Communication

More easily studied than olfaction, vocalizations have been invaluable for understanding the social behavior of galagos and, to a lesser degree, of lorises (Bearder et al. 1995, 2002; Honess 1996; Zimmermann et al. 1988; Zimmermann 1990, 1995a; Anderson et al. 2000; Coultas 2002). Since animals can always remain silent, their calls invariably reflect cir-cumstances where they benefit in some way and, therefore, provide a strong clue to important aspects of their ecology and social behavior. For example, calls are given when it is advantageous to attract and maintain contact with com-panions, increase distance between rivals, warn kin of the presence of dangers, and warn potential predators that they have been detected. In the case of galagos in particular, the safety provided by living in trees at night and the ability to escape rapidly if detected means that they can communicate effectively by sound even when they appear to be alone. They have a rich vocal repertoire of 8–25 structurally dis-tinct calls, including sounds that are *discrete* (relatively in-variable) and others that are *graded* (continuously changing from one form to another). Added to this, galagos are able to mix different calls into rapidly changing sequences that can sometimes last for over 30 min at a time. Calls are used during short-range social interactions, with some variation between animals of different age and sex; but each species also has some calls that are loud and used when mobbing predators, attracting partners, or repelling rivals. Fortunately for researchers, every species has one particular loud call that is common to both sexes and used to advertise their pre-sence to companions and rivals. Since this call helps to bring mates together, it is invariably species-specific, remaining more or less constant across the entire geographical range of each species, thereby providing a convenient diagnostic tool for identifying new species (Courtenay and Bearder 1989; Masters 1991; Zimmermann 1995a,b; Anderson et al. 2000).

The less agile pottos and lorises as a group are not so obviously vocal, but unlike galagos, some of their calls in-clude sounds in the ultrasonic range that remain inaudible to humans without a bat detector (Zimmerman 1985, Schulze and Meier 1995b, Nekaris and Jayewardene 2004). Still, some species, such as three slender loris taxa (*L. t. tardigradus*, *L. l. lydekkerianus*, and *L. l. nordicus*), are known to call throughout the night. Although the calls of Mysore slender lorises were not bioacoustically analyzed, they have several functions, including spacing, aggression, affiliation, and dawn assembly (Nekaris 2000, Bearder et al. 2002). At least six loud whistles with different functions have been identified for both *L. t. tardigradus* and *L. l. nordicus* (Coultas 2002). The latter species in captivity clearly uses one of these whis-tles for territorial spacing (Schulze and Meier 1995b), and one of these calls also has this function in the wild (Nekaris and Jayewardene 2003). Further studies of vocal repertoires within these species should prove to be rewarding.

Social Behavior

Nocturnal primates in general are typically described as solitary, despite extensive efforts by individuals studying them to dispel the use of this term (Charles-Dominique 1978, Bearder 1987). Sterling (1993) recommended that three components be used to aid in emphasizing the diver-sity of nocturnal primate social organization. The first of these, the social system, relates to social behavior and relationships within a group. Many of the lorisiforms engage in considerable amounts of social behavior. Table 3.4 com-pares the percentage of the active period that lorisiforms were seen together or in close proximity. This percentage does not include time spent communicating by scent or vocal communication, as described above. Although these figures also include mothers with their dependent offspring (e.g., *A. aureus*), a number of authors have pointed out that many adult nocturnal primates spend time together outside the breeding season, foraging and feeding (e.g., lesser

galagos, Bearder and Martin 1980b, thick-tailed galagos, Clark 1985, Rhadakrishna and Singh 2002, Mysore slender lorises, Nekaris 2003a). Some taxa spend up to 50% of their time in social proximity with adult conspecifics. Variability also exists in choice of companions. Among *Galago moholi*, for example, females were the most common social partners (Bearder and Doyle 1974b), whereas in *L. l. lydekkerianus*, females formed positive affiliations only with multiple adult males (Nekaris 2002, 2003a; Rhadakrishna and Singh 2004). When compared with diurnal primates, the figures for social interactions among nocturnal primates fall well within the range of diurnal monkeys and apes (see Chapter 39). This is excluding the fact that most nocturnal lorisiforms sleep in close proximity (e.g., *Perodicticus* and *Nycticebus*) or in gregarious groups (most galagos and slender lorises) (Table 3.5), where social cohesion behaviors such as grooming and huddling take place.

Ranging

Determination of home range overlap via radio tracking or extended observation in open environments further elucidates the varied social relationships of the lorisiforms and defines the second descriptor recommended by Sterling (1993), that of the spacing system. Building on pioneering work by Bearder (1987), Müller and Thalmann (2000) have constructed a framework by which home range overlap, or spacing system, can be used to illustrate the diversity among nocturnal mammal social organization. In this framework, grouping systems can be cohesive and gregarious, dispersed yet social, or solitary, meaning no social contacts are made outside the mating system (Müller and Thalmann 2000, Sterling et al. 2000). Adult sex composition mirrors that seen among diurnal primate social organizations, with single male and female units, single male and multiple female groups, single female with multiple male groups, and multiple male and female groups. Nine long-term studies have been conducted, which have determined the size and degree of overlap of the home ranges of lorisiform primates (Table 3.6). In the case of rain forest primates, where observation by any other means might prove impossible, radio tracking has become invaluable to infer social organization based on spacing patterns.

Table 3.6 summarizes the inferred social organizations of those lorisiforms studied to date; social organization of these primates has also been the topic of two reviews (Bearder 1987, Müller and Thalmann 2000). Most galagos appear to exhibit a dispersed multimale system, whereby males have larger home ranges than females and females form matrilocal clusters of related females that may sleep together. These related females tend to be aggressive toward those from other groups, whereas males may be aggressive toward one another (Bearder and Doyle 1974a, Charles-Dominique 1974a, Bearder and Martin 1980b). These males may be of different types, relating to age and status. For example, smaller resident males may be tolerated by the larger territorial males, others may be constantly on the move ("floaters"), and finally some males remain solitary during the process of dispersing from their natal groups (Charles-Dominique 1972, Bearder 1987). A one male, multiple female system may be present in *S. gabonensis*, where males are exclusively associated with small groups of females and have nothing but extremely aggressive contact with other males (Charles-Dominique 1974a, 1977a,b). Another exception is found in *Galagoides cocos*, which may form one male/one female or one male/two or three female associations, although variability between study sites shows some convergence with the general multi-male social organization (Harcourt and Nash 1986b).

Two different systems have been shown for *P. p. edwardsi*, the only potto for which home range data are available. Charles-Dominique (1977a) studied this species in a restricted forest environment where no matriarchies were present, with female home ranges isolated from one another. However, males may overlap their ranges with more than one female but tend to avoid one another, probably using scent. Not enough data are available from this study in order to classify the social organization (Müller and Thalmann 2000). A more recent study of the same subspecies of potto found that males and females shared their home ranges to the exclusion of other male/female pairs. These same pairs also slept together or very near one another on most occasions, suggesting a single male/single female spacing system (Pimley 2002).

Mysore slender lorises (*L. l. lydekkerianus*) exhibited limited range overlap between females, who were aggressive at territorial boundaries. Male ranges were much larger than those of females. One or more adult males shared sleeping sites with females; males were aggressive only to males from other sleeping groups. The spacing indicates a single male/single female and single male/multiple female system but is also combined with promiscuous mating, suggesting a multimale/multifemale social organization (Nekaris 2003a). Greater slow lorises (*N. c. coucang*) appear to exhibit a single male/single female social organization, with the most common groupings being an adult male and female pair and their dependent offspring. This assessment corresponds with low testes volume for this taxon (Wiens and Zitzmann 2003b). Nevertheless, a polygynous mating system may exist (see below) (Elliot and Elliot 1967).

The final aspect recommended by Sterling (1993) as necessary to understand nocturnal primate social complexity is knowledge of the mating system, that is, which animal actually mates and produces offspring with another. The study of molecular ecology for the understanding of lemur mating systems has recently taken off (e.g., Fietz et al. 2000; Radespiel et al. 2001, 2002). Due to difficulties in gaining permits, only two such studies are available for the lorisiforms. A recent elegant study (Pullen 2000, Pullen et al. 2000) showed that, despite their spatial advantages and despite fathering a majority of offspring in the study population, "alpha" lesser galagos, *Galago moholi*, were not always the fathers of infants. Furthermore, not all twins were fathered

by the same individuals (Pullen et al. 2000). These results are in line with both the testicular and copulatory evidence for this species, which suggests polygynandry. Pimley's (2002) molecular data for *P. p. edwardsi* at Mt. Kupe showed that offspring of mothers were not fathered by the male with which they were spatially paired. These data were in contrast to testicular volume data, which implied monogamy (see below), suggesting that the social system differed from the mating system (Pimley 2002).

REPRODUCTIVE STRATEGIES AND LIFE HISTORY

The life history strategies of the lorisiforms have been the focus of a number of captive studies (e.g., Manley 1966, 1967; Ehrlich and Musicant 1977; Doyle 1979; Izard and Rasmussen 1985; Rasmussen 1986; Rasmussen and Izard 1988; Ehrlich and Macbride 1989; Nash 1993; Weisenseel et al. 1998; Fitch-Snyder and Ehrlich 2003), yielding much of the information summarized in Table 3.7. A number of recent field studies, however, have supplemented the captive data, enhancing our knowledge of lorisiform life history

parameters, mating behavior, mating systems, and infant care (Gursky and Nekaris 2003). Recent reviews have summarized in detail aspects of the development patterns of nocturnal primates (Nash 1993) and the reproductive biology of the African lorisiforms (Bearder et al. 2003) and the slender lorises (Nekaris 2003b).

A number of reproductive parameters characterize the galagos, pottos, and lorises. All taxa, with few exceptions, give birth to either singletons or twins, with twin births being known from more than half the taxa studied at present. A number of taxa have two litters per year. Little is known about survivorship ratios of lorisiforms in the wild, but when it is mentioned, it is not uncommon for only one infant out of a potential four to reach sexual maturity. *Infant parking* is common among the lorisiforms. In general, the practice is for the mother to leave her infants on a branch or in a tree hole while she goes off to forage. The only variation seems to be whether the infant is parked throughout the night (most pottos and lorises) or carried with the mother for short distances and cached in multiple sites throughout the night (most galagos). Variation across taxa also exists in whether or not infants cling to the fur while carried or are

Table 3.7 Reproductive and Life History Parameters

TAXA	INFANTS/YEAR[1]	LITTER SIZE[1]	PARKING[1]	INFANT CARRIAGE[1]	GESTATION (DAYS)	WEANING (DAYS)	WEIGHT AT BIRTH (G)	AGE AT SEXUAL MATURITY (MONTHS)	DISPERSING SEX[1]	BREEDING SEASON?
Galaginae										
Galagoides demidovii	1–2	1	Yes	Mouth	111–114	40–50	5–10	8–10	Male	—
G. thomasi	—	—	Yes	Mouth	111–114	—	5–12	—	—	—
G. cocos	2–4	1–2	Yes	Mouth	120	49	16.5	—	Male	—
G. rondoensis	2	1?	Yes	Mouth	—	—	—	—	—	—
G. zanzibaricus (*udzungwensis*)	2	1	Yes	Mouth	—	—	—	—	—	—
G. granti	—	—	Yes	Mouth	—	—	—	—	—	—
G. orinus	—	—	Yes	Mouth	—	—	—	—	—	—
Sciurocheirus gabonensis	1–2	1	Yes	Mouth	133	—	24	8–10	—	—
S. alleni cameronensis	1–2	1	Yes	Mouth	—	—	—		Male	Yes
Galago moholi	1–2	2	Yes	Mouth	120–126	—	11–12	8.5	Male	Jan–Feb/Oct–Nov
G. moholi	1–2	1	Yes	Mouth	141 ± 2	70–98	19 ± 2.6	12–18	Male	Feb–Mar/June–July
G. matschiei	—	—	Yes	Mouth	—	—	—	—	—	—
Euoticus elegantulus	1	1	No	Fur	—	—	—	—	—	—
E. pallidus	1	1	No	Fur	—	—	—	10	—	—
Otolemur garnettii	1	1	Yes	Mouth/fur	126–138	140	—	12–18	Male	Possibly Oct/Nov
O. crassicaudatus	2–3	1	Rare	Mouth/fur	136	70–134	—	18–24	Male	Possibly Oct/Nov
Perodicticinae										
Perodicticus potto edwardsi	1/(2)	1	Rare	Fur	197 (193–205)	120–180	52, 30–42	6	Male	No, Aug–Jan high rate
Arctocebus aureus	1	1	Yes	Fur	131–136	100–130[1]	24–30[1]	9–10	—	No
A. calabarensis	1–2	1	Yes	fur	130	115	35	—	—	?, common Jan–Apr
Lorisinae										
Loris lydekkerianus lydekkerianus	1–4	1–2[1]	Yes	Fur	164 (160–166)[1]				Male or female	No[1]
L. l. malabaricus	1–4	1–2	Yes	Fur	166–169	120–150		11	—	No
L. l. nordicus	1–4	1–2[1]	Yes	Fur					—	No[1]
L. tardigradus tardigradus	1–4	1–2[1]	Yes	Fur	167–175				—	No[1]
L. t. nycticeboides		2[1]	?		174[1]				—	—
Nycticebus coucang coucang	1	1	Yes	Fur	165–175	85–180[1]	43.5	16–21	?	—
N. pygmaeus	1–4	1/2	Yes	fur	[1]					

[1] Data from wild animals or animals recently caught from the wild; all other date are from captive animals. —, no data available.

transported in the mother's mouth. Contrasting rates of life history among the galagos, pottos, and lorises are considered by some authors to be related to other locomotor and ecological differences among the three subfamilies (see Rasmussen and Nekaris 1998 for a review). The pottos and lorises are noted for having among the longest life history of any primates of their body size, including long gestation lengths followed by low birth weights and long periods of lactation, in contrast to galagos, which fall more in line with other primates of their body size (Martin 1990).

Interestingly, another feature uniting the lorisiforms is the absence of a single observation of infanticide in the wild. Although adults may kill infants under captive conditions, this has been shown to be due to stress or poor management rather than infanticide as an evolutionary strategy (Nekaris 2003a). In fact, male slender lorises regularly play with infants outside their sleeping groups. Males dispersing to a new area also show this behavior, even though it is highly unlikely that they are the fathers of infants. High reproductive output among twin-bearing lorisiforms with much opportunity for males to sire offspring suggests that infanticide has not played an important role in this infraorder (Manley 1966, Nekaris 2002, Bearder et al. 2003).

Dixson (1995, 1998) has pointed out that a number of features of the genital morphology and the copulatory behavior of nocturnal lorisiforms may provide evidence that the spacing system does not necessarily coincide with the mating system. For example, larger testes size or increase of testes size during a breeding season should be linked with a multiple male, multiple female mating system (*polygynandry*). The elaborate penile morphology of most lorisiforms might also serve to enhance female receptivity or genital lock or to break up copulatory plugs left by other males and might also provide a clue to the mating systems of these primates.

Information on dispersal is limited for most taxa. Many galagos appear to be matrilineal in their social organization, with males dispersing at sexual maturity and females either sharing a range with their mother or moving into a neighboring range (Bearder 1987). In Mysore slender lorises (*L. l. lydekkerianus*) and greater slow lorises (*N. c. coucang*), both males and females have been seen to disperse (Wiens 2002, Nekaris 2003b, Rhadakrishna and Singh 2004).

CONSERVATION STATUS

A cursory examination of Table 3.1 is enough to emphasize that very little is known about the conservation status of most nocturnal lorisiforms. Despite a number of surveys conducted for galagos (e.g., Honess 1996; Honess and Bearder 1996; Weisenseel et al. 1998; Butynski et al. 1998; Ambrose 1999; Ambrose and Perkin 2000; Perkin 2001a,b, 2002), pottos (Oates and Jewell 1967), and lorises (e.g., Barrett 1981; Duckworth 1994; Nekaris 1997; Singh et al. 1999, 2000; Fitch-Snyder and Vu 2002; Nekaris and Jayewardene 2004), a large proportion of species have been

described as "data-deficient." Where systematic studies have been conducted, they have almost always resulted in worrying conservation rankings (e.g., Nekaris 2003c). For example, one Sri Lankan loris (*L. t. nycticeboides*) and an unnamed species of galago (*Galagoides* sp. nov. 3) from Tanzania are considered critically endangered, and have been included on the recent list of the world's top 25 most endangered primates (Nekaris and Jayewardene 2004, Rylands et al. 2004). Although at this stage ranked as vulnerable, systematic surveys of pygmy lorises (*N. pygmaeus*) where virtually none have been seen suggest that they are more seriously threatened than the high availability in markets would suggest (Nekaris and Schulze 2004).

The paucity of studies on these African and Asian primates may lead them to be ignored at a time when they are facing severe human-induced threats. The bushmeat trade in Africa and the pet and biomedical trades in Asia are having detrimental effects on lorisiform populations (Ratajszczak 1998, Schulze and Groves 2004, Nekaris and Schulze 2004). Habitat loss in both Africa and Asia as a result of human population pressures also poses a severe threat to these species, which often go unconsidered in habitat development and planning (Erdelen 1988, Butynski 1996/97, Ratajszczak 1998). In Africa, human population growth rates are still increasing at 2.9% per annum (Butynski 1996/97). In Africa and Asia, clearing of the land for agriculture and deforestation for logging are the chief causes of forest loss (Mill 1995). Nocturnal prosimians may be at the greatest risk as they are asleep during the times of mass forest clearance, whereas other primates have the chance to flee. Sleeping nocturnal primates may be more easily burned alive or chopped down with the trees, collected, and sent to animal markets (Ratajszczak 1998, Schulze and Groves 2004). The tendency for lorises to cling to trees as they are cut, rather than fleeing, makes them an easy target for removal for the pet trade. Thus, whereas other animals can escape capture, lorises can be completely drained from areas of deforestation (Fitch-Snyder and Vu 2002, Streicher 2004). Furthermore, logging and human disturbance have been shown to adversely affect lorisiform density (Weisenseel et al. 1993, Nekaris and Jayewardene 2004). It is inappropriate to assume that healthy diurnal primate populations signify a healthy nocturnal primate population as the substrate and sleeping site requirements of these two groups of primates differ and surveys have often shown an inverse relationship in the presence of strepsirhine and haplorhine primates (e.g., Singh et al. 1999, 2000; Perkin 2001a; Nekaris and Jayewardene 2004).

Luckily, an increasing number of sanctuaries and reintroduction programs are being developed for Asian lorises, where the trade for pets and medicines is especially dire (Sanfey 2003, Nekaris and Schulze 2004, Streicher 2004). These sanctuaries operate in the face of stiff opposition from those who consider that priority should be given to "the more important" primates, such as gibbons and orangutans. Prosimians (strepsirhines and tarsiers) are in the unfortunate position of being relatively ignored by other conservation

action groups because they are primates and ignored by primatologists because they are not anthropoids. With advances in the understanding of species-level biology and the uncovering of more and more species, there is a genuine chance that species can be lost or assigned the status of critically endangered before they are even named (Bearder 1999). Future studies of individual species, equivalent to those conducted for day-living primates, will ensure that this genetically diverse and interesting group is no longer excluded from conservation initiatives.

REFERENCES

Alterman, L. (1995). Toxins and toothcombs: potential allospecific chemical defenses in *Nycticebus* and *Perodicticus*. In: Alterman, L., Doyle, G. A., and Izard, M. K. (eds.), *Creatures of the Dark: The Nocturnal Prosimians*. Plenum Press, New York. pp. 413–424.

Ambrose, L. (1999). Species diversity in West and central African galagos (Primates, Galagonidae): the use of acoustic analysis [PhD thesis]. Oxford Brookes University, Oxford.

Ambrose, L. (2003). Three acoustic forms of Allen's galagos (Primates; Galagonidae) in the central African region. *Primates* 44:25–39.

Ambrose, L., and Perkin, A. W. (2000). A survey of nocturnal prosimians at Moca on Bioko Island, Equatorial Guinea. *Afr. Primates* 4:4–10.

Anderson, M. (1998). Comparative morphology and speciation in galagos. *Folia Primatol.* 69(suppl. 1):325–331.

Anderson, M. J. (2000). Penile morphology and classification of bush babies (subfamily Galagoninae). *Int. J. Primatol.* 21:815–836.

Anderson, M. J. (2001). The use of hair morphology in the classification of galagos (Primates, subfamily Galagonidae). *Primates* 42:113–121.

Anderson, M. J., Ambrose, L., Bearder, S. K., Dixson, A. F., and Pullen, S. (2000). Intraspecific variation in the vocalizations and hand pad morphology of southern lesser bush babies (*Galago moholi*): a comparison with *G. senegalensis*. *Int. J. Primatol.* 21:537–555.

Barrett, E. (1981). The present distribution and status of the slow loris in peninsular Malaysia. *Malays. Appl. Biol.* 10:205–211.

Barrett, E. (1984). The ecology of some nocturnal, arboreal mammals in the rainforests of peninsular Malaysia [PhD thesis]. Cambridge University, Cambridge.

Bayes, M. K. (1998). A molecular phylogenetic study of the galagos, strepsirhine primates and archontan mammals [PhD thesis]. Oxford Brookes University, Oxford.

Bearder, S. K. (1969). Territorial and intergroup behaviour of the lesser bushbaby, *Galago senegalensis moholi* (A Smith), in semi-natural conditions and in the field [MSc diss.]. University of Witwatersrand, Johannesburg.

Bearder, S. K. (1974). Aspects of the ecology and behaviour of the thick-tailed bushbaby *Galago crassicaudatus* [PhD thesis]. University of Witwatersrand, Johannesburg.

Bearder, S. K. (1987). Lorises, bushbabies and tarsiers: diverse societies in solitary foragers. In: Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W., and Struhsaker, T. T. (eds.), *Primate Societies*. University of Chicago Press, Chicago. pp. 11–24.

Bearder, S. K. (1999). Physical and social diversity among nocturnal primates: a new view based on long term research. *Primates* 40:267–282.

Bearder, S. K., Ambrose, L., Harcourt, C., Honess, P., Perkin, A., Pimley, E., Pullen, S., and Svoboda, N. (2003). Species-typical patterns of infant contact, sleeping site use and social cohesion among nocturnal primates in Africa. *Folia Primatol.* 74:337–354.

Bearder, S. K., and Doyle, G. A. (1974a). Field and laboratory studies of social organisation in bushbabies (*Galago senegalensis*). *J. Hum. Evol.* 3:37–50.

Bearder, S. K., and Doyle, G. A. (1974b). Ecology of bushbabies *Galago senegalensis* and *Galago crassicaudatus*, with some notes on their behaviour in the field. In: Martin, R. D., Doyle, G. A., and Walker, A. C. (eds.), *Prosimian Biology*. Duckworth Press, London. pp. 109–130.

Bearder, S. K., Honess, P. E., and Ambrose, L. (1995). Species diversity among galagos with special reference to mate recognition. In: Alterman, L., Doyle, G., and Izard, M. K. (eds.), *Creatures of the Dark: The Nocturnal Prosimians*. Plenum Press, New York. pp. 331–352.

Bearder, S. K., and Martin, R. D. (1980a). Acacia gum and its use by bushbabies, *Galago senegalensis* (Primates: Lorisidae). *Int. J. Primatol.* 1:103–128.

Bearder, S. K., and Martin, R. D. (1980b). The social organisation of a nocturnal primate revealed by radio tracking. In: Amlaner, C. J., and MacDonald, D. W. (eds.), *A Handbook on Biotelemetry and Radio Tracking*. Pergamon Press, London. pp. 633–648.

Bearder, S. K., Nekaris, K. A. I., and Buzzell, C. A. (2002). Dangers of the night: are some primates afraid of the dark? In: Miller, L. E. (ed.), *Eat or Be Eaten: Predator Sensitive Foraging in Primates*. Cambridge University Press, Cambridge. pp. 21–43.

Bearder, S. K., Nekaris, K. A. I., and Curtis, D. J. (in press). A reevaluation of the role of vision in the activity and communication of nocturnal primates. *Folia Primatol.*

Boyd, R., and Silk, J. B. (2003). *How Humans Evolved*. W. W. Norton, New York.

Butynski, T. M. (1996/97). African primate conservation—the species and the IUCN/SSC primate specialist group network. *Primate Conserv.* 17:87–100.

Butynski, T. M., Ehardt, C. L., and Struhsaker, T. T. (1998). Notes on two dwarf galagos (*Galagoides udzungwensis* and *Galagoides orinus*) in the Udzungwa Mountains, Tanzania. *Primate Conserv.* 18:69–75.

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 Press, Chicago. pp. 97–122.

Charles-Dominique, P. (1972). Ecologie et vie sociale de *Galago demidovii* (Fisher 1808, Prosimii). *Z. Tierpsychol. Suppl.* 9:7–41.

Charles-Dominique, P. (1974a). Vie sociale de *Perodicticus potto* (Primates Lorisides). Étude de terrain en forêt equatorial de l'ouest africain au Gabon. *Mammalia* 38:355–379.

Charles-Dominique, P. (1974b). Ecology and feeding behaviour of five sympatric lorisids in Gabon. In: Martin, R. D., Doyle, G. A., and Walker, A. C. (eds.), *Prosimian Biology*. Duckworth Press, London. pp. 131–150.

Charles-Dominique, P. (1977a). *Ecology and Behaviour of Nocturnal Primates*. Duckworth Press, London.

Charles-Dominique, P. (1977b). Urine marking and territoriality in *Galago alleni* (Waterhouse, 1837-Lorisoidea, Primates)— a field study by radio-telemetry. *Z. Tierpsychol.* 43:113–138.

Charles-Dominique, P. (1978). Solitary and gregarious prosimians: evolution of social structures in primates. In: Chivers, D. J., and Joysey, K. A. (eds.), *Recent Advances in Primatology*, vol. 3. Academic Press, New York. pp. 139–149.

Charles-Dominique, P., and Bearder, S. K. (1979). Field studies of lorisid behavior: methodological aspects. In: Doyle, G. A., and Martin, R. D. (eds.), *The Study of Prosimian Behavior*. Academic Press, London. pp. 567–629.

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

Clark, A. B. (1978a). Olfactory communication, *Galago crassicaudatus*, and the social life of prosimians. In: Chivers, D. J., and Joysey, K. A. (eds.), *Recent Advances in Primatology*. Evolution, vol. 3. Academic Press, New York. pp. 109–117.

Clark, A. B. (1978b). Sex ratio and local resource competition in a prosimian primate. *Science* 201:163–165.

Clark, A. B. (1982a). Scent marks as social signals in *Galago crassicaudatus* I. Sex and reproductive status as factors in signals and responses. *J. Chem. Ecol.* 8:1133–1151.

Clark, A. B. (1982b). Scent marks as social signals in *Galago crassicaudatus*. II. Discrimination between individuals by scent. *J. Chem. Ecol.* 8:1153–1165.

Clark, A. B. (1985). Sociality in a nocturnal "solitary" prosimian: *Galago crassicaudatus*. *Int. J. Primatol.* 6:581–600.

Coultas, D. S. (2002). Bioacoustic analysis of the loud call of two species of slender loris (*Loris tardigradus* and *L. lydekkerianus nordicus*) from Sri Lanka [MSc thesis]. Oxford Brookes University, Oxford.

Courtenay, D. O., and Bearder, S. K. (1989). The taxonomic status and distribution of bushbabies in Malawi with emphasis on the significance of vocalisations. *Int. J. Primatol.* 10:17–34.

Crompton, R. H. (1980). A leap in the dark: locomotor behaviour and ecology in *Galago senegalensis* and *Galago crassicaudatus* [PhD thesis]. Harvard University, Cambridge, MA.

Crompton, R. H. (1983). Age differences in locomotion in two subtropical Galaginae. *Primates* 24:241–259.

Crompton, R. H. (1984). Foraging, habitat structure, and locomotion in two species of *Galago*. In: Rodman, P. S., and Cant, J. G. H. (eds.), *Adaptations for Foraging in Non-Human Primates*. Columbia University Press, New York. pp. 73–111.

Crovella, S. J. C., Masters, J. C., and Rumpler, Y. (1994). Highly repeated DNA sequences as phylogenetic markers among Galaginae. *Am. J. Primatol.* 32:177–185.

DelPero, M., Masters, J. C., Zuccon, D., Cervella, P., Crovella, S., and Ardito, G. (2000). Mitochondrial sequences as indicators of generic classification in bush babies. *Int. J. Primatol.* 21:889–904.

Demes, B., Fleagle, J. G., and Lemelin, P. (1998). Myological correlates of prosimian leaping. *J. Hum. Evol.* 34:385–399.

Dixson, A. F. (1989). Effects of sexual selection upon the genitalia and copulatory behaviour in male primates. *Int. J. Primatol.* 10:47–55.

Dixson, A. F. (1995). Sexual selection and the evolution of copulatory behavior in nocturnal prosimians. In: Alterman, L., Doyle, G. A., and Izard, M. K. (eds.), *Creatures of the Dark: The Nocturnal Prosimians*. Plenum Press, New York. pp. 93–118.

Dixson, A. F. (1998). *Primate Sexuality: Comparative Studies of the Prosimians, Monkeys, Apes and Human Beings*. Oxford University Press, Oxford.

Doyle, G. A. (1979). Development of behaviour in prosimians with special reference to the lesser bushbaby, *Galago senegalensis moholi*. In: Doyle, G. A., and Martin, R. D. (eds.), *The Study of Prosimian Behaviour*. Academic Press, London. pp. 157–189.

Duckworth, J. W. (1994). Field sighting of the pygmy loris (*Nycticebus pygmaeus*) in Laos. *Folia Primatol.* 63:99–101.

Dunbar, R., and Barrett, L. (2000). *Cousins: Our Primate Relatives*. Bookman-Huntingdon, London.

Dykyj, D. (1980). Locomotion of the slow loris in a designed substrate context. *Am. J. Phys. Anthropol.* 52:577–586.

Ehrlich, A., and Macbride, L. (1989). Mother–infant interactions in captive slow lorises (*Nycticebus coucang*). *Am. J. Primatol.* 19:217–228.

Ehrlich, A., and Musicant, A. (1977). Social and individual behaviors in captive slow lorises (*Nycticebus coucang*). *Behaviour* 60:195–220.

Elliot, O., and Elliot, M. (1967). Field notes on the slow loris in Malaya. *J. Mammal.* 48:497–498.

Erdelen, W. (1988). Forest ecosystems and nature conservation in Sri Lanka. *Biol. Conserv.* 43:115–135.

Falk, D. (2000). *Primate Diversity*. Norton, New York.

Fietz, J., Zischler, H., Schwieg, C., Tomiuk, J., Dausmann, K. H., and Ganzhorn, J. U. (2000). High rates of extra-pair young in the pair-living fat-tailed dwarf lemur, *Cheirogaleus medius*. *Behav. Ecol. Sociobiol.* 49:8–17.

Fisher, H. S., Swaisgood, R. R., and Fitch-Snyder, H. (2003a). Odor familiarity and female preferences for males in a threatened primate, the pygmy loris *Nycticebus pygmaeus*: applications for genetic management of small populations. *Naturwissenschaften* 90:509–512.

Fisher, H. S., Swaisgood, R. R., and Fitch-Snyder, H. (2003b). Countermarking by male pygmy lorises (*Nycticebus pygmaeus*): do females use odor cues to select mates with high competitive ability? *Behav. Ecol. Sociobiol.* 53:123–130.

Fitch-Snyder, H., and Ehrlich, A. (2003). Mother–infant interactions in slow lorises (*Nycticebus bengalensis*) and pygmy lorises (*Nycticebus pygmaeus*). *Folia Primatol.* 74:259–271.

Fitch-Snyder, H., and Vu, N. T. (2002). A preliminary survey of lorises (*Nycticebus* spp.) in northern Vietnam. *Asian Primates* 8:1–3.

Fleagle, J. G. (1999). *Primate Adaptation and Evolution*. Academic Press, San Diego.

Fry, B. G., and Fry, A. (2003). The loris: a venomous primate. *Fauna* 4:8–11.

Gebo, D. L. (1986). Miocene lorisids: the foot evidence. *Folia Primatol.* 47:217–225.

Glassman, D. M., and Wells, J. P. (1984). Positional and activity behavior in a captive slow loris: a quantitative assessment. *Am. J. Primatol.* 7:121–132.

Gray, J. E. (1863). Revision of the species of lemuroid animals, with the description of some new species. *Proc. Zool. Soc. Lond.* 1863:129–152.

Groves, C. P. (1998). Systematics of tarsiers and lorises. *Primates* 39:13–27.

Groves, C. P. (2001). *Primate Taxonomy*. Smithsonian Institute Press, Washington DC.

Grubb, P., Butynski, T. M., Oates, J. F., Bearder, S. K., Disotell, T. R., Groves, C., and Struhsaker, T. (2003). An assessment of the diversity of African primates. *Int. J. Primatol.* 24:1301–1357.

Gursky, S., and Nekaris, K. A. I. (2003). An introduction to mating, birthing and rearing systems of nocturnal prosimians. *Folia Primatol.* 74:272–284.

Happold, D., and Happold, M. (1992). Termites as food for the thick-tailed bushbaby (*Otolemur crassicaudatus*) in Malawi. *Folia Primatol*. 58:118–120.

Harcourt, C. S. (1980). Behavioural adaptations of South African galagos [MSc diss.]. University of Witwatersrand, Johannesburg.

Harcourt, C. S. (1981). An examination of the function of urine washing in *Galago senegalensis*. *Z. Tierpsychol*. 55:119–128.

Harcourt, C. S. (1984). The behaviour and ecology of galagos in Kenyan coastal forest [PhD thesis]. University of Cambridge, Cambridge.

Harcourt, C. (1986a). *Galago zanzibaricus*: birth seasonality, litter size and perinatal behaviour of females. *J. Zool*. 210:451–457.

Harcourt, C. S. (1986b). Seasonal variation in the diet of South African galagos. *Int. J. Primatol*. 7:491–506.

Harcourt, C. S., and Bearder, S. K. (1989). A comparison of *Galago moholi* in South Africa with *Galago zanzibaricus* in Kenya. *Int. J. Primatol*. 10:35–45.

Harcourt, C. S., and Nash, L. T. (1986a). Species differences in substrate use and diet between sympatric galagos in two Kenyan coastal forests. *Primates* 27:41–52.

Harcourt, C. S., and Nash, L. T. (1986b). Social organization of galagos in Kenyan coastal forests, I. *Galago zanzibaricus*. *Am. J. Primatol*. 10:339–356.

Hladik, C. M. (1979). Diet and ecology of prosimians. In: Doyle, G. A., and Martin, R. D. (eds.), *The Study of Prosimian Behavior*. Academic Press, London. pp. 307–357.

Honess, P. E. (1996). Speciation among galagos (Primates, Galagidae) in Tanzanian forests [PhD thesis]. Oxford Brookes University, Oxford.

Honess, P. E., and Bearder, S. K. (1996). Descriptions of the dwarf galago species of Tanzania. *Afr. Primates* 2:75–79.

Ishida, H., Hirasaki, E., and Matano, S. (1992). Locomotion of the slow loris between discontinuous substrates. In: Matano, S., Tuttle, R. H., and Ishida, H. (eds.), *Topics in Primatology. Evolutionary Biology, Reproductive Endocrinology and and Virology*, vol. 3. University of Tokyo Press, Tokyo. pp. 139–152.

Izard, M. K., and Rasmussen, D. T. (1985). Reproduction in the slender loris (*Loris tardigradus malabaricus*). *Am. J. Primatol*. 8:153–165.

Jewell, P. A., and Oates, J. F. (1969). Ecological observations of the lorisoid primates of African lowland forest. *Zool. Afr*. 4:231–248.

Kingdon, J. (1997). *The Kingdon Field Guide to African Mammals*. Academic Press, London.

Le Gros Clark, W. (1956). *British Museum (Natural History). Fossil Mammals of Africa, No. 9: A Miocene Lemuroid Skull from East Africa*. British Museum, London. p. 6.

MacDonald, D. (2001). *The New Encyclopedia of Mammals*. Oxford University Press, Oxford.

Manley, G. H. (1966). Reproduction in lorisoid primates. *Symp. Zool. Soc. Lond*. 15:493–509.

Manley, G. H. (1967). Gestation periods in the Lorisidae. *Int. Zool. Ybk*. 7:80–81.

Martin, R. D. (1990). *Primate Origins and Evolution: A Phylogenetic Reconstruction*. Chapman and Hall, London.

Martin, R. D. (2000). Origins, diversity and relationship of lemurs. *Int. J. Primatol*. 21:1021–1049.

Martin, R. D. (2003). Combing the fossil record. *Nature* 422:388–391.

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

Masters, J. C. (1991). Loud calls of *Galago crassicaudatus* and *G. garnettii* and their relation to habitat structure. *Primates* 32:153–167.

Masters, J. C. (1998). Speciation in the lesser galagos. *Folia Primatol*. 69(suppl. 1):357–370.

Masters, J. C., and Brothers, D. J. (2002). Lack of congruence between morphological and molecular data in reconstructing the phylogeny of the Galagonidae. *Am. J. Phys. Anthropol*. 117:79–93.

Masters, J. C., Rayner, H., Ludewig, H., Zimmermann, E., Molez-Verriere, F., Vincent, F., and Nash, L. T. (1994). Phylogenetic relationships among the Galaginae as indicated by erythrocytic allozymes. *Primates* 35:177–190.

McCrossin, M. L. (1992). New species of bushbaby from the middle Miocene of Maboko Island, Kenya. *Am. J. Phys. Anthropol*. 89:215–233.

Mill, R. R. (1995). Regional overview: Indian subcontinent. In: *Centres of Plant Diversity: A Guide to Strategy for Their Conservation. Asia, Australia and the Pacific*, vol. 2. World Wildlife Fund for Nature and IUCN Press, Cambridge. pp. 62–135.

Müller, A. E., and Thalmann, U. (2000). Origin and evolution of primate social organisation: a reconstruction. *Biol. Rev. Camb. Philos. Soc*. 75:405–435.

Nash, L. T. (1986). Influence of moonlight level on traveling and calling patterns in two sympatric species of *Galago* in Kenya. In: Taub, D. M., and King, F. A. (eds.), *Current Perspectives in Primate Social Dynamics*. Van Nostrand Reinhold, New York. pp. 357–367.

Nash, L. T. (1989). Galagos and gummivory. *Hum. Evol*. 4:199–206.

Nash, L. T. (1993). Juveniles in nongregarious primates. In: Pereira, M. E., and Fairbanks, L. A. (eds.), *Juvenile Primates: Life History, Development, and Behavior*. Oxford University Press, Oxford. pp. 119–137.

Nash, L. T., Bearder, S. K., and Olson, T. (1989). Synopsis of galago species characteristics. *Int. J. Primatol*. 10:57–80.

Nash, L. T., and Harcourt, C. H. (1986). Social organization of galagos in Kenyan coastal forest II: *Galago garnettii*. *Am. J. Primatol*. 10:357–369.

Nash, L. T., and Whitten, P. L. (1998). Preliminary observations on the role of *Acacia* gum chemistry in *Acacia* utilization by *Galago senegalensis* in Kenya. *Am. J. Primatol*. 17:27–39.

Nekaris, K. A. I. (1997). A preliminary survey of the slender loris (*Loris tardigradus*) in south India. *Am. J. Phys. Anthropol. Suppl*. 24:176–177.

Nekaris, K. A. I. (2000). The socioecology of the Mysore slender loris (*Loris tardigradus lydekkerianus*) in Dindigul, Tamil Nadu, south India [PhD thesis]. Washington University, St. Louis.

Nekaris, K. A. I. (2001). Activity budget and positional behavior of the Mysore slender loris (*Loris tardigradus lydekkarianus*): implications for "slow climbing" locomotion. *Folia Primatol*. 72:228–241.

Nekaris, K. A. I. (2002). Slender in the night. *Nat. History* 2:54–59.

Nekaris, K. A. I. (2003a). Observations on mating, birthing and parental care in three taxa of slender loris in India and Sri Lanka (*Loris tardigradus* and *Loris lydekkerianus*). *Folia Primatol*. 74(suppl.):312–336.

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

Nekaris, K. A. I. (2003c). Rediscovery of the slender loris in Horton Plains National Park, Sri Lanka. *Asian Primates* 8:1–7.

Nekaris, K. A. I. (in press). Visual predation in the slender loris. *J. Hum. Evol.*

Nekaris, K. A. I., and 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.

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

Nekaris, K. A. I., Liyanage, W. K. D. D., and Gamage, S. (in press). 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.*

Nekaris, K. A. I., and Rasmussen, D. T. (2003). Diet of the slender loris. *Int. J. Primatol.* 24:33–46.

Nekaris, K. A. I., and Schulze, H. (2004). Historical and recent developments of human–loris interactions in south and southeast Asia. Invited lecture for Primate Society of Great Britain winter meeting, London. *Primate Eye* 84:17–18.

Nekaris, K. A. I., and Stevens, N. J. (2005). All lorises are not slow: rapid arboreal locomotion in the newly recognised red slender loris (*Loris tardigradus tardigradus*) of southwestern Sri Lanka. *Am. J. Phys. Anthropol. Suppl.* 40:156.

Nietsch, A. A., and Kopp, M. L. (1998). Role of vocalization in species differentiation of Sulawesi tarsiers. *Folia Primatol.* 69(suppl. 1):371–378.

Oates, J. F. (1984). The niche of the potto, *Perodicticus potto. Int. J. Primatol.* 5:51–61.

Oates, J., and Jewell, P. A. (1967). Westerly extent of the range of three African lorisoid primates. *Nature* 215:778–779.

Olson, T. R. (1979). Studies on aspects of the morphology and systematics of the genus *Otolemur* (Coquerel, 1859) (Primates: Galagidae) [PhD thesis]. University of London, London.

Osman Hill, W. C. (1953). *Primates. Comparative Anatomy and Taxonomy. I. Strepsirhini*. Edinburgh University Press, Edinburgh.

Oxnard, C. E., Crompton, R. H., and Lieberman, S. S. (1990). *Animal Lifestyles and Anatomies*. University of Washington Press, Seattle.

Pariente, G. (1979). The role of vision in prosimian behaviour. In: Doyle, G. A., and Martin, R. D. (eds.), *The Study of Prosimian Behaviour*. Academic Press, London. pp. 411–459.

Pastorini, J., Thalmann, U., and Martin, R. D. (2003). A molecular approach to comparative phylogeography of extant Malagasy lemurs. *Proc. Natl. Acad. Sci. USA* 100:5879–5884.

Paterson, H. E. H. (1985). The recognition concept of species. In: Vbra, E. S. (ed.), *Species and Speciation*. Transvaal Museum, Pretoria. pp. 21–29.

Perkin, A. W. (2000). Bushbabies of Tanzania: an update. *Miombo* 20:4.

Perkin, A. W. (2001a). A field study on the conservation status and species diversity of galagos in the West Kilombero Scarp Forest Reserve. In: Doody, K. Z., Howell, K. M., and Fanning, E. (eds.), *West Kilombero Scarp Forest Reserve—Zoological Report*. Matumizi Endeleyu Mazingira, Iringa, Tanzania. pp. 149–159.

Perkin, A. W. (2001b). The taxonomic status and distribution of bushbabies (galagos) in the Uluguru Mountains, Tanzania. *Miombo* 23:5–7.

Perkin, A. W. (2002). The Rondo galago *Galagoides rondoensis* (Honess & Bearder, 1996): a primate conservation priority. *Primate Eye* 77:14–15.

Perkin, A. W., Bearder, S. K., Butynski, T., Bytebier, B., and Agwanda, B. (in press). The Taita Mountain dwarf galago *Galagoides* sp.: a new primate for Kenya. *J. East Afr. Nat. Hist.*

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

Petter, J., and Petter-Rousseaux, A. (1979). Classification of the prosimians. In: Doyle, G. A., and Martin, R. D. (eds.), *The Study of Prosimian Behaviour*. Academic Press, London. pp. 1–44.

Pimley, E. R. (2002). The behavioural ecology and genetics of the potto (*Perodicticus potto edwardsi*) and Allen's bushbaby (*Galago alleni cameronensis*) [PhD thesis]. University of Cambridge, Cambridge.

Pimley, E. R., Bearder, S. K., and Dixson, A. F. (2002). Patterns of ranging and social interactions in pottos (*Perodicticus potto edwardsi*) in Cameroon [abstract]. XIX Congress of the International Primatological Society, Beijing, PR China.

Pimley, E. R., Bearder, S. K., and Dixson, A. F. (in press). Examining the social organization of the Milne-Edward's potto *Perodicticus potto edwardsi. Am. J. Primatol.*

Pullen, S. L. (2000). Behavioural and genetic studies of the mating system in a nocturnal primate: the lesser galago (*Galago moholi*) [PhD thesis]. University of Cambridge, Cambridge.

Pullen, S. L., Bearder, S. K., and Dixson, A. F. (2000). Preliminary observations on sexual behavior and the mating system in free-ranging lesser galagos (*Galago moholi*). *Am. J. Primatol.* 51:79–88.

Radespiel, U., Dal Secco, V., Drogemuller, C., Braune, P., Labes, E., and Zimmermann, E. (2002). Sexual selection, multiple mating and paternity in grey mouse lemurs, *Microcebus murinus. Anim. Behav.* 63:259–268.

Radespiel, U., Funk, S. M., Zimmermann, E., and Bruford, M. W. (2001). Isolation and characterization of microsatellite loci in the grey mouse lemur (*Microcebus murinus*) and their amplification in the family Cheirogaleidae. *Mol. Ecol. Note* 1:16–18.

Rasmussen, D. T. (1986). Life history and behavior of slow lorises and slender lorises [PhD thesis]. Duke University, Durham, NC.

Rasmussen, D. T., and Izard, M. K. (1988). Scaling of growth and life-history traits relative to body size, brain size and metabolic rate in lorises and galagos (Lorisidae, Primates). *Am. J. Phys. Anthropol.* 75:357–367.

Rasmussen, D. T., and Nekaris, K. A. I. (1998). Evolutionary history of the lorisiform primates. *Folia Primatol.* 69(suppl. 1):250–285.

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.

Rhadakrishna, S. (2001). The social behavior of the Mysore slender loris (*Loris tardigradus lydekkerianus*) [PhD thesis]. University of Mysore, Manasagangotri.

Rhadakrishna, S., and Singh, M. (2002). Social behaviour of the slender loris (*Loris tardigradus lydekkerianus*). *Folia Primatol.* 73:181–196.

Rhadakrishna, S., and Singh, M. (2004). Reproductive biology of the slender loris (*Loris lydekkerianus lydekkerianus*). *Folia Primatol.* 75:1–13.

Roonwal, M. L., and Mohnot, S. M. (1977). *Primates of South Asia: Ecology, Sociobiology and Behavior*. Harvard University Press, Cambridge, MA.

Roos, C. (2003). Molekulare Phylogenie der Halbaffen, Schlankaffen, und Gibbons [diss.]. University of Munich, Munich.

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

Ross, C. (1996). Adaptive explanation for the origins of the Anthropoidea (Primates). *Am. J. Primatol.* 40:205–230.

Sanfey, P. (2003). Study of re-released semi-free ranging slow and pygmy lorises in Thailand [MSc diss.]. Oxford Brookes University, Oxford.

Sarmiento, E. (1998). The validity of *Pseudopotto martini*. *Afr. Primates* 3:44–45.

Schilling, A. (1979). Olfactory communication in prosimians. In: Doyle, G. A., and Martin, R. D. (eds.), *The Study of Prosimian Behaviour*. Academic Press, London. pp. 461–542.

Schulze, H., and Groves, C. P. (2004). Asian lorises: taxonomic problems caused by illegal trade. In: Nadler, T., Streicher, U., and Thang Long, H. (eds.), *Conservation of Primates in Vietnam*. Frankfurt Zoological Society, Frankfurt. pp. 33–36.

Schulze, H., and Meier, B. (1995a). The subspecies of *Loris tardigradus* and their conservation status: a review. In: Alterman, L., Doyle, G. A., and Izard, M. K. (eds.), *Creatures of the Dark: The Nocturnal Prosimians*. Plenum Press, New York. pp. 193–209.

Schulze, H., and Meier, B. (1995b). Behaviour of captive *Loris tardigradus nordicus*: a qualitative description including some information about morphological bases of behavior. In: Alterman, L., Doyle, G. A., and Izard, M. K. (eds.), *Creatures of the Dark: The Nocturnal Prosimians*. Plenum Press, New York. pp. 221–250.

Schwartz, J. H. (1996). *Pseudopotto martini*: a new genus and species of extant lorisiform primate. *Anthropol. Papers Am. Mus. Nat. Hist.* 78:1–14.

Seiffert, E. F., Simon, E. L., and Attia, Y. (2003). Fossil evidence for an ancient divergence of lorises and galagos. *Nature* 422:421–424.

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., Kumar, M. A., Kumara, H. N., and Mohnot, S. M. (2000). Distribution and conservation of slender lorises in southern Andhra Pradesh, south India. *Int. J. Primatol.* 21:721–730.

Singh, M., Lindburg, D. G., Udhayan, A., Kumar, M. A., and Kumara, H. N. (1999). Status survey of the slender loris in Dindigul, Tamil Nadu, India. *Oryx* 33:31–37.

Sterling, E. J. (1993). Patterns of range use and social organization in aye-ayes (*Daubentonia madagascariensis*) on Nosy Mangabe. In: Kappeler, P. M., and Ganzhorn, J. U. (eds.), *Lemur Social Systems and Their Ecological Basis*. Plenum Press, New York. pp. 1–10.

Sterling, E. J., Nguyen, N., and Fashing, P. (2000). Spatial patterning in nocturnal prosimians: a review of methods and relevance to studies of sociality. *Am. J. Primatol.* 51:3–19.

Streicher, U. (2003). Saisonale Veränderungen in Fellzeichnung und Fellfärbung beim Zwergplumplori *Nycticebus pygmaeus* und irhe taxonomische Bedeutung. *Zool. Garten N.F.* 73:368–373.

Streicher, U. (2004). Aspects of the ecology and conservation of the pygmy loris *Nycticebus pygmaeus* in Vietnam [inaugural diss.]. Ludwig-Maximilians University, Munich.

Tan, C. L., and Drake, J. H. (2001). Evidence of tree gouging and exudate eating in pygmy slow lorises (*Nycticebus pygmaeus*). *Folia Primatol.* 72:37–39.

Tavare, S., Marshall, C. R., Will, O., Soligo, C., and Martin, R. D. (2002). Using the fossil record to estimate the age of the last common ancestor of extant primates. *Nature* 416:726–729.

Walker, A. C. (1969). The locomotion of the lorises, with special reference to the potto. *E. Afr. Wildlife J.* 7:1–5.

Weisenseel, K., Chapman, C. A., and Chapman, L. J. (1993). Nocturnal primates of Kibale Forest: effects of selective logging on prosimian densities. *Primates* 34:445–450.

Weisenseel, K. A., Izard, M. K., Nash, L. T., Ange, R. L., and Poorman-Allen, P. (1998). A comparison of reproduction in two species of *Nycticebus*. *Folia Primatol.* 69(suppl. 1):321–324.

Welker, C. (1973). Ethologic significance of the urine washing by *Galago crassicaudatus* E. Geoffroy, 1812 (Lorisiformes: Galagidae). *Folia Primatol.* 20:429–452.

Wickings, E. J., Ambrose, L., and Bearder, S. K. (1998). Sympatric populations of *Galagoides demidoff* and *G. thomasi* in the Haut Ogooué region of Gabon. *Folia Primatol.* 69(suppl. 1):389–393.

Wiens, F. (1995). Verhaltensbeobachtungen am plumplori, *Nycticebus coucang* (Primates: Lorisidae) im Freiland [diplomarbeit]. Universität Frankfurt am Main, Frankfurt am Main.

Wiens, F. (2002). Behavior and ecology of wild slow lorises (*Nycticebus coucang*): social organisation, infant care system and diet [PhD thesis]. Bayreuth University, Bayreuth.

Wiens, F., and Zitzmann, A. (2003a). Social dependence of infant slow lorises to learn diet. *Int. J. Primatol.* 24:1007–1021.

Wiens, F., and Zitzmann, A. (2003b). Social structure of the solitary slow loris *Nycticebus coucang* (Lorisidae). *J. Zool.* 261:35–46.

Yoder, A. D., Irwin, J. D., and Payseur, B. A. (2001a). Failure of the ILD to determine data combinability for slow loris phylogeny. *Syst. Biol.* 50:408–424.

Yoder, A. D., Rasoloarison, R. M., Goodman, S. M., Irwin, J. A., Atsalis, S., Ravosa, M., and Ganzhorn, J. U. (2001b). Remarkable species diversity in Malagasy mouse lemurs (Primates, *Microcebus*). *Proc. Natl. Acad. Sci. USA* 97:11325–11330.

Zimmerman, E. (1985). Vocalisations and associated behaviours in adult slow loris (*Nycticebus coucang*). *Folia Primatol.* 44:52–64.

Zimmermann, E. (1990). Differentiation of vocalisations in bushbabies (Galaginae, Prosimii, Primates) and the significance for assessing phylogenetic relationships. *Z. Zool. Syst. Evol.* 28:217–239.

Zimmermann, E. (1995a). Loud calls in nocturnal prosimians: structure, evolution and ontogeny. In: Zimmermann, E., Newman, J. D., and Jürgens, U. (eds.), *Current Topics in Primate Vocal Communication*. Plenum Press, New York. pp. 47–72.

Zimmermann, E. (1995b). Acoustic communication in nocturnal prosimians. In: Alterman, L., Doyle, G. A., and Izard, M. K. (eds.), *Creatures of the Dark: The Nocturnal Prosimians*. Plenum Press, New York. pp. 311–330.

Zimmermann, E., Bearder, S. K., Doyle, G. A., and Anderson, A. B. (1988). Variations in vocal patterns of Senegal and South African lesser bushbabies and their implications for taxonomic relationships. *Folia Primatol.* 51:87–105.

4

Lemuriformes

Lisa Gould and Michelle Sauther

INTRODUCTION

Behavioral and ecological research on the Malagasy primates began in the late 1950s, when Petter (1962) surveyed Madagascar's fauna and published preliminary information on several lemur species at a variety of sites around the island (Fig. 4.1). In the 1960s and 1970s, a number of primate biologists undertook the first in-depth studies of *Lemur catta* and *Propithecus verreauxi* at the Berenty site in the far south of the island (Jolly 1966) and comparative studies of *P. verreauxi* in the northwest and south (Richard 1973, 1974), *L. catta* and *Eulemur fulvus rufus* in the southwest (Sussman 1972, 1974), and *Indri* in the eastern rain forest (Pollock 1975, 1977). Some of the nocturnal

lemurs were also studied for the first time in the 1970s by Martin (1972a), who focused on *Microcebus*, while Charles-Dominique and Hladik (1971) documented early information on *Lepilemur*. On the nearby Comoro Islands, the only place outside of Madagascar where lemurs are found, Tattersall (1976, 1977b) conducted research on *Eulemur mongoz* on Moheli and Anjouan Islands as well as on the one subspecies of brown lemur not found on Madagascar, *E. f. mayottensis*, the Mayotte brown lemur, on the island of the same name.

In the 1970s, the political situation in Madagascar precluded most lemur research; but in the 1980s, many Malagasy,

Figure 4.1 National parks and reserves in Madagascar. Based on a map from Madagascar: The Bradt Travel Guide, 7th ed., 2002. Reprinted with kind permission of the editor, H. Bradt.
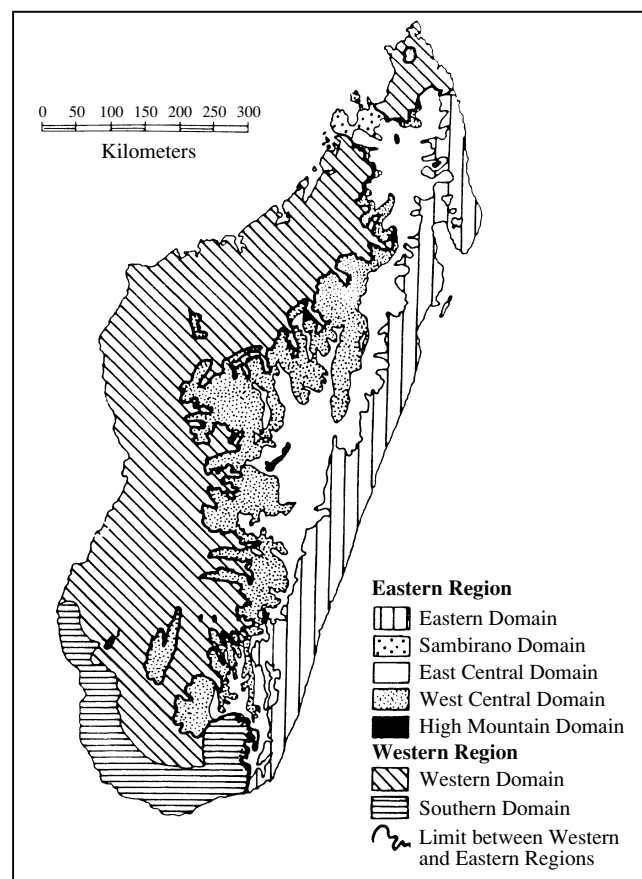

Figure 4.2 Map of vegetation zones in Madagascar. From Sussman (1999), based on Humber's (1955) original.

North American, European, and Japanese researchers began a new phase of field studies on most of the extant lemur species. Lemur research has grown remarkably in the past two and a half decades as topics such as geographic distribution; behavior and ecology of previously unknown species; correlations between climate, diet, and dominance patterns; long-term demographic and life history studies; hormonal correlates of behavior; health studies; and genetics have been and are being investigated.

In this chapter, we will first present information on the origins of the Malagasy primates, taxonomy and classification of the living lemurs, lemur morphology, and current explanations relating to the evolution of behavioral traits which distinguish lemurs from other primate groups. We will then give an overview of the ecology of the extant lemurs and end the chapter with a note concerning the extinct subfossil lemurs.

ORIGIN OF THE LEMURS

The landmass which is now Madagascar split from mainland Africa approximately 165 million years ago (mya) and drifted southward to its present position, 400 kms from mainland East Africa around 121 mya (Yoder et al. 2003). At this time, Madagascar was part of a larger landmass which included India. About 88 mya, the landmass split again, and India drifted northward, eventually colliding with Asia (Yoder et al. 2003). Madagascar has thus been isolated from any other landmass for 88 million years. How then did lemurs end up on Madagascar, when primates did not exist at the time of the landmass separation? Lemur ancestors arose in Africa either during the Eocene epoch (55–37 mya) or even earlier as Martin (2000) notes, that Deoxyribonucleic acid (DNA) sequencing suggests they may have begun to colonize Madagascar as early as 80 mya. The most accepted explanation as to how they got to Madagascar is via over-water dispersal, or "rafting," on large clumps of floating vegetation (Martin 1972b, 2000; Mittermeier et al. 1994; Yoder et al. 2003). It has been suggested that the ancestral lemurs survived this long journey because they may have had the ability to go into a state of torpor for lengths of time, which would have offset the problem of food shortages (Martin 1972b, 2000; Kappeler 2000). Tattersall (2004) argues that some form of "island hopping" may have occurred by means of paleogeographic "stepping stones" in the form of seabed exposures in the Mozambique channel at different times during the Tertiary and that these small islands would have reduced the distances between points of land that mammals crossing over to Madagascar would have had to travel. Whether today's lemurs arose from just one or several separate waves of migration (Yoder et al. 2003, Tattersall 2004), once on Madagascar these ancestral species underwent a large adaptive radiation over many millions of years, resulting in the living lemurs of today and the extinct (subfossil) lemurs.

CLASSIFICATION OF THE LEMURS

There are five taxonomic families of living Malagasy primates: the Lemuridae, Indriidae, Cheirogaleidae, Lepilemuridae (sometimes classified as Megaladapidae), and Daubentoniidae. Within these families we find 14 genera of extant lemurs, which represent 25% of all extant primate genera in the world (Fleagle 1999) and 43 living species. There are also six genera of very recently extinct lemurs (Burney 1997). Table 4.1 lists current extant lemur and extinct sub-fossil taxonomy.

Morphology

Like other strepsirhines, lemurs are morphologically characterized by a number of primitive features of the skull, including a postorbital bar rather than postorbital closure, a primitive mammalian nasal region, reduced upper incisors, and a toothcomb, made up of the lower incisors and canines

Table 4.1   Taxonomy of the Malagasy Primates

Extant lemurs

Family Lemuridae

Lemur catta (ring-tailed lemur)

Eulemur fulvus (**7 subspecies**)
  E. f. fulvus (common brown lemur), *E. f. rufus* (red-fronted brown lemur), *E. f. sanfordi* (Sanford's brown lemur), *E. f. albifrons* (white-fronted brown lemur), *E. f. collaris* (collared brown lemur), *E. f. albocollaris* (white-collared brown lemur), *E. f. mayottensis* (Mayotte brown lemur, on Mayotte Island in the Comoros)

Eulemur macaco (**2 subspecies**)
  E. m. macaco (black lemur), *E. m. flavifrons* (Sclater's black lemur)

Eulemur coronatus (crowned lemur)

Eulemur rubriventer (red-bellied lemur)

Eulemur mongoz (mongoose lemur)

Hapalemur griseus (**3 subspecies**)
  H. g. griseus (eastern lesser bamboo lemur), *H. g. occidentalis* (western lesser bamboo lemur), *H. g. alaotrensis* (Lac Alaotra bamboo lemur)

Hapalemur aureus (golden bamboo lemur)

Hapalemur simus (greater bamboo lemur)

Varecia variegata (**2 subspecies**)
  V. v. variegata (black and white ruffed lemur), *V. v. rubra* (red ruffed lemur)

Family Indriidae

Propithecus verreauxi (**4 subspecies**)
  P. v. verreauxi (Verreaux's sifaka), *P. v. deckeni* (Decken's sifaka), *P. v. coronatus* (crowned sifaka), *P. v. coquereli* (Coquerel's sifaka)

Propithecus diadema (**4 subspecies**)
  P. d. diadema (diademed sifaka), *P. d. edwardsi* (Milne-Edwards sifaka), *P. d. candidus* (silky sifaka), *P. d. perreri* (Perrier's sifaka)

Propithecus tattersalli (golden-crowned sifaka)

Indri indri (indri)

Avahi laniger (eastern woolly lemur)

Avahi occidentalis (western woolly lemur)

Avahi unicolor (unicolor avahi)

Table 4.1   (*cont'd*)

Family Lepilemuridae (also sometimes considered Megaladapidae)

Lepilemur mustelinus (weasel sportive lemur)

Lepilemur microdon (small-toothed sportive lemur)

Lepilemur leucopus (white-footed sportive lemur)

Lepilemur ruficaudatus (red-tailed sportive lemur)

Lepilemur edwardsi (Milne-Edwards sportive lemur)

Lepilemur dorsalis (gray-backed sportive lemur)

Lepilemur septentrionalis (northern sportive lemur)

Family Cheirogalidae

Microcebus murinus (gray mouse lemur)

Microcebus rufus (eastern rufous mouse lemur)

Microcebus myoxinus (pygmy mouse lemur)

Microcebus ravelobensis (golden-brown mouse lemur)

Microcebus tavaratra (northern rufous mouse lemur)

Microcebus sambiranensis (Sambirano mouse lemur)

Microcebus berthae (Berthe's mouse lemur)

Microcebus griseorufus (gray-brown mouse lemur)

Allocebus trichotis (hairy-eared dwarf lemur)

Cheirogaleus major (greater dwarf lemur)

Cheirogaleus crossleyi (Crossley's greater dwarf lemur)

Cheirogaleus ravus (large iron-gray dwarf lemur)

Cheirogaleus minisculus (lesser iron-gray dwarf lemur)

Cheirogaleus sibreei (Sibree's dwarf Lemur)

Cheirogaleus medius (fat-tailed dwarf lemur)

Cheirogaleus adapicaudatus (southern dwarf lemur)

Phaner furcifer (4 subspecies)
   P. f. furcifer (eastern fork-marked lemur), *P. f. pallescens* (pale fork-marked lemur), *P. f. parienti* (Pariente's fork-marked lemur), *P. f. electromontis* (Amber Mountain fork-marked lemur), *Mirza coquereli* (Coquerel's dwarf lemur)

Family Daubentoniidae

Daubentonia madagascariensis (aye-aye)

Subfossil lemurs

Subfossil Lemuridae

Pachylemur insignis

Pachylemur jullyi

Subfossil Daubentoniidae

Daubentonia robusta

Subfossil Megaladapidae

Megaladapis grandidieri

Megaladapis madagascariensis

Megaladapis edwardsi

Family Paleopropithecidae (all subfossils)

Mesopropithecus globiceps

Mesopropithecus pithecoides

Mesopropithecus dolichobrachion

Babakotia radofilai

Paleopropithecus ingens

Paleopropithecus maximus

Archaeoindris fontoynontii

Source: Adapted from Tattersall (1982), Mittermeier et al. (1994), Groves (2000), Rasoloarison et al. (2000), Jungers et al. (2002).

(with the exception of the aye-aye, see below). They also possess a moist rhinarium, or "wet nose," a primitive mammalian trait which aids in their very keen sense of smell (Fleagle 1999). Scent marking is used by all species in various forms and contexts: scent glands are situated on heads and palms in *Eulemur*, under wrist spurs in *L. catta*, on chest glands in *Propithecus*, and in the anogenital area in all species, with the scent glands situated under the tail. Scent is used commonly to denote the presence of a group or individual and extensively during the mating season.

All lemurs possess a grooming claw on the second toe of each foot (Fleagle 1999).

The dental formula is variable. In both the cheirogaleids and the lemurids, the dental formula is 2.1.3.3. Lepilemurids lack permanent upper incisors, so their upper dental formula is 0.1.3.3. and the lower, 2.1.3.3. The indriids have quite different dentition from the above lemurs. Their dental formula is the same as that found in the Old World monkeys, apes, and hominids, 2.1.2.3; and their toothcomb includes the incisors only, not the canine as in the above taxa. The oddest dentition of all lemurs, and probably of all primates, is that of the aye-aye (*Daubentonia madagascariensis*), the only living member of the Daubentoniidae family. Its dental formula is 1.0.1.3, and the middle two incisors grow constantly, like those found in rodents and lagomorphs (rabbits and hares) (Fleagle 1999).

Mean weights of species captured in the wild can be found in Table 4.2.

Nocturnal Lemur Postcranial Morphology and Locomotion

Most nocturnal lemurs have relatively short, pointed snouts and large, moveable ears. The mouse lemurs (*Microcebus*) are branch runners. Their arms and legs are short relative to their trunk, and their tail is as long as their body. Dwarf lemurs (*Cheirogaleus*) have a shorter tail and legs that are longer than the arms. Sportive lemurs (*Lepilemur*) have an enlarged cecum, to help digest the cellulose in their mostly folivorous diet (Fleagle 1999). Sportive lemurs are not branch runners; rather, they travel by vertical leaping (Ganzhorn 1993). The woolly lemur (*Avahi*) is the only nocturnal indriid. It is much smaller than its close relatives, the diurnal sifakas (*Propithecus*) and indri (*Indri*); but its mode of locomotion is the same: vertical clinging and leaping. Using vertical clinging and leaping, the animal begins the leap with its back toward its destination tree, takes a large leap, twists in midair, and lands facing forward (Richard 1985). The legs of both *Lepilemur* and *Avahi* are much longer than their arms, a necessary adaptation for this type of locomotion (Fleagle 1999). The aye-aye, an extremely unusual-looking primate, is covered in black, shaggy hair and has enormous bat-like ears, a large bushy tail, and an extremely elongated third digit on its hands, which it uses in extractive foraging for grubs, insects under bark, and egg yolks (Erickson 1991, 1994; Fleagle 1999).

Table 4.2   Mean Body Weights of Wild–Caught Diurnal Lemur species

SPECIES	MEAN WEIGHT (AND/OR WEIGHT RANGE)	SOURCE
Diurnal lemurs		
Lemur catta	2.2 kg	Sussman 1991
Eulemur fulvus ssp.	1.8–2.6 kg	Glander et al. 1992, Mittermeier et al. 1994, Freed 1996, Terranova and Coffman 1997, Vasey 2000
E. mongoz	1.5 kg	Terranova and Coffman 1997
E. macaco	2.4 kg	Mittermeier et al. 1994
E. rubriventer	2.0 kg	Glander et al. 1992
E. coronatus	1.77 kg	Terranova and Coffman 1997
Hapalemur griseus griseus *H. g. occidentalis*	700–1,000 g	Mittermeier et al. 1994, Tan 1998
H. g. alaotrensis	1.2 kg	Mutschler 2002
H. aureus	1.5–1.6 kg	Glander et al. 1992, Tan 1998
H. simus	2.4 kg	Meier et al. 1987, Tan 1998
Varecia variegata	3–4.5 kg	Tattersall 1982, Morland 1993, Terranova and Coffman 1997, Britt et al. 2001, Vasey 2002
Propithecus verreauxi verreauxi	2.8 kg	Richard et al. 2002
P. diadema edwardsi	5–6.5 kg	Glander et al. 1992, Wright 1995
P. d. diadema	5–6 kg	Powzyk 1997
P. tattersalli	3.5 kg	Meyers and Wright 1993
Indri indri	6.5–6.9 kg	Powzyk 1997, Britt 2000
Nocturnal lemurs		
Cheirogaleus medius	Body weight changes seasonally (range = 75–200 g)	Hladik et al. 1980
C. major	Body weight changes seasonally (mean = 400 g)	Martin 1984
C. crossleyi	Body weight changes seasonally (mean = 400 g)	Petter et al. 1977
Allocebus trichotis	75–80 g	Meier and Albignac 1991
Mirza coquereli	300 g	Tattersall 1982
Microcebus murinus	50–90 g (mean = 62.3)	Martin 1973, Rasoloarison et al. 2000
M. rufus	50 g	Harcourt 1987
M. myoxinus	49 g	Rasoloarison et al. 2000
M. ravelobensis	71.7 g	Rasoloarison et al. 2000
M. tavaratra	61.1 g	Rasoloarison et al. 2000
M. sambirianensis	44.1 g	Rasoloarison et al. 2000
M. berthae	30.6 g	Rasoloarison et al. 2000
M. griseorufus	62.6 g	Rasoloarison et al. 2000
Phaner furcifer	360–500 g	Petter et al. 1977
Avahi laniger	900–1,200 g and 600–700 g	Razanahoera-Rakotomalala 1981, Petter et al. 1977
A. occidentalis	700–900 g	Razanahoera-Rakotomalala 1981
Daubentonia madagascariensis	3 kg	Tattersall 1982
Lepilemur mustelinus	1 kg	Jenkins 1987
L. dorsalis	500 g	Tattersall 1982
L. septentrionalis	700–800 g	Tattersall 1982
L. edwardsi	600–900 g	Tattersall 1982
L. leucopus	550 g	Petter et al. 1977, Petter and Petter-Rousseaux 1979
L. ruficaudatus	600–900 g	Petter et al. 1977, Petter and Petter-Rousseaux 1979
L. microdon	1 kg	Petter et al. 1977, Petter and Petter-Rousseaux 1979

Because there is very little sexual dimorphism in terms of body weight, "mean weight" is presented here as the actual mean in kilograms when data are combined for both males and females.

Postcranial Morphology and Locomotion of the Diurnal Lemurs

Lemur, *Eulemur*, and *Varecia*, are quadrupedal walkers and runners; but they also leap from branch to branch. *Varecia* also uses suspensory postures for feeding (Fleagle 1999). *L. catta*, the only species within the genus *Lemur*, spends about 30% of its time on the ground (Jolly 1966, Sussman 1974). Unlike other lemurs, the fleshy pads of its hands and feet extend upward to the wrist and beyond the heel.

The three *Hapalemur* species have shorter faces than the other lemurids. Their arms are short and legs are proportionally long (Jungers 1979), an adaptation to their primary mode of locomotion, vertical clinging and leaping, although the three species also move quadrupedally along branches when feeding (Fleagle 1999).

The longest leg in proportion to arm length is found in the indriids and is an adaptation to the vertical clinging and leaping mode of locomotion: the indriids are extraordinary leapers. Some sifaka (*Propithecus* spp.) occasionally come to the ground, particularly Verreaux's sifaka, which lives in dry forests. Because their legs are so long, they must move along the ground by hopping bipedally. Indriids also possess very long fingers and toes, which aid them when adopting suspensory feeding postures.

EVOLUTION OF UNIQUE BEHAVIORAL TRAITS IN MALAGASY PRIMATES, INCLUDING FEMALE DOMINANCE

Not only do lemurs exhibit aspects of morphology which differ from anthropoids but some unique behavioral traits have evolved in this group of primates which are not found in other strepsirhines or the haplorhines. These traits include female dominance in the majority of species, targeted female–female aggression, lack of notable sexual dimorphism, strict seasonal breeding (in all but two species, the aye-aye and the Lac Alaotra bamboo lemur), high infant mortality, and cathemerality (exhibiting both day and night activity). Why do we find such a combination of characteristics in the lemurs? A number of explanations have been offered and are explained in detail in Wright (1999) and Sussman (1999). These hypotheses are briefly presented below.

The *energy conservation hypothesis* involves a synthesis of explanations presented by Jolly (1984), Richard (1987), Young et al. (1990), Wright (1993), Sauther (1993), and Pereira (1993a,b). This hypothesis proposes that the combination of extreme and largely unpredictable climatic seasonality in Madagascar and high pre- and postreproductive costs have resulted in the evolution of female dominance. More specifically, strong food resource seasonality and climatic factors have resulted in energetic stress with respect to reproductive females. In group-living lemurs, all females in a social group are pregnant and lactating at the same time, which leads to strong female–female feeding competition during both gestation and lactation periods. Furthermore, in both group- and non-group-living lemur species, females give birth to altricial, quickly growing infants for which they must lactate. Female lemurs may have responded to such reproductive stress through the evolution of female priority of access to food resources, which can help them offset energy demands experienced in this situation. In addition to seasonal reproduction which is largely tied to availability of good weaning foods for growing infants, the relatively lengthy winter season in parts of Madagascar is proposed to have led to the evolution of seasonal energy storage in some species, strategies for temperature regulation, modulation of metabolic and growth rates and activity levels, and timing of aggressive behaviors.

Wright (1999) argues that not all of the unique behavioral traits found in lemurs are strictly related to the conservation of energy and suggests that some are more tailored to maximizing the extraction of scarce resources. She proposes that low basal metabolic rate, small group size, torpor, sperm competition, and seasonal breeding are adaptations related to energy conservation and that others, such as female dominance, weaning synchrony, fibrous diets, territoriality, and cathemerality (found in some species), have evolved as strategies to maximize the use of scarce resources resulting from seasonal resource shortages. Thus, Wright (1999) suggests that it may be appropriate to consider the energy conservation hypothesis as more of an "energy frugality" hypothesis.

The *evolutionary disequilibrium hypothesis* (van Schaik and Kappeler 1996) suggests that recent extinctions, particularly of large diurnal predators such as raptors, have allowed many lemur species to switch from a nocturnal activity pattern to diurnality (and cathemerality). Because of such extinctions, adaptation to a diurnal activity pattern is suggested to have occurred rapidly and recently: between 1,000 and 500 years ago. Also, the social systems of today's diurnal lemurs (species living in relatively small mixed-sex groups) may be an outgrowth of an ancestral nocturnal, monogamous condition; and pair-living animals may have been sufficiently tolerant, once diurnal, to form larger groups. van Schaik and Kappeler (1996) propose that cathemeral activity may be an ancestral and stable activity pattern among lemurs, or, conversely, may have evolved relatively recently as an occasional habit of nocturnal animals. With respect to the evolution of female dominance, van Schaik and Kappeler suggest that in group-living lemurs today female dominance may be a relic of pair-living in ancestral times since female priority of access to resources seems to be the case in pair-living species that do not exhibit sexual dimorphism and where male polygyny, and male–male competition, does not occur. They argue that the expansion of female feeding priority to overall female dominance in *group*-living lemurs (emphasis ours) suggests that female needs in ancestral monogamous species were greater in lemurs than in other primate taxa.

OVERVIEW OF THE ECOLOGY, SOCIAL ORGANIZATION, AND SOME ASPECTS OF BEHAVIOR OF THE EXTANT LEMURS

Mean group size and home range size of extant lemur species (Fig. 4.3) can be found in Table 4.3, and mean weights of wild-caught animals are presented in Table 4.2.

Lemuridae (*Lemur, Eulemur, Hapalemur, Varecia*)

Lemur catta *(Ring-Tailed Lemur)*

L. catta is one of the two lemur species that has been studied over the longest period of time, beginning with Jolly's (1966) pioneering work. Ring-tailed lemurs have been studied primarily at three sites in the south and

(A)

(B)

(C)

(D)

Figure 4.3 (A) *Lemur catta* (photo by L. Gould). (B) *Eulemur coronatus* (photo by B. Z. Freed). (C) *Hapalemur simur* (photo by D. Haring). (D) *Propithecus verreauxi verreauxi* (photo by M. L. Sauther).

(E)

(F)

(G)

(H)

Figure 4.3 (*cont'd*) (E) *Propithecus diadema edwardsi* (photo by S. Arrigo-Nelson). (F) *Varecia variegata variegata* (photo by S. Arrigo-Nelson). (G) *Lepilemur leucopus* (photo by L. Gould). (H) *Microcebus ravelobensis* (photo by U. Radespiel).

Table 4.3 Group Size, Home Range Size, and Habitat of Several Lemur Species at Sites in Madagascar

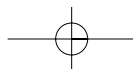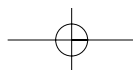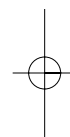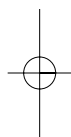| SPECIES	MEAN GROUP SIZE (OR RANGE OF GROUP SIZE)	MEAN HOME RANGE SIZE (RANGE)	HABITAT AND WHERE STUDIED	STUDIED BY OR CITED BY
Diurnal lemurs				
Lemur catta	11.5 and 16 (at two sites), range 3–27	6–35 depending on local habitat	South and southwestern riverine, xerophytic, spiny, and limestone forest: Beza Mahafaly Special Reseve and Berenty Reserve	Budnitz and Dainis 1975; Sussman 1977, 1991; Jolly et al. 2002; Koyama et al. 2002; Gould et al. 2003
Eulemur fulvus rufus (eastern)	6.8	100 ha	Southeastern submontane rain forest: Ranomafana National Park	Overdorff 1993a, Overdorff et al. 2003
E. f. rufus (western)	9.4	1–9 ha	Western dry deciduous forest: Mangoky River, Kirindy Forest	Sussman 1974, Kappeler and Erkert 2003
E. f. fulvus	12	~7 ha (west), >20 (east)	Northwestern dry deciduous forest, eastern rain forest: Ampijoroa (west), Andasibe (east)	Harrington 1975, Ganzhorn 1988, Mittermeier et al. 1994
E. f. sanfordi	Range 5–9	5–9 ha	Northern dry deciduous forest: Mt. d'Ambre	Freed 1996
E. f. albifrons	Range 7–11	13 ha	Northeastern rain forest: Masoala Peninsula	Vasey 2000
E. f. collaris	–	–	Southeastern rain forest and littoral forest: St. Luce	Mittermeier et al. 1994, Donati and Borgognini-Tarli 2002a
E. f. albocollaris	–	–	Restricted range, southeastern rain forest remnants	Tattersall 1982, Mittermeier et al. 1994
E. rubriventer	2–4	19 ha	Southeastern submontane rain forest: Ranomafana National Park	Overdorff 1993a
E. coronatus	Range 5–9	6.5–15.5 ha	Northern dry deciduous forest: Ankarana Reserve, Montagne d'Ambre National Park	Wilson et al. 1989, Freed 1996
E. macaco	10, range 5–14	3.5–7 ha	Northwestern dry forest: Sambirano, Nosy Be	Colquhoun 1993, Andrews and Birkenshaw 1998
E. mongoz	Range 3–8	2.8 ha (0.5–1.0)	Northwestern dry forest: Comoran Islands of Anjouan and Mohéli Humid forest: Ampijoroa Reserve	Tattersall 1977b, Harrington 1978, Curtis and Zaramody 1997
Hapalemur griseus griseus	Range 2–9	6–10 ha/14–20 ha	Eastern rain forest, southeastern submontane forest: Andasibe National Park, Ranomafana National Park	Wright 1986, Tan 1998, Grassi 2001
H. g. occidentalis	Range 1–4	26 ha	Isolated forest regions: western Madagascar, Manongarivo Reserve	Petter and Peyriéras 1970b, Tattersall 1982, Raxworthy and Rakotondraparany 1988
H. g. alaotrensis	Range 3–9	–	Reed beds: Lac Alaotra, east-central Madagascar	Mutschler 2002
H. aureus	Range 2–6	26–80 ha	Restricted range—found only at two sites in southeastern submontane rain forest: Ranomafana and Andringitra National Parks	Wright et al. 1987, Meier and Rumpler 1987, Mittermeier et al. 1994, Tan 1998
H. simus	Range 4–12	62 ha	Southeastern submontane rain forest: Ranomafana region, spotted in Andringitra National Park	Meier and Rumpler 1987, Wright et al. 1987, Tan 1998
Varecia variegata variegata	Range 2–6 and 8–16 (at Nosy Mangabe)	30–150 ha (depends on site and habitat disturbance)	Lowland, mid-altitude, and higher-altitude rain forests in northern, eastern, and east-central Madagascar: Nosy Mangabe, Ranomafana National Park, Manombo, Betampona	Morland 1991, Balko 1998, White 1989, Ratsimbazafy 2002, Britt et al. 2001
V. v. rubra	2–6 (Rigamonti)	25–58 ha	Northeastern rain forest: Masoala Peninsula	Rigamonti 1993, Vasey 2002
Propithecus verreauxi	2–14, mean = 6	3–10 ha	South, southwestern, western dry deciduous forest, spiny forest: Beza Mahafaly Reserve, Kirindy Reserve	Richard et al. 2002
P. v. coquereli	Range 3–10	?	Northwestern mixed-deciduous and evergreen forests, and brush and scrub forest: Ankarafatsika Reserve	Petter 1962, Albignac 1981b
P. v. coronatus	?	?	Northwestern Madagascar	Petter et al. 1977, Mittermeier et al. 1994

Table 4.3   (*cont'd*)

SPECIES	MEAN GROUP SIZE (OR RANGE OF GROUP SIZE)	MEAN HOME RANGE SIZE (RANGE)	HABITAT AND WHERE STUDIED	STUDIED BY OR CITED BY
P. v. deckeni	?	?	Western deciduous (fragments): Tsingy de Bemaraha Reserve	Mittermeier et al. 1994
P. diadema edwardsi	Range 2–9, mean = 5.3	400 ha	Southeastern submontane rain forest: Ranomafana National Park	Wright 1995, Pochron and Wright 2003
P. d. diadema	Range 3–8, mean = 4.83	33–42 ha	Eastern rain forest: Mantadia National Park	Powzyk 1997, Powzyk and Mowry 2003
P. d. perrieri	Range 2–6	30 ha	Northern dry forest: Analamera Reserve, Ankarana Reserve	Meyers and Ratsirarson 1989, Hawkins et al. 1990
P. d. candidus	Range 3–7, mean = 4.3	?	Northeastern humid forest: Marojejy Reserve	Safford et al. (unpub. report cited in Mittermeier et al. 1994)
P. tattersallli	Range 3–10, mean = 5	9–12 ha	Northeastern dry deciduous forest and semi-evergreen forest patches: Daraina region	Meyers 1993, Meyers and Wright 1993, Mittermeier et al. 1994, Vargas et al. 2002.
Indri indri	2 + offspring	34–40 ha	Eastern rain forest: Mantadia National Park	Powzyk 1997, Powzyk and Mowry 2003
Nocturnal lemurs				
Cheirogaleus medius	2 + offspring (monogamous)	4 ha	Dry deciduous forest: south and southwestern Madagascar	Hladik et al. 1980; Müller 1998, 1999; Fietz 1999
C. major	Solitary	?	Eastern lowland rain forest	Petter et al. 1977, Tattersall 1982
C. ravus	?	?	Eastern rain forest	Groves 2000
C. crossleyi	?	?	Northeastern Madagascar plateau	Groves 2000
C. adapicaudatus	?	?	Southern spiny forest	Groves 2000
C. minisculus	?	?	Central Madagascar: Ambositra	Groves 2000
C. sibreei	?	?		
Allocebus trichotis	Sleeps in groups of 2–6	?	Northern tropical evergreen forest	Meier and Albignac 1991
Mirza coquereli	Sleeps in groups up to 6 at some sites	~4 ha	Western coastal forests	Tattersall 1982
Microcebus murinus	Sleeps in groups of 1–15	0.22–3.2 ha (males), 0.24–1.8 ha (females)	Dry deciduous forest, spiny forest, littoral forest: western and southern Madagascar	Martin 1972a, 1973; Pagès-Feuillade 1989; Radespiel et al. 1998; Ramanamanjato and Ganzhorn 2001
M. rufus	?	?	Northwest and eastern rain forest	Tattersall 1982, Atsalis 2000
M. myoxinus	?	?	Dry forests: southern and western Madagascar	Petter et al. 1971, Rasoloarison et al. 2000
M. ravelobensis	Sleeps in groups	0.44–0.79 ha	Northwestern Madagascar	Petter 1962, Zimmerman et al. 1998
M. tavaratra	?	?	Northern dry deciduous forest: Ankanrana	Rasoloarison et al. 2000
M. berthae	Solitary/dispersed, do not sleep in groups	Male home ranges larger than female, size not known	Western dry deciduous forest: Kirindy, Andranomena, Analabe	Schmid and Kappeler 1994, Rasoloarison et al. 2000, Schwab 2000
M. griseorufus	?	?	Southestern dry deciduous forest, spiny forest: Beza Mahafaly	Rasoloarison et al. 2000, Rasoazanabary personal comm.
Phaner furcifer	Dispersed pairs (male–female pairs sleep together in nests)	3.8–4 ha	Humid, dry, and secondary forest: western and northern Madagascar	Petter and Petter-Rousseaux 1979, Schulke and Kappeler 2003
Avahi laniger	Male–female pairs and offspring	1–2 ha	Rain forest, coastal forest: eastern Madagascar	Albignac 1981a, Ganzhorn et al. 1985, Harcourt 1988
A. occidentalis	Male–female pairs and offspring	?	Dry deciduous forest: northwestern Madagascar	Petter et al. 1977, Tattersall 1977a
A. unicolor	Male–female pairs and offspring	?	Dry deciduous forest: northwestern Madagascar, Sambirano region	Thalmann and Geissmann 2000
Daubentonia madagascariensis	Solitary	mean = 35.6 (females), 170.3 (males)	Eastern, western, and northern Madagascar; primary rain forest, deciduous forest, secondary growth, cultivation, and dry scrub forest: Nosy Mangabe	Tattersall 1982, Sterling 1993, Sterling and Richard 1995
Lepilemur mustelinus	Solitary	1.5	Eastern rain forest	Ratsiraron and Rupler 1988

Table 4.3   (*cont'd*)

SPECIES	MEAN GROUP SIZE (OR RANGE OF GROUP SIZE)	MEAN HOME RANGE SIZE (RANGE)	HABITAT AND WHERE STUDIED	STUDIED BY OR CITED BY
L. dorsalis	Solitary	?	Humid forest, northwestern Madagascar: Nosy Be	Petter et al. 1977, Tattersall 1982
L. septentrionalis	Solitary	1 ha	Dry deciduous forest and humid forest: northern Madagascar	Tattersall 1982, Ratsirarson et al. 1987, Hawkins et al. 1990
L. edwardsi	Dispersed pairs (male–female pairs sleep together in tree holes)	1 ha	Dry deciduous forests: western Madagascar	Petter and Petter-Rousseaux 1979; Albignac 1981a,b; Warren 1994
L. leucopus	Solitary/dispersed (male–female pairs or mother–daughter pairs sleep together)	0.18–0.3 ha	Spiny and gallery forests: southern Madagascar, Beza Mahafaly Reserve	Petter and Petter-Rousseaux 1979, Sussman and Richard 1986
L. ruficaudatus	Solitary or male–female pairs	0.8 ha	Dry forest: western Madagascar	Petter and Petter-Rousseaux 1979
L. microdon	?	?	Eastern rain forest	Petter et al. 1977

southwest of Madagascar: Berenty, Beza Mahafaly, and Antserananomby.

While this species is found primarily in riverine, *xerophytic* (drought-adapted), and scrub forests in south and southwestern Madagascar (Jolly 1966, Sussman 1977), it is also found in spiny forests and low-lying limestone forests; and one population has even been found at Andringitra National Park in the central southeast, living above the tree line at an elevation of 2,500 m (Goodman and Langrand 1996).

L. catta has been defined as a very flexible "edge" species, able to withstand relatively extreme temperatures and to recover from serious droughts (Sussman 1977, Gould et al. 1999, Sauther et al. 1999). It is the most terrestrial species of lemur, spending up to 30% of the time on the ground (Jolly 1966, Sussman 1974).

Social Organization.   *L. catta* lives in multimale/multifemale groups (Jolly 1966, Sussman 1977). Group fission commonly occurs when groups reach a critical size, and they split along matrilines (Sussman 1991, Koyama 1991, Hood and Jolly 1995, Jolly et al. 2002, Gould et al. 2003). This species is female-philopatric, and males disperse at 3–4 years of age (Sussman 1992).

Diet and Feeding Ecology.   Ring-tailed lemurs have been described as "opportunistic omnivores" (Sauther et al. 1999), feeding on fruit (particularly tamarind), leaves and stems, flowers, some insects, and soil from both the ground and termite mounds (Jolly 1966, Sussman 1977, Sauther 1992, Sauther et al. 1999). Food resources are extremely seasonal, and the regions where *L. catta* are found often experience severe droughts (Jolly 1966, Sussman 1977, Sauther 1992, Gould et al. 1999). As a result, ring-tailed lemurs are very flexible and can switch their primary food resources to follow ecological unpredictability. For example, *L. catta* groups will expand their home ranges into those of other groups when particular seasonal resources are unavailable

in their own home range (Budnitz 1978, Jolly et al. 1993, Sussman 1991, Sauther and Sussman 1993).

Reproduction.   Reproductive synchrony is marked in this species and strongly tied to the specific nature of seasonal food resources (Jolly 1966; Sauther 1992, 1998). Average gestation length is 141 days (Sauther 1991). Although females normally give birth to a single infant, twinning in the wild has occasionally been reported (Koyama et al. 2002, Jolly et al. 2002, Bauer, personal communication). Infants are born near the end of the dry season in September and October and weaned at 4–5 months, during the rainy season, when weaning foods are available (Jolly 1966, Sussman 1977, Gould 1990, Sauther 1992). Alloparental care is common (Gould 1992).

Sauther (1994) found that pregnant females feed primarily on fruit and flowers but, when lactating, switch to low-cost, predictable, high-protein plant foods.

Infant mortality differs at the two different sites where it has been documented. Koyama et al. (2002) report 32%–37% at Berenty, where many groups are water-provisioned; but at Beza, where no provisioning occurs, a range of 52%–80% has been reported, depending on rainfall (Gould et al. 1999, 2003).

Eulemur

Within the *Eulemur* genus, we find five species and many subspecies. *E. fulvus* (the brown lemur) is the most geographically widespread, and as a result, there are seven subspecies (Table 4.1). All subspecies except *E. f. mayottensis*, the Mayotte brown lemur which lives on the island of Mayotte in the neighboring Comoros, inhabit continuous forest throughout Madagascar (Freed 1999).

Sexual Dichromatism.   One interesting morphological feature of *Eulemur* is that most species and subspecies are sexually dichromatic, making it easy to distinguish males from females, even in relatively high canopy. The extent

of dichromatism ranges from completely different pelage color in *E. macaco macaco* and *E. m. flavifrons* (males black, females russet brown) to different-colored ventrums, beards, heads, and face markings in *E. fulvus spp., E. rubriventer*, and *E. mongoz. E. f. fulvus* is the only lemur in this group that exhibits no sexual dichromatism (Harrington 1975, Mittermeier et al. 1994).

Reproduction. Gestation in *Eulemur* in the wild is reported to be between 120 and 126 days, and infants in most species are born between September and November (Colquhoun 1993, Mittermeier et al. 1994, Sussman 1999). Females normally give birth to just one infant, which, like most diurnal lemurs, can cling immediately. Interbirth intervals are 1 year, though Overdorff et al. (1999) found that in an *E. f. rufus* population which had been studied for 7 years, the mean interbirth interval between surviving offspring was 2.1 years. In *E. mongoz*, which is often monogamous, adult males frequently carry the infant after it is 2 weeks old (Curtis and Zaramody 1997).

Cathemerality. Cathemerality has been observed in all *Eulemur* species. Most species exhibit year-round cathemeral activity but with some seasonal variation (Overdorff 1988; Rasmussen 1999; Donati et al. 1999, 2001; Donati and Borgognini Tarli 2002b; Andrews and Birkenshaw 1998; Freed 1996; Overdorff and Rasmussen 1995; Kappeler and Erkert 2003). For example, *E. mongoz* exhibits greater nocturnal activity during the cooler, dry seasons, which may correlate with thermoregulation during long cool nights (Curtis et al. 1999). Low nocturnal light during the wet season compromises nighttime activity in *E. mongoz* (Rasmussen 1999), and Colquhoun (1998), Donati et al. (2001, 2002b), and Kappeler and Erkert (2003) stress that nocturnal activity in *E. m. macaco, E. f. collaris*, and *E. f. rufus* is strongly dependent on phases of the moon and available light. Rasmussen (1999) also suggests that in seasonally dry forests cathemeral activity may function as an antipredator strategy during times when canopy cover is thin.

Rasmussen (1999) divides cathemerality into three types: seasonal differences in day and night activity, found in *E. mongoz*; seasonal shift from diurnal to 24 hr activity, found in *E. f. fulvus* (Rasmussen 1999) and *E. f. rufus* (Donati et al. 1999); and year-round 24 hr activity, found in all *Eulemur* species that have been studied in rain forest habitats (Andrews and Birkenshaw 1998, Freed 1996, Overdorff 1988, Overdorff and Rasmussen 1995) as well as in some dry forest habitats (Kappeler and Erkert 2003).

Van Schaik and Kappeler (1996) propose that cathemerality may have occurred in formerly nocturnal taxa, due to an "evolutionary disequilibrium" related to human activities causing the subsequent extinction of both the aforementioned large-bodied lemurs as well as large raptors. These authors suggest that the extinctions of large raptors allowed for greater diurnal activity in the relatively small-bodied *Eulemur* species. Colquhoun (1993) suggests that cathemeral activity may be an ancestral trait for the entire *Eulemur* genus. Kappeler and

Erkert (2003) argue that cathemerality evolved from nocturnal ancestors, perhaps relatively recently, and may have occurred by adding some diurnal activity to a largely nocturnal baseline. Because cathemeral primates are primarily restricted to Madagascar, Kappeler and Erkhart suggest that the unusual aspects of Madagascar's ecology, outlined in Richard and Dewar (1991) and Wright (1999), have allowed for such a transition in activity pattern.

Eulemur fulvus *(Brown Lemur, six Subspecies: Common Brown Lemur, Red-Fronted Brown Lemur, White-Fronted Brown Lemur, Sanford's Lemur, Collared Lemur, White-Collared Brown Lemur, Mayotte Brown Lemur)*

Social Organization. Social organization of all subspecies is mixed-sex groups (Sussman 1974, 1999; Overdorff 1992, 1993a, 1996, 1998; Gerson 2001; Harrington 1975; Mittermeier et al. 1994; Vasey 2000). In *E. f. rufus* (rufous brown lemur), however, groups sometimes fission during periods of food scarcity (Overdorff 1998); and individuals of this subspecies also form strong affiliative dyadic relationships, primarily between males and females but also between other sex/age combinations (Overdorff 1998, Gerson 2001). Overdorff (1998) notes that dyads occurred more often in feeding contexts during the mating season and during periods of food scarcity and may be related to the unclear dominance hierarchies found in rufous brown lemurs, the distribution and density of food patches in the habitat, and vulnerability to predators.

Diet and Feeding Ecology. Diet in the wild has been noted in *E. f. fulvus* in a western dry forest (Harrington 1975); *E. f. rufus* at Ranomafana, a rain forest site (Overdorff 1992, 1993b, 1996); *E. f. sanfordi* in a northern dry forest at Montagne d'Ambre (Freed 1996, 1999); *E. f. collaris* in a southeastern littoral (coastal) forest (Donati and Borgognini Tarli 2002a); *E. f. albifrons* in a northern montane rain forest (Vasey 2000); and three populations in three different areas of the southeastern rain forests (Johnson and Overdorff 2002). The diet of all subspecies is described as highly frugivorous, but leaves, buds, flowers, invertebrates, and nectar are also consumed. In most areas where *E. fulvus* occurs, there can be marked seasonal fluctuation in amount and type of food resources available. During times of fruit scarcity (usually the dry season), animals include more leaves, flowers, and figs in their diets; and *E. f. rufus* groups have been observed to move well out of their home ranges during these periods to seek alternative resources or fission into smaller groups (Overdorff 1993a,b, 1996; Johnson and Overdorff 2002; Overdorff et al. 2003). Both common brown lemurs and rufous brown lemurs ingest a significant amount of tannins and alkaloids from unripe fruit and mature leaves in their diet, and Ganzhorn (1988) and Vasey (2000) suggest that tolerance of secondary compounds combined with ecological flexibility in *E. fulvus* spp. may explain the wide geographic range of this species. Vasey

also notes that because of such flexibility, *E. fulvus* is able to avoid overt competition with sympatric lemur species.

Sympatry between *E. fulvus* and other lemur taxa has been documented in a number of geographic areas. Sympatry and polyspecific associations between *E. f. sanfordi* and *E. coronatus* are discussed below in the section on crowned lemurs, and information on sympatry and niche separation in *E. f. rufus* and *E. rubriventer* is presented in the section on *E. rubriventer*.

E. coronatus *and* E. f. sanfordi*: Sympatry and Polyspecific Assoications*

Sanford's brown lemurs (*E. f. sanfordi*) and crowned lemurs (*E. coronatus*) are sympatric throughout the same region at the northern tip of Madagascar (Wilson et al. 1989; Freed 1996, 1999). Freed studied these two species at Montagne d'Ambre National Park in northern Madagascar, while Wilson's group focused on the two species in the unusual habitat of Ankarana, which is composed of dry forest growing on and around limestone karst pinnacles (*tsingy*) as well as xerophytic scrub and semideciduous dry forest.

Both species inhabit forests which vary in elevation, climate, structure, and disturbance. One difference, however, is that Sanford's lemurs are restricted to closed, continuous-canopy forest and share highly overlapping home ranges (Freed 1996). Both live in small, multimale/multifemale groups (Freed 1996, Wilson et al. 1989), but group cohesion and spacing differ by species. In the dry season, crowned lemur groups are less cohesive than those of Sanford's lemurs, and crowned lemurs sometimes divide into small foraging subgroups during the day (Freed 1996).

Both species are highly frugivorous; however, proportions of fruit and flowers differ between them, and both occasionally feed on leaves and insects.

At Ankarana, Wilson et al. (1989) found that the two species often fed together but did not travel in mixed-species groups. Conversely, Freed (1996) observed frequent polyspecific associations, the first report of such in sympatric lemurs. The two species tolerated the presence of each other well, and when interspecific agonism occurred (in 20%–25% of encounters), they were initiated by the Sanford's lemur group in response to feeding competition. Polyspecific associations varied according to season and were most frequent during the wet season. Freed suggests that both species benefit from one another's familiarity with food resources in different forest levels but not in relation to enhanced predator protection since there were few predators in the area and actual predation on these lemurs was rare.

E. mongoz *(Mongoose Lemur)*

E. mongoz occurs in the subhumid, seasonal forests of northwestern Madagascar as well as on two of the Comoro Islands: Anjouan and Moheli, where they were likely introduced by humans (Tattersall 1982, Mittermeier et al. 1994).

Social Organization. Social organization of *E. mongoz* is variable as it has been observed in both pair-bonded (monogamous) family groups and larger mixed-sex groups (Harrington 1978, Tattersall 1977a, Curtis and Zaramody 1997). Offspring of both sexes disperse and establish their own social groups. Females leave the natal family unit at 27–30 months and males, at 31–42 months (Curtis and Zaramody 1997, 1998).

Diet and Feeding Ecology. The mongoose lemur diet can be categorized as highly nectivorous during the dry season and frugivorous/folivorous during the wet season (Sussman and Tattersall 1976, Curtis and Zaramody 1997).

Reproduction. Infants are born in October–November. At 3 weeks, infants began to explore the environment. Adult males frequently carry the infant between weeks 2 and 5, and at 9 weeks, infants begin to move and feed independently. Females give birth annually (Tattersall 1976, Curtis and Zaramody 1997).

E. m. macaco *(Black Lemur) and* E. m. flavifrons *(Sclater's Black Lemur)*

E. macaco exhibits marked sexual dichromatism: males are black with black ear tufts, and females are golden/reddish/rust brown with off-white ventrum and white ear tufts (Tattersall 1982, Mittermeier et al. 1994).

E. m. flavifrons and *E. m. macaco* × *E. m. flavifrons* hybrids are restricted to dry northwestern forests, just south of the geographic range of the black lemur. Sclater's black lemur differs from the black lemur in that it lacks tufted ears, but more strikingly, its eye color ranges from turquoise blue to gray, as opposed to the amber brown eyes of *E. m. macaco* (Koenders et al. 1985, Mittermeier et al. 1994). Hybrids exhibit either duller blue eyes and no beard or light brown eyes and a less prominent beard and ear tufts compared to the black lemur (Rabarivola et al. 1991).

Social Organization. Social organization is multimale/multifemale. At Ambato Massif in the northwest, Colquhoun (1993) found that larger groups often fissioned into smaller sub-groups.

Diet and Feeding Ecology. Marked wet and dry seasons occur in this area, and seasonal variation was noted with respect to dietary patterns. Fruit was the dominant food item during the rainy season, supplemented by mushrooms and millipedes. During the dry season, flowers, nectar, seed pods, and some leaves were eaten (Colquhoun 1993). Andrews and Birkenshaw (1998) found differences in daytime and nighttime feeding, with more variation in fruit species and leaves consumed in the day and more nectar consumed at night.

Cathemerality. Colquhoun (1993) and Andrews and Birkenshaw (1998) noted year-round cathemeral activity in black lemurs, with nocturnal activity following phases of the moon. Cathemeral activity was seen more in the cooler, dry season and, as with *E. mongoz*, may be related to thermoregulation, allowing these lemurs to avoid cold stress by being physically active during cool nights in the dry season.

Reproduction. Females usually give birth annually to a single infant, in September or October, after a gestation period of 125–126 days (Colquhoun 1993, Mittermeier et al. 1994).

E. rubriventer *(Red-Bellied Lemur)*

One of the few pair-bonded lemurs, *E. rubriventer* has been closely studied at Ranomafana National Park by Overdorff (1992, 1993a,b, 1996).

Social Organization and Group Size. The red-bellied lemur lives in monogamous pairs with offspring and maintains exclusive use of its home range, actively defending the boundaries.

Diet, Feeding Ecology, and Sympatry with E. f. rufus. *E. rubriventer* is a highly frugivorous primate and includes some leaves and nectar in the diet (Overdorff 1992). At the Ranomafana site, *E. rubriventer* and *E. f. rufus* are sympatric. Even though the composition of their diets is similar, Overdorff (1992, 1993b) notes that *E. f. rufus* ate more unripe fruits, mature leaves, and insects than did *E. rubriventer*; and she suggests that *E. f. rufus* may have a higher tolerance than *E. rubriventer* for secondary compounds, which may also help with niche separation. The two species also used flowers in different ways: *E. rubriventer* licked flower nectar and *E. f. rufus* consumed the entire flower.

Both of these species may serve as pollinators for some of the plant species that they use, but Overdorff (1992) notes that *E. rubriventer* may be a more efficient pollinator since it does not destroy the reproductive parts of the flower. Overdorff (1996) suggests that the two sympatric species may avoid direct competition during periods of scarce resources by differing both their activity patterns and habitat use, and subtle and consistent differences in diet throughout the seasons allow these two species to coexist.

Reproduction. Females give birth to one infant annually, in September or October. As in some pair-bonded anthropoid species, male red-bellied lemurs help with infant care, often holding or carrying the infant. Males have been noted to carry infants up to 100 days (Overdorff 1993a, Mittermeier et al. 1994).

Hapalemur *(Bamboo Lemurs)*

All species of *Hapalemur* are highly unusual because they specialize on bamboo, a dietary focus not found in other primates. There are three species of *Hapalemur* and two subspecies (see Table 4.1). *H. aureus*, an extremely rare lemur so far found only in very small populations in two southeastern national parks (see Table 4.3), was discovered only in 1986 (Meier and Rumpler 1987, Wright et al. 1987).

Social Organization. *H. griseus griseus* is reported to have flexible social organization. Grassi (2001) found monogamous pairs as well as polygynous and multimale/multifemale social groups at her field site. Alaotran gentle lemurs (*H. g. alaotrensis*) also live in varying kinds of group: monogamous pairs, groups with two breeding females,

and some groups with three adult males, though there is only one breeding male per group (Mutschler et al. 2000, Mutschler 2002). Mutschler found that sexes disperse. Females leave their natal group as subadults, and males make their first migration as adults.

Tan (1998) notes that *H. aureus* live in monogamous pairs, and the one group of *H. simus* which Tan studied was multimale/multifemale, with three adult males, two adult females, and offspring.

Diet and Feeding Ecology. As their common names suggest, all *Hapalemur* species are bamboo specialists, and all three species ingest the cyanide found in the giant bamboo without harm, a remarkable dietary adaptation (Glander et al. 1989, Tan 1998). More than 85% of *Hapalemur* diets are made up of bamboo and grasses (Tan 1998, Mutschler 2002). Tan found that the three species are able to coexist sympatrically in the Ranomafana National Park habitat because each specializes on different parts of the bamboo plant. They also feed on several other plant species, fungus, and, at times, soil (Tan 1998, Grassi 2001). *H. griseus* and *H. aureus* both consume some fruit, and Grassi notes that both new and mature leaves were eaten by *H. griseus* at the higher-elevation Vato site in Ranomafana Park. She suggests that increased dietary diversity by female *H. g. griseus* during reproductive periods helps offset high metabolic needs.

Reproduction. *H. griseus* and *H. aureus* have similar gestation lengths of 137–140 and 138 days, respectively, while the gestation period of the larger *H. simus* is somewhat longer, at 149 days (Tan 2001, Grassi 2001).

The Alaotran gentle lemur does not have as strict and discrete a mating season as that found in most other lemur species. Mating season begins in September and ends in February (Mutschler 2002). Mutschler suggests that a year-round, consistent resource base is a key factor in the absence of strict breeding seasonality.

H. aureus mothers have been noted to nest their infants in thick foliage during the first 2 weeks of life (Tan 2001). Tan also found that *H. griseus* and *H. aureus* females both park and orally transport infants, but *H. simus* females carry their newborns.

Grassi (2001) reports high infant mortality (67%) in *H. g. griseus* at the Vato site, Ranomafana. Surviving infants were fully weaned by 5 months. There is a 1-year interbirth interval in *Hapalemur*.

Varecia *(Ruffed Lemur)*

The genus *Varecia* contains two subspecies: the black and white ruffed lemur (*V. variegata variegata*) and the red ruffed lemur (*V. v. rubra*), the latter having a very restricted range in the northern Masoala Peninsula. In all areas where these lemurs have been studied, populations have experienced occasional and sometimes devastating cyclones (Balko 1998; Ratsimbazafy 2001, 2002).

Social Organization. Both monogamy and multimale/multifemale mating systems have been reported (Morland 1991,

White 1989, Balko 1998, Britt 2000). Rigamonti's (1993) two study groups of red ruffed lemurs fissioned into subgroups of two or three animals. During the cool wet season, they lived in these small subgroups for several weeks at a time, and groups were cohesive in the transitional dry months. Ratsimbazafy (2002) found that after a severe cyclone black and white ruffed lemurs at Manombo on the southeastern coast foraged singly rather than as a group as 95% of larger trees in the area stopped fruiting.

Diet and Feeding Ecology.   *Varecia* is highly frugivorous, with fruit making up 75%–95% of the diet, and the remainder is comprised of nectar, flowers, and some leaves (Morland 1991, Britt 2000, Vasey 2000). During times of low fruit availability, *Varecia* will consume large amounts of young leaves (Balko 1998). After the above-mentioned cyclone at Manombo, ruffed lemurs at this site relied on fruit from nonendemic, invasive plant species, as well as fungus (Ratsimbazafy 2002). *Varecia* has been observed to come to the ground and ingest soil at particular times of the year (Morland 1991, White 1989, Britt 2000). Such geophagy may serve to neutralize secondary compounds in the diet as well as provide a source of minerals (Ganzhorn 1988, Britt 2000). Britt suggests that even though *Varecia* are marked frugivores, their ability to use other food items may be an important adaptation for dealing with low or absent fruit productivity during times of environmental stress because these lemurs live in areas of Madagascar where cyclones are common and important food trees can be destroyed.

Ruffed lemurs are considered important seed dispersers and pollinators in the eastern Madagascar rain forests (Balko 1998, Britt 2000), and Britt (2000) stresses that, as such, it is of utmost importance to develop conservation strategies that will aid in the survival of ruffed lemurs.

Reproduction.   Reproduction and infant care in *Varecia* differ from other diurnal lemurs. *Varecia* is the only diurnal prosimian in which females possess two sets of mammary glands and regularly exhibit multiple (two to four infants) births (Morland 1990, Mittermeier et al. 1994). Infants do not cling to the mother as do other diurnal lemur infants; rather, the mother transports infants one at a time by mouth and parks them in nests or in trees (Petter et al. 1977, Tattersall 1982). Morland (1990) noted frequent alloparental care consisting of guarding infants at nest sites and allonursing. Nests are constructed by pregnant females a few weeks prior to parturition 10–20 m above ground (Morland 1990, Balko 1998). Furthermore, ruffed lemur infants develop more quickly than do other diurnal lemur offspring, and in captivity they have been noted to weigh up to 70% of adult body weight by 4 months of age (Pereira et al. 1987). In the wild, infants grow rapidly (Balko 1998) and appear to reach nearly adult size at about 6 months of age (Morland 1990).

Ruffed lemurs commonly experience cyclones in their geographic range. In Ratsimbazafy's (2001, 2002) study, females ceased reproduction for 3 years after a cyclone destroyed most of their resource base. He suggests that plasticity in diet, small group size, solitary foraging, and reproductive cessation following a severe natural disaster are important reasons why *Varecia* groups can persist in such a highly disturbed habitat. Ratsimbazafy (2002) points out the link between environmental variability and female fertility in this species.

Gestation length is estimated at around 102 days in the wild, and infants are born in September and October (Morland 1990, Mittermeier et al. 1994).

Indriidae (*Propithecus* and *Indri*)

Propithecus *(Sifakas)*

Propithecus species are extraordinary vertical clingers and leapers. With three species and eight subspecies (Table 4.1), sifakas are found in many habitats and many regions of Madagascar, although some, like *P. tattersalli*, are found only in very restricted ranges and several are very rare, with populations threatened by habitat destruction.

The remainder of this section will focus on the four most-studied *Propithecus* species: *P. verreauxi verreauxi*, *P. tattersalli*, *P. diadema edwardsi*, and *P. d. diadema*.

P. v. verreauxi *(Verreaux's Sifaka)*

Social Organization.   Verreaux's sifaka is found in small multimale/multifemale groups; however, this species also fissions into small foraging parties at times. The social organization of Verreaux's sifaka has been sometimes been referred to as "neighborhoods" because of the fluidity of groups, the fact that males make temporary visits to adjacent groups, and the frequency of adult male intergroup transfer (Jolly 1966, Richard 1978, Richard et al. 1993).

Diet and Feeding Ecology.   Verreaux's sifaka lives in the dry west, south, and southwest of Madagascar and experiences dramatic shifts in seasonal resource distribution between the wet and dry seasons. Sifakas (and all indriids) are considered folivores; however, during the wet season, 60%–70% of their diet is made up of fruit and flowers, with young leaves accounting for 20%. During the dry season, mature leaves make up 70% of the diet, with fruit and flowers contributing only 20%. Bark makes up the remainder of the diet in both seasons (Richard 1978, Sussman 1999).

Reproduction.   Gestation in this species is 150–160 days (Petter-Rousseaux 1964). The infant is carried ventrally at first, then dorsally; and infants will continue to ride on the mother until 6–7 months (Jolly 1966). At the Beza Mahafaly site in southwestern Madagascar, Richard et al. (2002) found that more than half of the females in this population did not reproduce for the first time until they were 6 years old. Such a delay in reproduction for such a small primate is considered by Richard et al. (2002) to be "bet hedging," i.e. a slowing down of female reproductive life history where first births are later than expected and females reproduce into old age, also later than expected. This unusual reproductive

strategy is suggested to be an evolutionary response to the climatic unpredictability in this species' geographic region, such as extremely varied annual rainfall patterns and frequent droughts (Richard et al. 2002). Infant mortality is high, averaging 52% in the first year of life (Richard et al. 2002). High mortality may be related to a combination of starvation after weaning in particularly dry years, hypothermia in the cold and dry season, disease, and predation. Adult males mate at 3–4 years of age (Richard et al. 2002).

P. tattersalli *(Golden-Crowned Sifaka)*

The golden-crowned sifaka has recently been reported to exist slightly outside of the original restricted area in the Daraina region of northeastern Madagascar, with an effective population size of these rare lemurs estimated at 2,520–3,960 individuals (Vargas et al. 2002).

Social Organization.   The golden-crowned sifaka lives in small, multimale/multifemale groups (Meyers and Wright 1993).

Diet and Feeding Ecology.   Seasonal variation in food resources occurs in *P. tattersalli*'s geographic range. Meyers and Wright (1993) note that the diet consists of immature and mature leaves (22% and 17%, respectively), 37% unripe fruit and seeds, 9% fruit pulp, and 13% flowers. These items peaked in availability in the wet season, but seeds, available year-round, formed the staple food item. Bark is also sometimes eaten during the dry season (Mittermeier et al. 1994).

Reproduction.   In *P. tattersalli*, mating season occurs in late January and infants are born in late July. Weaning occurs at 5–6 months and is timed to coincide with peak immature leaf availability. As in many other lemur species, late lactation/weaning occurs in the early wet season so that infants have access to abundant weaning foods (Meyers and Wright 1993).

P. d. edwardsi *(Milne-Edwards Sifaka)*

A population of Milne-Edwards sifaka has been studied continuously since 1986 by Wright and her students and colleagues at Ranomafana National Park in southeastern Madagascar (see, e.g., Wright et al. 1987, Meyers and Wright 1993, Wright 1995, Hemingway 1996, Wright et al. 1997, Erhardt and Overdorff 1998, Overdorff et al. 2003, Pochron and Wright 2003, Pochron et al. 2004). Consequently, much is known about this species of rain forest sifaka.

Social Organization.   Pochron and Wright (2003) and Pochron et al. (2004) report variable social organization in this species. Multimale/multifemale groups, unimale polygynous, polyandrous, and male–female pair groups have been observed. Pochron and Wright (2003) suggest that since females sometimes mate with males outside of their groups, such flexibility may reduce pressure for males to join groups with several females and result in the variability seen in group composition in this species.

Pochron and Wright (2003) suggest that Madagascar's harsh and unpredictable environment may have resulted in *P. d. edwardsi* living and foraging in small groups, which would reduce feeding competition yet help somewhat with predator protection (vs. living/foraging solitarily).

Diet and Feeding Ecology.   Ripe fruit and seeds make up the majority (55%) of *P. d. edwardsi*'s diet, supplemented by vine leaves (15%), flowers (3%), and immature leaves (26%) (Meyers and Wright 1993). As in most lemur habitats, seasonal variation in resource availability is found in *P. d. edwardsi*'s habitat, with more immature leaves available during the wet season. Fruit production can vary annually (Meyers and Wright 1993).

Reproduction.   Average gestation length is 179 days, 1 month longer than in the smaller *P. verreauxi* (Wright 1995). Infants are primarily independent by 7 months of age and fully weaned by 1 year. Most females begin reproducing at 4 years of age. However, Pochron et al. (2004) have found that only 24% of all females survive to the age of 4 years.

Average interbirth interval is 1.5 years, and average infant mortality is 50%.

P. d. diadema *(Diademed Sifaka)*

Powzyk (1997) studied sympatric *P. d. diadema* and *Indri* at Mantadia National Park in the eastern rain forest. She notes that in parts of their former distribution, diademed sifaka populations have disappeared due to overhunting or habitat destruction.

Social Organization.   Diademed sifakas live in multimale/multifemale groups. Females choose mates within their group but have also been observed mating with novel males from other groups (Powzyk 1997).

Diet and Feeding Ecology.   Diademed sifakas are primarily folivorous. Powzyk (1997) and Powzyk and Mowry (2003) note that 42% of their diet consists of immature leaves. They supplement their diet with fruits and flowers. Feeding differences between *P. d. diadema* and sympatric *Indri* at Mantadia are presented in the section on *Indri* below.

Reproduction.   The average birth rate over 3 years was 0.50/year, and infant mortality over this period was 50% (Powzyk 1997).

Indri indri *(Indri)*

There is only one species of *Indri*, and the common name is also indri. In addition to its large size (see Table 4.2), *Indri* can be distinguished from most other lemurs by its rudimentary tail (Pollock 1975). It is also known because of its loud, wailing morning calls, which can be heard up to 3 km away (Pollock 1975, Mittermeier et al. 1994).

Indri has been characterized as the largest extant lemur species; however, Glander and Powzyk (1995) and Powzyk (1997) found that both *Indri* and *P. d. diadema* were similar in body weight, and Powzyk suggests that both species be considered the largest two extant lemurs. In both species, females weighed slightly more than males.

Geographic Range/Habitat.   Indri inhabit the eastern rain forests, from near, but not in, the Masoala Peninsula in the

northeast to east central Madagascar (Petter et al. 1977, Tattersall 1982).

Social Organization.   *Indri* is one of the few monogamous lemur species, living in pairs or small groups consisting of a pair and offspring (Pollock 1975, Powzyk 1997, Britt et al. 2001). The mated pair use morning calls to announce both their location to other pairs and their mated status (Powzyk 1997).

Diet and Feeding Ecology.   Like other indriids, *Indri*'s diet consists of leaves, flowers, fruit, bark, and seeds (Pollock 1975, Powzyk 1997, Britt et al. 2001, Powzyk and Mowry 2003). Powzyk found that leaves made up 71% of the diet at Mantadia. Britt et al. note that *Indri* at Betampona, farther north, fed on more mature leaves than those at Mantadia and that in the winter season they increased consumption of bark and fruit. Pollock (1975) notes that *Indri* regularly came to the ground to ingest earth; however, Powzyk and Mowry (2003) note that sympatric diademed sifaka at Mantadia engaged in geophagy twice as often as did *Indri*. Powzyk (1997) suggests that *Indri*'s specialization for plant fiber has allowed these two large-bodied diurnal lemur species to coexist in over 90% of their range.

Reproduction.   A single infant is born in May, after a gestation period of 120–150 days (Pollock 1975, Mittermeier et al. 1994). Infants are carried on the ventrum until 4 months, then carried dorsally until 8 months. Infants are weaned between 8 and 12 months (Pollock 1975). Powzyk (1997) calculated Indri average birth rates as 0.33/year and infant mortality as 0.67 over a 3-year period.

Nocturnal Lemurs

During the past 10 years, the nocturnal lemurs of Madagascar have been the focus of a number of behavioral and phylogenetic studies that have greatly expanded what is known of their socioecology and biology. Exciting new data on their behavioral ecology indicate that nocturnal prosimians live in complex societies and exhibit high interspecific diversity in lemur social and mating systems. Indeed, it has been suggested that nocturnal lemur social systems contain three types: gregarious, for animals living in cohesive groups; dispersed, for solitary foragers with social networks; and solitary, for completely solitary animals (Müller and Thalmann 2000).

There are three families that contain only nocturnal lemuriformes: Cheirogaleidae, Megaladapidae, and Daubentoniidae. The primarily diurnal Indriidae contains two nocturnal species: *Avahi laniger* and *A. occidentalis*.

Cheirogaleidae

Members of the family Cheirogaleidae are small, quadrupedal lemurs that sleep in nests of leaves or in tree holes during the day. The genus *Cheirogaleus* has recently undergone a number of taxonomic changes, and seven species are now recognized (Groves 2000). The scientific and common names

for these species are found in Table 4.1. *Allocebus trichotis*, the hairy-eared dwarf lemur, was originally thought extinct but was rediscovered in 1989 (Meier and Albignac 1991). The genus *Mirza* is comprised of one species, *Mirza coquereli*, Coquerel's dwarf lemur. Fork-marked lemurs include *Phaner furcifer* and a number of newly described subspecies (see Groves and Tattersall 1991).

Microcebus *(Mouse Lemurs)*

Recent phylogenetic analyses of mitochondrial deoxyribonucleic acid (mtDNA) sequence data and newly collected mouse lemur specimens have also resulted in designations of several new species of *Microcebus* (Schmid and Kappeler 1994, Zimmerman et al. 1998, Rasoloarison et al. 2000, Yoder et al. 2000, Pastorini et al. 2001). There are now eight species of mouse lemur recognized, and these are listed in Table 4.1.

Cheirogaleus medius *Group:* C. medius *and* C. adipicaudatus *(Dwarf Lemurs)*

Social Organization.   While home ranges of *Cheirogaleus medius* and *C. adipicaudatus* may overlap, same-sexed individuals are intolerant of one another (Hladik et al. 1980). *C. medius* is monogamous and lives in dispersed family groups (Müller 1998, 1999; Fietz 1999). This species deals with seasonal variation in food resources by entering torpor. During torpor, nesting size is variable, from one to as many as five individuals sharing a nest in a hollow tree trunk. Males, however, emerge from torpor sooner than do females, and this may be a form of paternal investment as males patrol their home range and by doing so may maintain access to its resources for their family group (Müller 1999). Males dramatically lose weight during this time (Müller 1999).

Diet and Feeding Ecology.   *C. medius* focuses on a variety of high-quality foods, including fruits, nectar, vertebrates, and insects (Hladik 1979, Hladik et al. 1980, Wright and Martin 1995). Of particular note is their ability to store substantial fat in their tails (during which the volume of the tail triples), which is used during the torpid state in seasons of low food abundance (Hladik et al. 1980, Wright and Martin 1995).

Reproduction.   Fat-tailed dwarf lemurs are seasonal breeders. The gestation period is 61–64 days (Petter 1978, Hladik et al. 1980), and a female normally produces twins, although this can vary from one to four infants (Foerg 1982). In captivity, these lemurs become sexually mature in their first year of life (Foerg 1982); however, in the wild, sexual maturity may not occur until 2 years of age (Müller 1999).

Cheirogaleus major *Group:* C. major *and* C. crossleyi

Social Organization.   Little is known regarding the ranging or social behavior of the *C. major* group. They are essentially solitary and may nest together in groups of two (Petter et al. 1977).

Diet and Feeding Ecology. Like the *C. medius* group, these lemurs feed on young leaves, fruit, nectar, pollen, and insects (Petter et al. 1977) and can tolerate a medium level of tannins in their diet (Ganzhorn 1988). They also enter a period of torpor during the dry season and store fat in the tail to accommodate this period.

Reproduction. Gestation length is 70 days with two or three infants born in January (Petter-Rousseaux 1964, Petter et al. 1977). They are carried by the mother in her mouth as they are unable to cling at birth (Petter-Rousseaux 1964). Lactation lasts only 1.5 months, and infants develop quickly, being able to follow their mothers within a month and to eat fruit at about 25 days of age (Petter-Rousseaux 1964).

Al. trichotis *(Hairy-Eared Dwarf Lemur)*

Social Organization. As *Al. trichotis* has yet to be systematically studied in the wild, little information is available. It does sleep in tree holes in groups of two to six (Meier and Albignac 1991).

Diet and Feeding Ecology. Observations in captivity indicate that *Allocebus* feeds on fruit, honey, and locusts; and its long tongue is suggestive of nectar feeding (Meier and Albignac 1991). Seasonal body fat storage occurs but over the entire body, not just in the tail (Meier and Albignac 1991).

Reproduction. Little is known about its reproduction, but infants may be born in January or February (Meier and Albignac 1991).

Mirza coquereli *(Coquerel's Dwarf Lemur)*

Social Organization. Adult males are heavier than adult females, and this increases most dramatically prior to and during the mating season (Kappeler 1997). Female home ranges are 4 ha, remain stable over time, and overlap considerably, with little evidence of actively defended territories (Kappeler 1997). Male home ranges increase during the mating season and overlap with other home ranges only at that time (Kappeler 1997). Genetic data indicate that females are organized into matrilines, most females show philopatry, and dispersed multimale/multifemale is the social organization of this species (Kappeler et al. 2002).

Diet and Feeding Ecology. Coquerel's dwarf lemur has an eclectic diet that includes fruit, flowers, buds, gums, insects and insect secretions, spiders, frogs, chameleons, and small birds (Pagès 1980, Andrianarivo 1981).

Reproduction. Mating occurs in October, followed by a 3-month gestation (Petter-Rousseaux 1980). Infants develop quickly and can leave their nests after 1 month (Pagès 1980). Females may become reproductive within their first year (Kappeler 1997).

Microcebus

Considerable advances in the study of the behavior and ecology of *Microcebus* have revealed great flexibility in this genus. Many of the newer species have yet to be completely described, including *M. myoxinus*, *M. tavaratra*, *M. sambiranensis*, and *M. griseorufus.*

M. murinus *(Gray Mouse Lemur)*

Social Organization. The gray mouse lemur appears to exhibit a multimale/multifemale system within a dispersed social network (Fietz 1999, Radespiel 2000). While commonly observed foraging alone at night, during the nonmating season, this lemur sleeps in groups of up to 15 individuals in nests made of leaves or in tree hollows (Martin 1972a, 1973; Radespiel et al. 1998). Females will sleep with the same female partners, and these individuals often share home ranges; however, different female groups use nearly exclusive home ranges (Radespiel 2000). Males often sleep alone (Radespiel et al. 1998, Radespiel 2000), but during the mating season it is common to find mixed-sex groups in these nests, with a single male nesting with as many as seven females (Martin 1973). Home ranges overlap substantially (Barre et al. 1988, Fietz 1999, Radespiel 2000), and male home ranges are larger than those of females (Table 4.3) (Pagès-Feuillade 1989). Males prefer nests near those preferred by females (Rasoazanabary 2004). Preferred nests may have superior thermoregulation and protection from predators, and female nests are better insulated, suggesting that this may be a contested resource between the sexes (Radespiel et al. 1998, Schmid 1998). Genetic data indicate male-biased natal dispersal in this species (Radespiel et al. 2003b).

Diet and Feeding Ecology. The gray mouse lemur stores fat in its tail and may enter torpor, but time spent in torpor varies by sex; also, while females become inactive during periods of low food availability, males are more active (Rasoazanabary 2004). This species is omnivorous, but fruit and invertebrates are a major component of the diet. Other foods include flowers, nectar, leaves, sap and gum, homopteran larvae secretions, and small invertebrates (Martin 1972a, 1973; Petter 1978; Hladik 1979; Barre et al. 1988; Corbin and Schmid 1995). Insect prey is often caught on the ground (Martin 1972a, 1973).

Reproduction. Mating occurs in September, with a gestation of 59–62 days (Martin 1972a, Radespiel 2000). Normally, twins are born and are parked in tree holes and/or carried until 3 weeks of age. Infants develop quickly and exhibit adult behaviors by 2 months of age (Petter-Rousseaux 1964, 1980; Martin 1972a). In captivity, females first give birth at 18 months (Petter-Rousseaux 1964).

M. rufus *(Eastern Rufous Mouse Lemur)*

Social Organization. The brown mouse lemur remains understudied, and little is known of its social organization. Like other *Microcebus* species, it sleeps in tree holes or nests but may also use old birds' nests (Martin 1973). Mark–recapture data suggest overlapping home ranges and a multimale/multifemale social organization (Atsalis 2000).

Diet and Feeding Ecology. With a diet similar to that of *M. murinus*, this species consumes fruits, insects, and flowers

(Martin 1972a, Harcourt 1987) as well as, more rarely, young leaves (Ganzhorn 1988). *M. rufus* stores some fat in its tail and may enter torpor depending on the habitat (Atsalis 1998).

Reproduction. No data are available on its reproduction in the wild. This species is also difficult to maintain in captivity, but data from a breeding colony of wild-caught *M. rufus* indicate an estrous cycle of 59 days, 2.5 cycles per season, seasonal reproduction with a seasonal change in testicular size, and a gestation length of 56.5 days, with litter size ranging from one to three offspring. Mating behavior varied among pairs but copulation appeared to be limited to a single day per estrus (Wrogemann and Zimmermann 2001).

M. berthae *(Berthe's Mouse Lemur)*

Social Organization. Current data indicate that this newly discovered species is nongregarious and forages solitarily. It does not form sleeping associations but instead sleeps alone in a tangle of lianas rather than in self-constructed nests or tree holes. It has been suggested that such a sleeping pattern may occur as a result of both competition for nest sites from other nocturnal sympatric animals, including lemurs, as well as an antipredator strategy in this smallest of the living primates (Schwab 2000). Male home ranges appear to be larger than female home ranges at least during the mating season (Schwab 2000). Indirect data (e.g., changes in testicle size, presence of sperm plugs) suggest this species has a multimale mating system that includes promiscuous mating and sperm competition (Schwab 2000).

Diet and Feeding Ecology. In-depth studies of their feeding ecology have yet to be carried out, but males and females forage separately (Schwab 2000).

Reproduction. Female cycles are not synchronized during the mating season. Males are heavier than females during the mating period, but females are heavier than males during the nonreproductive season (Schwab 2000).

M. ravelobensis *(Golden-Brown Mouse Lemur)*

Social Organization. The golden-brown mouse lemur lives in a dispersed multimale/multifemale society with promiscuous mating (Radespiel et al. 2003a). Conspecifics interact frequently. Sleeping groups can contain only females or both females and males and are maintained over time even though sleeping sites may change (Radespiel et al. 2003a, Weidt et al. 2004). It is suggested that thermoregulation may explain such groupings and that sleeping groups are the basic social unit in brown mouse lemur society (Weidt et al. 2004).

Diet and Feeding Ecology. The diet is omnivorous and similar to that of *M. murinus* (Reimann 2002, Radespiel et al. 2003a). Individuals forage alone, remain active despite changes in environmental conditions, and do not appear to alter fat storage in their tails across different seasons and photoperiods (Randrianambinina et al. 2003). Daily torpor occurs in this species (Radespiel et al. 2003a).

Reproduction. There is a distinct mating season in this species, although females' estrus does not appear to be strongly synchronized (Schmelting et al. 2000, Randrianambinina et al. 2003).

Ph. furcifer *(Fork-Marked Lemur, Four Subspecies: Eastern Fork-Marked Lemur, Pale Fork-Marked Lemur, Pariente's Fork-Marked Lemur, Amber Mountain Fork-Marked Lemur)*

Social Organization. The highly vocal *Ph. furcifer* (a mean of 30 loud calls an hour emitted by males has been counted in a radius of about 200 m) can be found in holes in baobab trees, old *Mirza coquerli* nests, and leaf nests (Petter et al. 1971, 1975; Schulke and Kappeler 2003). Meetings between neighboring family groups occur where home ranges intersect, during which females may interact affiliatively with females of other groups (Schulke and Kappeler 2003). Males often interact agonistically with neighboring males and females during such encounters (Schulke and Kappeler 2003). Male–female pairs can maintain vocal contact throughout the night and may nest together during the day (Charles-Dominique and Petter 1980, Schulke and Kappeler 2003). *Phaner*'s social organization may be described as "dispersed pairs" because although there is pair stability for as many as 3 years and their territories overlap nearly completely, actual interaction between male and female pairs is very low (Schulke and Kappeler 2003).

Diet and Feeding Ecology. The fork-marked lemurs' primary food is gum, particularly from *Terminalia* trees; but they also consume insects, sap, buds, flowers, and insect exudates (Charles-Dominique and Petter 1980). Gum feeding correlates with this species' highly specialized toothcomb, which is used to create holes to access tree gum and sap (Charles-Dominique and Petter 1980).

Reproduction. Mating is in June (Charles-Dominique and Petter 1980), with a single infant born in November or December that is first carried and then rides on the mother's back (Petter et al. 1971, 1975; Charles-Dominique and Petter 1980).

Avahi Group *(Woolly Lemurs)*

Social Organization. Short-term studies indicate that the woolly lemur is monogamous. An adult male, female, and offspring make up the group; usually, it is encountered in pairs or trios, but as many as five individuals can be together (Pollock 1975, Petter and Charles-Dominique 1979, Albignac 1981a, Ganzhorn et al. 1985, Harcourt 1988, Thalmann 2001). Individuals forage alone but may meet throughout the night to groom and rest together (Harcourt 1988, Razanahoera-Rakotomalala 1981). Group members sleep together in dense foliage (Albignac 1981a).

Diet and Feeding Ecology. Although primarily active at night, woolly lemurs have also been observed feeding during the day (Ganzhorn et al. 1985). *Avahi* feeds primarily

on leaves, an unexpected diet given its relatively small body size. Such folivory may explain its high level of resting during the evening (Albignac 1981a, Razanahoera-Rakotomalala 1981, Ganzhorn et al. 1985, Ganzhorn 1988, Harcourt 1988, Thalmann 2001). Males and females forage together and feed in the same trees (Thalmann 2001).

Reproduction.   Woolly lemurs give birth to a single infant in August or September. Infants initially cling to the mother's ventrum and then later ride on her back (Martin 1972b, Petter et al. 1977, Ganzhorn et al. 1985, Harcourt 1988).

D. madagascariensis *(Aye-Aye)*

Originally believed to be extinct, the highly specialized aye-aye was rediscovered in 1957 (Petter and Petter-Rousseaux 1959).

Social Organization.   The aye-aye builds its nest in the fork of trees and normally forages alone, but it can be found near other individuals (Petter et al. 1977; Iwano and Iwakawa 1988; Sterling 1992, 1993). Studies at Nosy Mangabe indicate that females have exclusive ranges and rarely interact with one another or do so aggressively (Sterling and Richard 1995). Males have large, overlapping ranges and interact both aggressively and affiliatively with one another (Sterling and Richard 1995). Male and female ranges overlap, and most interactions appear to be affiliative, with individuals communicating through vocalizations and scent marking (Sterling and Richard 1995).

Diet and Feeding Ecology.   The aye-aye exhibits a number of specializations, including continuously growing rodent-like incisors and a long and thin third digit that allows it to forage for wood-boring larvae and to feed on hard seeds of the genus *Canarium* (Sterling et al. 1994). It also focuses on other high-quality foods that include fruit, especially coconuts; adult insects; fungus; and nectar (Petter et al. 1977, Iwano and Iwakawa 1988, Sterling 1993, Sterling et al. 1994). This species is able to inhabit a wide variety of habitats, from rain forest to cultivated areas (especially coconut groves) (Tattersall 1982).

Reproduction.   Females in estrus give loud calls that attract males and will mate with some, but not all, attracted males (Sterling and Richard 1995). Aye-ayes are reported to give birth only every 2–3 years (Petter and Peyriéras 1970a,b; Petter et al. 1977). Births appear to not be seasonal, and infants may be weaned at 7 months (Petter and Peyriéras 1970a,b; Sterling 1993).

Lepilemur (Sportive Lemurs)

Lepilemur leucopus *(White-Footed Sportive Lemur)*

Social Organization.   Found primarily in the Didierea bush and southern dry forests of Madagascar, males and females may sleep in separate tree holes or bundled lianas; but in some studies, they are also found sleeping in pairs (Russell 1977, 1980). Females may share ranges with young offspring and perhaps even with adult daughters (Charles-Dominique and Hladik 1971).

Diet and Feeding Ecology.   Highly folivorous, the white-footed sportive lemur focuses on low-quality leaves or flowers of the Didereaceae species *Alluadia procera* and *Alluadia ascendens* (Charles-Dominique and Hladik 1971, Hladik and Charles-Dominique 1974). While ingestion of feces (*coecotrophy*) has been reported in some studies (Hladik and Charles-Dominique 1974), it appears to be absent in others (Russell 1977, 1980).

Reproduction.   Mating in this species occurs in May–July, gestation is 4.5 months, with singleton births in September–November (Petter et al. 1977). Individuals are sexually mature at 18 months (Richard 1984).

Lepilemur edwardsi *(Milne-Edwards Sportive Lemur)*

Social Organization.   Found within the dry deciduous forests of western Madagascar, male and female *L. edwardsi* commonly sleep together in tree holes or near one another in separate holes (Albignac 1981b, Petter et al. 1977, Warren 1994, Rasoloharijaona et al. 2003). Two to three individuals may forage together and regularly engage in grooming bouts (Warren 1994). Current studies indicate this species may be characterized by dispersed monogamy, with each pair defending its home range by branch shaking and vocal displays (Rasoloharijaona 1998, Zimmermann 1998, Rasoloharijaona et al. 2003). Fidelity of these pairs may last as long as 4 years (Altrichter 2001).

Diet and Feeding Ecology.   As in other lepilemurs that have been studied in the wild, the Milne-Edwards sportive lemur forages solitarily and its diet is primarily leaves (Thalmann 2001), which are selected for their protein value and low alkaloid content (Ganzhorn 1988, 1993). Fruit, flowers, and fleshy seeds are also eaten but at much lower levels (Razanahoera-Rakotomalala 1981, Albignac 1981b, Ganzhorn 1988, Thalmann 2001).

Reproduction.   Females give birth at the end of September to a single infant (Rasoloharijaona et al. 2003). Infants are left in a tree hole or within dense foliage while the mother forages (Rasoloharijaona et al. 2003).

Subfossil Lemurs

About 17, or nearly one-third, of the known lemur species became extinct in the late Holocene due to human habitation (overhunting, habitat destruction) and aridification (Burney 1997, Dewar 1997). These extinct species are referred to as "subfossil" lemurs since most became extinct relatively recently, that is, within the first 1,000 years of the 2,000 years of human habitation on Madagascar (Simons et al. 1995, Fleagle 1999). All extinct species were larger than living lemurs, and this is the most striking difference between extant and extinct species. Some extinct lemurs are

Figure 4.4 Some subfossil lemur species, with extant *Indri*, one of the two largest living lemurs, shown for size comparison. Drawing by Stephen Nash, reprinted with kind permission of the artist.
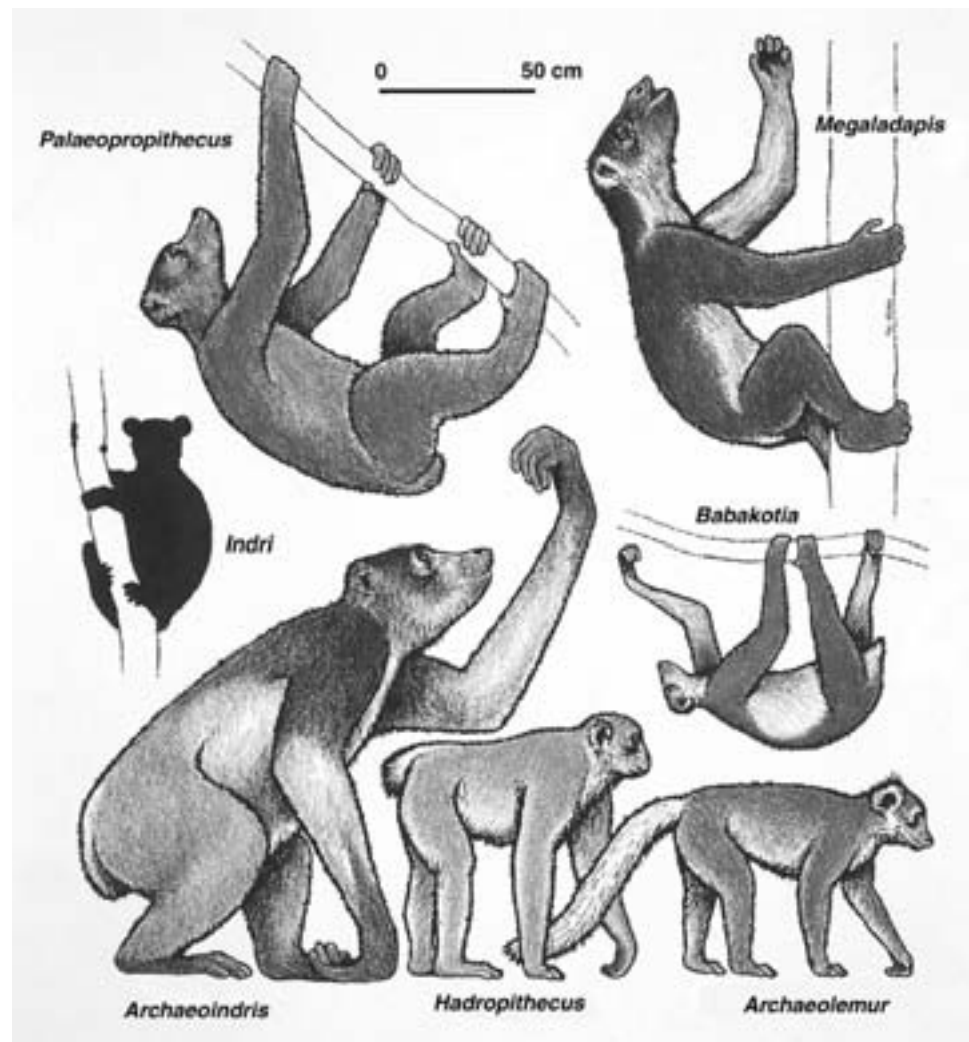
considered to be as large as the largest living anthropoids today (Fig. 4.4).

Godfrey et al. (1993) found that lack of sexual dimorphism is a morphological trend in all lemurs. Even in the largest and most terrestrial of these subfossil lemurs, there is little evidence for sexual dimorphism.

Walker (1967), Gingerich and Martin (1981), and Martin (1990) suggest, based on orbit size measurements and comparisons, that all subfossil lemur species were diurnal, although Jungers et al. (2002) note that the actual ancestral condition for all lemurs was nocturnality. Thus, the subfossil species became diurnal as a later adaptation during the speciation and adaptive radiation which occurred on Madagascar after the first lemur ancestors arrived.

Diet in subfossil lemurs has been inferred based on dental morphology and molar microwear analysis (Jungers et al. 2002, Rafferty et al. 2002, Godfrey et al. 2004). The very large *Megaladapis* species were likely arboreal leaf browsers (Godfrey et al. 1997, 2004). The large *Paleopropithecus* species (extinct relatives of the extant

Propithecus genus) were probably folivorous seed predators which supplemented their diet with a variety of fruits, similar to *Propithecus* today (Godfrey et al. 1997, 2004). The diet of the partially terrestrial *Hadropithecus* was misinterpreted for a number of years as being gramnivorous, rather like the gelada baboon (Jolly 1970, Mittermeier et al. 1994, Jungers et al. 2002); however, recent molar microwear analysis strongly suggests that the diet of this extinct lemur consisted of hard objects such as seeds but not grass seeds, rhizomes, or tubers (Rafferty et al. 2002, Godfrey et al. 2004). *Archaeolemur* species were likely hard-object feeders and may have been omnivorous with a seasonally diverse diet (Godfrey et al. 1997, Jungers et al. 2002, Rafferty et al. 2002). The dental morphology of *Pachylemur* suggests frugivory (Godfrey et al. 1997, 2004).

Despite the large body size of subfossil species, some exhibit skeletal characteristics that indicate some degree of arboreality; and Jungers et al. (2002) note that the large terrestrial species would have been awkward and slow-moving on the ground. *Paleopropithecus* would have used a

suspensory posture. Jungers et al. suggest that the subfossil species were not vertical clingers and leapers (as is seen in extant indriids and *Lepilemur*) as they all had relatively short and robust hindlimbs.

While we will unfortunately never see these large and unusual extinct lemurs, research and conservation efforts are occurring in many areas of Madagascar today on extant species and new protected areas are being designated. Hopefully, these conservation programs, along with the continued work and training of both Malagasy and foreign primatologists, will inform us further as to the behavior and ecology of the lemurs and help protect these beautiful and fascinating primates through the twenty-first century and beyond.

REFERENCES

Albignac, R. (1981a). Variabilité dans l'organisation territoriale et l'écologie de Avahi laniger (Lémurien nocturne de Madagascar). *C. R. Acad Sci. III* 292:331–334.

Albignac, R. (1981b). Lemurine social and territorial organization in a northwestern Malagasy forest (restricted area of Ampijoroa). In: Chiarelli, A. B., and Corruccini, R. S. (eds.), *Primate Behavior and Sociobiology*. Springer-Verlag, Berlin. pp. 25–29.

Altrichter, H. (2001). Playback zur Erkennung und Diskrimination von Informationskategorien in den Sozialrufen von Edward-Wieselmakis (*Lepilemur edwardsi*) in NW-Madagascar [diplomarbeit]. Universität Osnabrück, Osnabrück.

Andrews, J. R., and Birkinshaw, C. R. (1998). A comparison between the daytime and night-time diet, activity and feeding height of the black lemur *Eulemur macaco* (Primates: Lemuridae), in Lokobe Forest, Madagascar. *Folia Primatol.* 69(suppl. 1):175–182.

Andrianarivo, A. J. (1981). Étude comparée de l'organisation sociale chez *Microcebus coquereli* [diss.]. University of Madagascar, Antananarivo.

Atsalis, S. (1998). Seasonal fattening and changes in activity levels in the brown mouse lemur (*Microcebus rufus*) in Ranomafana National Park, Madagascar. *Am. J. Primatol.* 45:165.

Atsalis, A. (2000). Spatial distribution and population composition of the brown mouse lemur (*Microcebus rufus*) in Ranomafana National Park, Madagascar, and its implications for social organization. *Am. J. Primatol.* 51:61–78.

Balko, E. A. (1998). A behaviorally plastic response to forest composition and logging disturbance by *Varecia variegata variegata* in Ranomafana National Park, Madagascar [PhD diss.]. State University of New York, Syracuse.

Barre, V., Lebac, A., Petter, J. J., and Albignac, R. (1988). Étude du Microcèbe par radiotracking dans la forêt de l'Ankarafantsika. In: Rakotovao, L., Barre, V., and Sayer, J. (eds.), *L'Equilibre des Ecosystèmes Forestiers a Madagascar: Actes d'un Séminaire International*. IUCN, Gland, Switzerland. pp. 61–71.

Britt, A. (2000). Diet and feeding behaviour of the black-and-white ruffed lemur (*Varecia variegata variegata*) in the Betampona Reserve, eastern Madagascar. *Folia Primatol.* 71:133–141.

Britt, A., Randriamandatonirina, N. J., Glasscock, K. D., and Iambana, B. R. (2001). Diet and feeding behaviour of *Indri indri* in a low-altitude rain forest. *Folia Primatol.* 73:225–239.

Budnitz, N. (1978). Feeding behavior of *Lemur catta* in different habitats. In: Bateson, P. P. G., and Klopfer, P. H. (eds.), *Perspectives in Ethology. Social Behavior*, vol. 3. Plenum Press, New York. pp. 85–108.

Budnitz, N., and Dainis, K. (1975). *Lemur catta*: ecology and behavior. In: Tattersall, I., and Sussman, R. W. (eds.), *Lemur Biology*, Plenum Press, New York. pp. 219–236.

Burney, D. A. (1997). Theories and facts regarding Holocene environmental change before and after human colonization. In: Goodman, S. M., and Patterson, B. D. (eds.), *Natural Change and Human Impact in Madagascar*. Smithsonian Institution Press, Washington DC. pp. 75–89.

Charles-Dominique, P., and Hladik, C. M. (1971). Le *Lepilemur* du sud de Madagascar: écologie, alimentation et vie sociale. *Terre Vie* 25:3–66.

Charles-Dominique, P., and Petter, J.-J. (1980). Ecology and social life of *Phaner furcifer*. In: Charles-Dominique, P., Cooper, H. M., Hladik, A., Hladik, C. M., Pages, E., Pariente, G. F., Petter-Rousseaux, A., Petter, J.-J., and Schilling, A. (eds.), *Nocturnal Malagasy Primates: Ecology, Physiology and Behavior*. Academic Press, New York. pp. 75–95.

Colquhoun, I. C. (1993). The socioecology of *Eulemur macaco*. In: Kappeler, P. M., and Ganzhorn, J. U. (eds.), *Lemur Social Systems and Their Ecological Basis*. Plenum Press, New York. pp. 11–23.

Colquhoun, I. C. (1998). Cathemeral behavior of *Eulemur macaco macaco* at Ambato Massif, Madagascar. *Folia Primatol.* 69(suppl. 1):22–34.

Corbin, G. D., and Schmid, J. (1995). Insect secretions determine habitat use patterns by a female lesser mouse lemur (*Microcebus murinus*). *Am. J. Primatol.* 37:317–324.

Curtis, D. J., and Zaramody, A. (1997). Monogamy and mate monopolization by females in *Eulemur mongoz* [abstract]. *Primate Rep.* 48–2:16–17.

Curtis, D. J., and Zaramody, A. (1998). Group size, home range use, and seasonal variation in the ecology of *Eulemur mongoz*. *Int. J. Primatol.* 19:811–835.

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

Dewar, R. E. (1997). Were people responsible for the extinction of Madagacar's subfossils, and how will we ever know? In: Goodman, S. M., and Patterson, B. D. (eds.), *Natural Change and Human Impact in Madagascar*. Smithsonian Institution Press, Washington DC. pp. 364–377.

Donati, G., and Borgognini Tarli, S. M. (2002a). Feeding ecology of the collared brown lemur, *Eulemur fulvus collaris*, in the Sainte Luce Littoral Forest. *Folia Primatol.* 73:315.

Donati, G., and Borgognini Tarli, S. M. (2002b). The role of abiotic factors in influencing cathemeral activity of collared brown lemurs (*E. fulvus collaris*) in the Sainte Luce Littoral Forest. *Folia Primatol.* 73:305–306.

Donati, G., Lunardini, A., and Kappeler, P. M. (1999). Cathemeral activity of red-fronted brown lemurs (*Eulemur fulvus rufus*) in the Kirindy Forest. In: Rakotosamimanana, B., Rasamimanana, H., Ganzhorn, J. U., and Goodman, S. M. (eds.), *New Directions in Lemur Studies*. Kluwer/Plenum, New York. pp. 119–137.

Donati, G., Lunardini, A., Kappeler, P. M., and Borgognini Tarli, S. M. (2001). Nocturnal activity in the cathemeral red-fronted lemur (*Eulemur fulvus rufus*) with observations during a lunar eclipse. *Am. J. Primatol.* 53:69–78.

Erhardt, E. M. and Overdorff, D. J. (1998). Infanticide in *Propithecus diadema edwardsi*: an evaluation of the sexual selection hypothesis. *Into. J. Primatol*. 19:73–81.

Erickson, C. J. (1991). Percussive foraging in the aye-aye, *Daubentonia madagascariensis*. *Anim. Behav*. 41:793–801.

Erickson, C. J. (1994). Tap-scanning and extractive foraging in aye-ayes, *Daubentonia madagascariensis*. *Folia Primatol*. 62:125–135.

Fietz, J. (1999). Mating system of *Microcebus murinus*. *Am. J. Primatol*. 48:127–133.

Fleagle, J. G. (1999). *Primate Adaptation and Evolution*, 2nd ed. Academic Press, London.

Foerg, R. (1982). Reproduction in *Cheirogaleus medius*. *Folia Primatol*. 39:49–62.

Freed, B. Z. (1996). Co-occurrence among crowned lemurs (*Eulemur coronatus*) and Sanford's lemurs (*Eulemur fulvus sanfordi*) of Madagascar [PhD diss.]. Washington University, St. Louis.

Freed, B. Z. (1999). An introduction to the ecology of daylight-active lemurs. In: Dolhinow, P., and Fuentes, P. A. (eds.), *The Non-Human Primates*. Mayfield Press, Mountain View, CA. pp. 123–132.

Ganzhorn, J. U. (1988). Food partitioning among Malagasy primates. *Oecologica* 75:436–450.

Ganzhorn, J. U. (1993). Flexibility and constraints of *Lepilemur* ecology. In: Kappeler, P. M., and Ganzhorn, J. U. (eds.), *Lemur Social Systems and Their Ecological Basis*. Plenum Press, New York. pp. 153–166.

Ganzhorn, J. U., Abraham, J. P., and Razanahoera-Rakotomalala, M. (1985). Some aspects of the natural history and food selection of *Avahi laniger*. *Primates* 26:452–463.

Gerson, J. S. (2001). Social relationships in wild red-fronted brown lemurs (*Eulemur fulvus rufus*) [PhD diss.]. Duke University, Durham, NC.

Gingerich, P. D., and Martin, R. D. (1981). Cranial morphology and adaptations in Eocene Adapidae II: the Cambridge skull of *Adapis parisiensis*. *Am. J. Phys. Anthropol*. 56:235–257.

Glander, K. E., Powzyk, J. A. (1998). Morphometrics of wild *Indri indri* and *Propithecus diadema diadema*. *Folia Primatol*. 69(suppl. 1):399.

Glander, K. E., Wright, P. C., Daniels, P. S., and Merenlender, A. M. (1992). Morphometrics and testicle size of rain forest lemur species from southeastern Madagascar. *J. Hum. Evol*. 22:1–17.

Glander, K. E., Wright, P. C., Seigler, D. S., and Randriansolo, B. (1989). Consumption of cyanogenic bamboo by a newly discovered species of bamboo lemur. *Am. J. Primatol*. 19:199–124.

Godfrey, L. R., Jungers, W. L., Reed, K. E., Simons, E. L., and Chatrath, P. S. (1997). Subfossil lemurs: inferences about past and present primate communities. In: Goodman, S. M., and Patterson, B. D. (eds.), *Natural Change and Human Impact in Madagascar*. Smithsonian Institution Press, Washington DC. pp. 218–256.

Godfrey, L. R., Lyon, S. K., and Sutherland, M. R. (1993). Sexual dimorphism in large-bodied primates: the case of the subfossil lemurs. *Am. J. Phys. Anthropol*. 90:315–334.

Godfrey, L. R., Semprebon, G. M., Jungers, W. L., Sutherland, M. R., Simons, E. L., and Solounias, N. (2004). Dental use wear in extinct lemurs: evidence of diet and niche differentiation. *J. Hum. Evol*. 47:145–169.

Goodman, S. M., and Langrand, O. (1996). A high mountain population of the ringtailed lemur *Lemur catta* on the Andringitra Massif, Madagascar. *Oryx* 30:259–268.

Gould, L. (1990). The social development of free-ranging infant *Lemur catta* at Berenty Reserve, Madagascar. *Int. J. Primatol*. 11:297–317.

Gould, L. (1992). Alloparental care in free-ranging *Lemur catta* at Berenty Reserve, Madagascar. *Folia Primatol*. 58:72–83.

Gould, L., Sussman, R. W., and Sauther, M. L. (1999). Natural disasters and primate populations: the effects of a two-year drought on a naturally occurring population of ringtailed lemurs in southwestern Madagascar. *Int. J. Primatol*. 20:69–84.

Gould, L., Sussman, R. W., and Sauther, M. L. (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.

Grassi, C. (2001). The behavioral ecology of *Hapalemur griseus griseus*: the influence of microhabitat and population density on this small-bodied prosimian folivore [PhD diss.]. University of Texas, Austin.

Groves, C. P. (2000). The genus *Cheirogaleus*: unrecognized biodiversity in dwarf lemurs. *Int. J. Primatol*. 21:943–962.

Groves, C. P., and Tattersall, I. (1991). Geographical variation in the fork-marked lemur, *Phaner furcifer* (Mammalia, Primates). *Folia Primatol*. 56:39–49.

Harcourt, C. (1988). *Avahi laniger*: a study in inactivity. *Primate Eye* 35:9.

Harcourt, C. S. (1987). Brief trap/retrap study of the brown mouse lemur (*Microcebus rufus*). *Folia Primatol*. 49:209–211.

Harrington, J. E. (1975). Field observations of social behavior of *Lemur fulvus fulvus* (E. Geoffroy 1812). In: Tattersall, I., and Sussman, R. W. (eds.), *Lemur Biology*. Plenum Press, New York. pp. 259–279.

Harrington, J. E. (1978). Diurnal behavior of *Lemur mongoz* at Ampijoroa, Madagascar. *Folia Primatol*. 29:291–302.

Hawkins, A. F. A., Chapman, P., Ganzhorn, J. U., Bloxam, Q. M., Barlow, S. C., and Tonge, S. J. (1990). Vertebrate conservation in Ankarana Special Reserve, northern Madagascar. *Biol. Conserv*. 54:83–110.

Hemingway, C. A. (1996). Morphology and phenology of seeds and whole fruit eaten by Milre-Edwards sifaka. *Propithecus diadema edwardsi* in Ranomafana National Park, Madagascar. *Int. J. Primatol*. 17:637–659.

Hladik, C. M. (1979). Diet and ecology of prosimians. In: Doyle, G. A., and Martin, R. D. (eds.), *The Study of Prosimian Behavior*. Academic Press, New York. pp. 307–357.

Hladik, C. M., and Charles-Dominique, P. (1974). The behavior and ecology of the sportive lemur (*Lepilemur mustelinus*) in relation to its dietary peculiarities. In: Martin, R. D., Doyle, G. A., and Walker, A. C. (eds.), *Prosimian Biology*. Duckworth Press, London. pp. 23–37.

Hladik, C. M., Charles-Dominique, P., and Petter, J. J. (1980). Feeding strategies of five nocturnal prosimians in the dry forest of the west coast of Madagascar. In: Charles-Dominique, P., Cooper, H. M., Hladik, A., Hladik, C. M., Pages, E., Pariente, G. F., Petter-Rousseaux, A., Petter, J. J., and Schilling, A. (eds.), *Nocturnal Malagasy Primates: Ecology*, *Physiology and Behavior*. Academic Press, New York. pp. 41–73.

Hood, L. C., and Jolly, A. (1995). Troop fission in female *Lemur catta* at Berenty Reserve, Madagascar. *Int. J. Primatol*. 16:997–1016.

Iwano, T., and Iwakawa, C. (1988). Feeding behaviour of the aye-aye (*Daubentonia madagascariensis*) on nuts of Ramy (*Canarium madagascariensis*). *Folia Primatol*. 50:136–142.

Jenkins, P. D. (1987). Catalogue of primates in the British Museum (Natural History) and elsewhere in the British Isles Part IV: Suborder strepsirrhini, including the subfossil Madagascar lemurs and family Tarsiidae. London: British Museum (Natural History). px. 189.

Johnson, S., and Overdorff, D. J. (2002). Scarce season diet and keystone resources in three brown lemur (*Eulemur fulvus* spp.) populations. *Am. J. Primatol.* 56:65–66.

Jolly, A. (1966). *Lemur Behavior*. University of Chicago Press, Chicago.

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. 197–215.

Jolly, A., Dobson, A., Rasamimanana, H. M., Walker, J., Solberg, M., and 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., Rasamimanana, H. R., Kinnaird, M. F., O'Brien, T. G., Crowley, H. M., Harcourt, C. S., Gardner, S., and Davidson, J. (1993). Territoriality in *Lemur catta* groups during the birth season at Berenty, Madagascar. In: Kappeler, P. M., and Ganzhorn, J. U. (eds.), *Lemur Social Systems and Their Ecological Basis*. Plenum Press, New York. pp. 85–109.

Jolly, C. J. (1970). *Hadropithecus*: A lemuroid small-object feeder. *Man* 5:619–626.

Jungers, W. L. (1979). Locomotion, limb proportions and skeletal allometry in lemurs and lorises. *Folia Primatol.* 32:8–28.

Jungers, W. L., Godfrey, L. R., Simons, E. L., Wunderlich, R. E., Richmond, B. G., and Chatrath, P. S. (2002). Ecomorphology and behavior of giant extinct lemurs from Madagascar. In: Plavcan, J. M., Kay, R. F., Jungers, W. L., and van Schaik, C. P. (eds.), *Reconstructing Behavior in the Primate Fossil Record*. Kluwer, New York. pp. 371–411.

Kappeler, P. M. (1997). Intrasexual selection in *Mirza coquereli*: evidence for scramble competition polygyny in a solitary primate. *Behav. Ecol. Sociobiol.* 45:115–127.

Kappeler, P. M. (2000). Lemur origins: rafting by groups of hibernators? *Folia Primatol.* 71:422–425.

Kappeler, P. M., and Erkert, H. G. (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.

Kappeler, P. M., Wimmer, B., Zinner, D., and Diethard, T. (2002). The hidden matrilineal structure of a solitary lemur: implications for primate social evolution. *Proc. R. Soc. Lond. B.* 269:1755–1763.

Koenders, L., Rumpler, Y., and Ratisirarson, J. (1985). *Lemur macaco flavifrons*: a rediscovered subspecies of primate. *Folia Primatol.* 44:210–215.

Koyama, N. (1991). Troop division and inter-troop relationships of ring-tailed lemurs (*Lemur catta*) at Berenty, Madagascar. In: Ehara, A., Kimura, T., and Iwamoto, M. (eds.), *Primatology Today*. Elsevier, Amsterdam. pp. 173–176.

Koyama, N., Nakamichi, M., Ichino, S., and Takahata, Y. (2002). Population and social dynamics changes in ring-tailed lemur troops at Berenty, Madagascar, between 1989–1999. *Primates* 43:291–314.

Martin, R. D. (1972a). A preliminary field study of the lesser mouse lemur (*Microcebus murinus* J. F. Miller 1777). *Z. Tierpsychol.* 9(suppl.):43–89.

Martin, R. D. (1972b). Adaptive radiation and behaviour of the Malagasy lemurs. *Phil. Trans. R. Soc. Lond. B.* 264:295–352.

Martin, R. D. (1973). A review of the behaviour and ecology of the lesser mouse lemur (*Microcebus murinus* J. F. Miller 1777). In: Michael, R. P., and Crook, J. H. (eds.), *Comparative Ecology and Behaviour of Primates*. Academic Press, London. pp. 1–68.

Martin, R. D. (1984). Dwarf and mouse lemurs. In: MacDonald, D. (ed.), *The Encyclopaedia of Mammals: 1*. George Allen and Unwin, London. p. 331.

Martin, R. D. (1990). *Primate Origins and Evolution*, Princeton University Press, Princeton, NJ.

Martin, R. D. (2000). Origins, diversity, and relationships of lemurs. *Int. J. Primatol.* 21:1021–1049.

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

Meier, B., Albignac, R., Peyrieras, A., Rumpler, Y., and Wright, P. C. (1987). A new species of *Hapalemur* (Primates) from southeast Madagascar. *Folia Primatol.* 48:211–215.

Meier, B., and Rumpler, Y., (1987). Preliminary survey of *Hapalemur simus* and of a new species of *Hapalemur* in eastern Betsileo, Madagascar. *Primate Conserv.* 8:40–43.

Meyers, D. M. (1993). The effects of resource seasonality on the behavior and reproduction of the golden-crowned sifaka (*Propithecus tattersalli*, Simons, 1988) in three Malagasy forests [PhD diss.]. Duke University, Durham, NC.

Meyers, D. M., and Ratsirarson, J. (1989). Distribution and conservation of two endangered sifakas in northern Madagascar. *Primate Conserv.* 10:82–87.

Meyers, D. M., and Wright, P.C. (1993). Resource tracking: food availability and *Propithecus* seasonal reproduction. In: Kappeler, P. M., and Ganzhorn, J. U. (eds.), *Lemur Social Systems and Their Ecological Basis*. Plenum Press, New York. pp. 179–192.

Mittermeier, R. A., Tattersall, I., Konstant, W. R., Meyers, D. M., and Mast, R. B. (1994). *Lemurs of Madagascar*. *Conservation International Tropical Field Guide Series*. Conservation International, Washington DC.

Morland, H. S. (1990). Parental behavior and infant development in ruffed lemurs (*Varecia variegata*) in a northeast Madagascar rain forest. *Am. J. Primatol.* 20:253–265.

Morland, H. S. (1991). Preliminary report on the social organization of ruffed lemurs (*Varecia variegata variegata*) in a northeast Madagascar rain forest. *Folia Primatol.* 56:157–161.

Morland, H. S. (1993). Seasonal behavioral variation and its relationship to thermoregulation in ruffed lemurs (*Varecia variegata variegata*). In: Kappeler, P. M., and Ganzhorn, J. U. (eds.), *Lemur Social Systems and their Ecological Basis*. Plenum Press, New York. pp. 193–203.

Müller, A. E. (1998). A preliminary report on the social organisation of *Cheirogaleus medius* (Cheirogaleidae; Primates) in north-west Madagascar. *Folia Primatol.* 69:160–166.

Müller, A. E. (1999). Aspects of social life in the fat-tailed dwarf lemur (*Cheirogaleus medius*): inferences from body weights and trapping data. *Am. J. Primatol.* 49:265–280.

Müller, A., and Thalmann, U. (2000). Origin and evolution of primate social organization: a reconstruction. *Biol. Rev.* 75:405–435.

Mutschler, T. (2002). Alaotran gentle lemur: some aspects of its behavioral ecology. *Evol. Anth. Suppl* 1:101–104.

Mutschler, T., Nievergelt, C. M., and Feistner, A. T. C. (2000). Social organization of the Alaotran gentle lemur (*Hapalemur griseus alaotrensis*). *Am J. Primatol.* 50:9–24.

Overdorff, D. J. (1988). Preliminary report on the activity cycle and diet of the red-bellied lemur (*Eulemur rubriventer*) in Madagascar. *Am. J. Primatol.* 16:143–153.

Overdorff, D. J. (1992). Differential patterns of flower feeding by *Eulemur fulvus rufus* and *Eulemur rubriventer* in Madagascar. *Am. J. Primatol.* 28:191–203.

Overdorff, D. J. (1993a). Ecological and reproductive correlates to range use in red-bellied lemurs (*Eulemur rubriventer*) and rufous lemurs (*Eulemur fulvus rufus*). In: Kappeler, P. M., and Ganzhorn, J. U. (eds.), *Lemur Social Systems and Their Ecological Basis*. Plenum Press, New York. pp. 167–178.

Overdorff, D. J. (1993b). Similarities, differences, and seasonal patterns in the diets of *Eulemur rubriventer* and *Eulemur fulvus rufus* in the Ranomafana National Park, Madagascar. *Int. J. Primatol.* 14:721–753.

Overdorff, D. J. (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.

Overdorff, D. J. (1998). Are *Eulemur* species pair-bonded? Social organization and mating strategies in *Eulemur fulvus rufus* from 1988–1995 in southeast Madagascar. *Am. J. Phys. Anthropol.* 105:153–166.

Overdorff, D. J., Erhart, E. M., and Mutschler, T. (2003). Fission–fusion in *Eulemur fulvus rufus* in southeastern Madagascar. *Am. J. Primatol.* 60(suppl. 1):42–43.

Overdorff, D. J., Merenlender, A. M., Talata, P., Telo, A., and Forward, Z. A. (1999). Life history of *Eulemur fulvus rufus* from 1988–1995 in southeastern Madagascar. *Am. J. Phys. Anthropol.* 108:295–310.

Overdorff, D. J., and Rasmussen, M. A. (1995). Determinants of nighttime activity in "diurnal" lemurid primates. In: Alterman, L., Doyle, G. A., and Izard, M. K. (eds.), *Creatures of the Dark: The Nocturnal Prosimians*. Plenum Press, New York. pp. 61–74.

Pagès, E. (1980). Ethoecology of *Microcebus coquereli* during the dry season. In: Charles-Dominique, P., Cooper, H. M., Hladik, A., Hladik, C. M., Pagès, E., Pariente, C. F., Petter-Rousseaux, A., Peter, J. J., and Schilling, A. (eds.), *Nocturnal Malagasy Primates: Ecology*, *Physiology and Behavior*. Academic Press, New York. pp. 17–116.

Pagès-Feuillade, E. (1989). Modalités de l'occupation de l'espace et interindividuelles chez un prosimien nocturne malagache (*Microcebus murinus*). *Folia Primatol.* 50:204–220.

Pastorini, J., Martin, R. D., Ehresmann, P., Zimmermann, E., and Forstner, M. R. J. (2001). Molecular phylogeny of the lemur family Cheirogaleidae (primates) based on mitochondrial DNA sequences. *Mol. Phylogenet. Evol.* 19:45–56.

Pereira, M. E. (1993a). Agonistic interactions, dominance relations and ontogenetic trajectories in ringtailed lemurs. In: Pereira, M. E., and Fairbanks, L. A. (eds.), *Juvenile Primates: Life History*, *Development and Behavior*. Oxford University Press, New York. pp. 285–305.

Pereira, M. E. (1993b). Seasonal adjustment of growth rate and adult body weight in ringtailed lemurs. In: Kappeler, P. M., and Ganzhorn, J. U. (eds.), *Lemur Social Systems and Their Ecological Basis*. Plenum Press, New York. pp. 205–221.

Pereira, M. E., Klepper, A., and Simons, E. L. (1987). Tactics of care for young infants by forest-living ruffed lemurs (*Varecia variegata variegata*): ground nests, parking, and biparental guarding. *Am. J. Primatol.* 13:129–144.

Petter, J. J. (1962). Recherches dur l'ecologie et l'ethologie des lemuriens malagashes. Mémoires Museum National Histoire Naturelle, Paris, 27:1–146.

Petter, J. J. (1978). Ecological and physiological adaptations of five sympatric nocturnal lemurs to seasonal variation in food production. In: Chivers, D. J., and Herbert, J. (eds.), *Recent Advances in Primatology. 1: Behaviour*. Academic Press, London. pp. 211–223.

Petter, J. J., Albignac, R., and Rumpler, Y. (1977). Lemurine mammals (Primates, Prosimians). *Faune Madagascar*, 44:1–513.

Petter, J. J., and Charles-Dominique, P. (1979). Vocal communication in prosimians. In: Doyle, G. A., and Martin, R. D. (eds.), *The Study of Prosimian Behavior*. Academic Press, New York. pp. 247–305.

Petter, J. J., and Petter-Rousseaux, A. (1959). Contribution to the study of the aye-aye. *Naturaliste Malagache* 11:153–164.

Petter, J. J., and Petter-Rousseaux, A. (1979). Classification of the prosimians. In: Doyle, G. A., and Martin, R. D. (eds.), *The Study of Prosimian Behavior*. Academic Press, London. pp. 1–44.

Petter, J. J., and Peyriéras, A. (1970a). Nouvelle contribution a l'étude d'un lémurien malagache, le aye-aye (*Daubentonia madagascariensis* E. Geoffroy). *Mammalia* 34:167–193.

Petter, J. J., and Peyriéras, A. (1970b). Observation éco-éthologiques sur les lemuriens malagaches du genre Hapalemur. *Terre Vie* 24:356–382.

Petter, J. J., Schilling, A., and Pariente, G. (1971). Observations éco-éthologiques sur deux lémuriens malagaches nocturnes: *Phaner furcifer* et *Microcebus coquereli*. *Terre Vie* 25:287–327.

Petter, J. J., Schilling, A., and Pariente, G. (1975). Observations on behavior and ecology of *Phaner furcifer*. In: Tattersall, I., and Sussman, R. W. (eds.), *Lemur Biology*. Plenum Press, New York. pp. 209–218.

Petter-Rousseaux, A. (1964). Reproductive physiology and behavior of the Lemuroidea. In: Buettner-Janusch, J. (ed.), *Evolutionary and Genetic Biology of Primates*, vol. 2. Academic Press, New York. pp. 91–132.

Petter-Rousseaux, A. (1980). Seasonal activity rhythms, reproduction, and body weight variations in five sympatric nocturnal prosimians, in simulated light and climatic conditions. In: Charles-Dominique, P., Cooper, H. M., Hladik, A., Hladik, C. M., Pages, E., Pariente, G. F., Petter-Rousseaux, A., Petter, J. J., and Schilling, A. (eds.), *Nocturnal Malagasy Primates: Ecology*, *Physiology and Behavior*. Academic Press, New York. pp. 137–152.

Pochron, S. T., Tucker, W. T., and Wright, P. C. (2004). Demography, life history and social structure in *Propithecus diadema edwardsi* from 1986 to 2000 in Ranomafana National Park, Madagascar. *Am. J. Phys. Anthropol.* 125:61–72.

Pochron, S. T., and Wright, P. C. (2003). Variability in adult group compositions of a prosimian primate. *Beh. Ecol. Sociobiol.* 54:285–293.

Pollock, J. I. (1975). Field observations on *Indri indri*: a preliminary report. In: Tattersall, I., and Sussman, R. W. (eds.), *Lemur Biology*. Plenum Press, New York. pp. 287–311.

Pollock, J. I. (1977). The ecology and socioecology of feeding in *Indri indri*. In: Clutton-Brock, T. (ed.), *Primate Ecology:*

Studies of Feeding and Ranging Behavior in Lemurs, Monkeys and Apes. Academic Press, London. pp. 37–69.

Powzyk, J. A. (1997). The socioecology of two sympatric indriids: *Propithecus diadema diadema* and *Indri indri*, a comparison of feeding strategies and their possible repercussions on species-specific behavior [PhD diss.]. Duke University, Durham, NC.

Powzyk, J. A., and Mowry, C. B. (2003). Dietary and feeding differences between sympatric *Propithecus diadema diadema* and *Indri indri*. *Int. J. Primatol.* 24:1143–1162.

Rabarivola, C., Meyers, D., and Rumpler, Y. (1991). Distribution and morphological characteristics of intermediate forms between the black lemur (*Eulemur macaco macaco*) and the Sclater's lemur (*E. m. flavifrons*). *Primates* 32:269–273.

Radespiel, U. (2000). Sociality in the gray mouse lemur (*Microcebus murinus*) in northwestern Madagascar. *Am. J. Primatol.* 51:21–40.

Radespiel, U., Cepok, S., Zimmermann, E., and Zietemann, V. (1998). Sex-specific usage patterns of sleeping-sites in grey mouse lemurs (*Microcebus murinus*) in northwestern Madagascar. *Am. J. Primatol.* 46:77–84.

Radespiel, U., Ehresmann, P., and Zimmerman, E. (2003a). Species-specific usage of sleeping sites in two sympatric mouse lemur species (*Microcebus murinus* and *M. ravelobensis*) in northwestern Madagascar. *Am. J. Primatol.* 59:139–151.

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

Rafferty, K. L., Teaford, M. F., and Jungers, W. L. (2002). Molar microwear of subfossil lemurs: Improving the resolution of dietary inferences. *J. Hum. Evol.* 43:645–657.

Ramanamanjato, J. B., and Ganzhorn, J. U. (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.

Randrianambinina, B., Rakotondravony, P., Radespiel, U., and Zimmermann, E. (2003). Seasonality in general activity, body mass and reproduction of the golden brown mouse lemur (*Microcebus ravelobensis*) in northwestern Madagascar and the brown mouse lemur (*M. rufus*) in eastern Madagascar. *Primates* 44:321–331.

Rasmussen, M. A. (1999). Ecological influences on activity cycle in two cathemeral primates, the mongoose lemur (*Eulemur mongoz*) and the common brown lemur (*Eulemur fulvus fulvus*) [PhD diss.]. Duke University, Durham, NC.

Rasoazanabary, E. A. (2004). Preliminary study of mouse lemurs in the Bezamahafaly Special Reserve, southwest Madagascar. *Lemur News* 9:4–7.

Rasoloarison, R. M., Goodman, S. M., and Ganzhorn, J. U. (2000). Taxonomic revision of mouse lemurs (*Microcebus*) in the western portions of Madagascar. *Int. J. Primatol.* 21:963–1019.

Rasoloharijaona, S. (1998). Vocal communication in a nocturnal lemur in northwestern Madagascar. XVIIth Congress of the International Primatological Society, Antananarivo, Madagascal. Abstract 170.

Rasoloharijaona, S. B., Rakotosamimanana, B., Randrianambinina, B., and Zimmermann, E. (2003). Pair-specific usage of sleeping sites and their implications for social organization in a nocturnal Malagasy primate, the Milne Edwards sportive lemur (*Lepilemur edwardsi*). *Am. J. Phys. Anthropol.* 122:251–258.

Ratsimbazafy, J. H. (2001). On the brink of extinction and the process of recovery: responses of black-and-white ruffed lemurs (*Varecia variegata variegata*) to disturbance in Manombo Forest, Madagascar [PhD diss.]. State University of New York, Stony Brook.

Ratsimbazafy, J. H. (2002). How do black and white ruffed lemurs still survive in a highly disturbed habitat? *Lemur News* 7:7–10.

Ratsirarson, J., Anderson, J., Warter, S., and Rumpler, Y. (1987). Notes on the distribution of *Lepilemur septentrionalis* and *L. mustelinus* in northern Madagascar. *Primates* 28:119–122.

Ratsirarson, J., and Rumpler, Y. (1988). Contribution à l'étude comparée de l'écoéthologie de deux espèces de lémuriens, *Lepilemur mustelinus* (I. Geoffroy 1850), *Lepilemur septentrionalis* (Rumpler and Albignac 1975). In: Rakotovao, L., Barre, V., and Sayer, J. (eds.), *L'Equilibre des Ecosystèmes forestiers à Madagascar. Actes d'un Séminaire International*. IUCN, Gland, Switzerland. pp. 100–102.

Raxworthy, C. J., and Rakotondraparany, F. (1988). Mammals report. In: Quansah, N. (ed.), *Manongarivo Special Reserve (Madagascar), 1987/88 Expedition Report*. Madagascar Environmental Research Group, London.

Razanahoera-Rakotomalala, M. (1981). Les adaptations alimentaires comparées de deux lémuriens folivores sympatriques: *Avahi Jourdan*, 1834—*Lepilemur* I. Geoffroy 1851 [PhD thesis]. University of Madagascar, Antananarivo.

Reimann, E. W. (2002). Coexistence and feeding ecology in female grey and golden-brown mouse lemurs (*Microcebus murinus* and *M. ravelobensis*) in north-western Madagascar [diss.]. Tierärztliche Hochschule, Hannover.

Richard, A. F. (1973). Social organisation and ecology of *Propithecus verreauxi*, Grandidier 1867 [PhD diss.]. University of London, London.

Richard, A. F. (1974). Intra-specific variation in the social organization and ecology of *Propithecus verreauxi*. *Folia Primatol.* 22:178–207.

Richard, A. F. (1978). *Behavioral Variation: Case Study of a Malagasy Lemur*. Associated University Press, Princeton, NJ.

Richard, A. F. (1984). Lemurs. In: MacDonald, D. (ed.), *The Encyclopedia of Mammals*, vol. 1. George Allen and Unwin, London. pp. 330–331.

Richard, A. F. (1985). *Primates in Nature*. W. H. Freeman, New York. pp. 98–99.

Richard, A. F. (1987). Malagasy prosimians: female dominance. In: Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W., and Struhsaker, T. T. (eds.), *Primate Societies*. University of Chicago Press, Chicago. pp. 227–239.

Richard, A. F., and Dewar, R. E. (1991). Lemur ecology. *Annu. Rev. Ecol. Syst.* 22:145–175.

Richard, A. F., Dewar, R. E., Schwartz, M., and 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.

Richard, A. F., Rakotomanga, P., and Schwartz, M. (1993). Dispersal by *Propithecus verreauxi* at Beza Mahafaly, Madagascar: 1984–1991. *Am. J. Primatol.* 30:1–20.

Rigamonti, M. M. (1993). Home range and diet in red ruffed lemurs (*Varecia variegata rubra*) on the Masoala Peninsula, Madagascar. In: Kappeler, P. M., and Ganzhorn, J. U. (eds.), *Lemur Social Systems and Their Ecological Basis*. Plenum Press, New York. pp. 25–39.

Russell, R. J. (1977). The behavior, ecology, and environmental physiology of a nocturnal primate, *Lepilemur mustelinus* (Strepsirhini, Lemuriformes, Lepilemuridae) [PhD thesis]. Duke University, Durham, NC.

Russell, R. J. (1980). The environmental physiology and ecology of *Lepilemur ruficaudatus* (*L. leucopus*) in arid southern Madagascar. *Am. J. Phys. Anthropol*. 52:273–274.

Sauther, M. L. (1991). Reproductive behavior of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. *Am. J. Phys. Anthropol*. 84:463–477.

Sauther, M. L. (1992). The effect of reproductive state, social rank and group size on resource use among free-ranging ringtailed lemurs (*Lemur catta*) of Madagascar [PhD diss.]. Washington University, St. Louis.

Sauther, M. L. (1993). Resource competition in wild populations of ringtailed lemurs (*Lemur catta*): implications for female dominance. In: Kappeler, P. M., and Ganzhorn, J. U. (eds.), *Lemur Social Systems and Their Ecological Basis*. Plenum Press, New York. pp. 135–152.

Sauther, M. L. (1994). Wild plant use by pregnant and lactating ringtailed lemurs; Implications for ringtailed lemur conservation. *Folia Primatol*. 69(suppl. 1):309–320.

Sauther, M. L. (1998). The interplay of phenology and reproduction in ringtailed lemurs: implications for ringtailed lemur conservation. *Folia Primatol*. 69(suppl. 1):309–320.

Sauther, M. L., and Sussman, R. W. (1993). A new interpretation of the social organization and mating system of the ringtailed lemur (*Lemur catta*). In: Kappeler, P. M., and Ganhorn, J. U. (eds.), *Lemur Social Systems and Their Ecological Basis*. Plenum Press, New York. pp. 111–122.

Sauther, M. L., Sussman, R. W., and Gould, L. (1999). The myth of the typical *Lemur catta*: 30 years of research on the ringtailed lemur. *Evol. Anthropol*. 8:120–132.

Schmelting, B., Ehresmann, P., Lutermann, H., Randrianambinina, B., and Zimmermann, E. (2000). Reproduction of two sympatric mouse lemur species (*Microcebus murinus* and *Microcebus ravelobensis*) in north-west Madagascar: first results of a long term study. In: Lourenco, W. R., and Goodmann, S. M. (eds.), *Diversity and Endemism in Madagascar*. Mémoires de la Société de Biogéographie, Paris. pp. 165–175.

Schmid, J. (1998). Tree holes used for resting by gray mouse lemurs (*Microcebus murinus*) in Madagascar: insulation capacities and energetic consequences. *Int. J. Primatol*. 19:797–809.

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

Schulke, O., and Kappeler, P. M. (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.

Schwab, D. (2000). A preliminary study of the social and mating system of pygmy mouse lemurs (*Microcebus myoxinus*). *Am. J. Primatol*. 51:41–60.

Simons, E. L., Burney, D. A., Chatrath, P. S., Godfrey, L. R., Jungers, W. L., and Rakotosamimanana, B. (1995). AMS ^{14}C dates for extinct lemurs from caves in the Ankarana Massif, northern Madagascar. *Quat. Res*. 43:249–254.

Sterling, E. J. (1992). Timing the reproduction of aye-ayes (*Daubentonia madagascariensis*) in Madagascar. *Am. J. Primatol*. 27:59–60.

Sterling, E. J. (1993). Patterns of range use and social organization in aye-ayes (*Daubentonia madagascariensis*) on Nosy

Mangabe. In: Kappeler, P. M., and Ganzhorn, J. U. (eds.), *Lemur Social Systems and Their Ecological Basis*. Plenum Press, New York. pp. 1–10.

Sterling, E. J., Dierenfeld, E. S., Ashbourne, C. G., and Feistner, A. T. C. (1994). Dietary intake, food composition and nutrient intake in wild and captive populations of *Daubentonia madagascariensis*. *Folia Primatol*. 62:115–124.

Sterling, E. J., and Richard, A. F. (1995). Social organization in the aye-aye (*Daubentonia madagascariensis*) and the perceived distinctiveness of nocturnal primates. In: Alterman, L., Doyle, G. A., and Izard, M. K. (eds.), *Creatures of the Dark: The Nocturnal Prosimians*. Plenum Press, New York. pp. 439–451.

Sussman, R. W. (1972). An ecological study of two Madagascan primates: *Lemur fulvus rufus* Audebert and *Lemur catta* Linnaeus [PhD diss.]. Duke University, Durham, NC.

Sussman, R. W. (1974). Ecological distinctions between two species of lemur. In: Martin, R. D., Doyle, D. A., and Walker, C. (eds.), *Prosimian Biology*. Duckworth, London. pp. 75–108.

Sussman, R. W. (1977). Socialization, social structure and ecology of two sympatric species of lemur. In: Chevalier-Skolnikoff, S., and Poirier, F. E. (eds.), *Primate Bio-Social Development: Biological, Social, and Ecological Determinants*. Garland, New York. pp. 515–528.

Sussman, R. W. (1991). Demography and social organization of free-ranging *Lemur catta* in the Beza Mahafaly Reserve, Madagascar. *Am. J. Phys. Anthropol*. 84:43–58.

Sussman, R. W. (1992). Male life histories and inter-group mobility among ringtailed lemurs (*Lemur catta*). *Int. J. Primatol*. 13:395–413.

Sussman, R. W. (1999). *Primate Ecology and Social Structure. Lorises. Lemurs and Tarsiers*, vol. 1. Pearson, Needham Heights, MA.

Sussman, R. W., and Richard, A. F. (1986). Lemur conservation in Madagascar: the status of lemurs in the south. *Primate Conserv*. 7:85–92.

Sussman, R. W., and Tattersall, I. (1976). Cycles of activity, group composition and diet of *Lemur mongoz* Linnaeus 1766 in Madagascar. *Folia Primatol*. 26:270–283.

Tan, C. L. (1998). Group composition, home range size, and diet of three sympatric bamboo lemur species (Genus *Hapalemur*) in Ranomafana National Park. *Int. J. Primatol*. 20:547–563.

Tan, C. L. (2001). Behavior and ecology of three sympatric bamboo lemur species (genus *Hapalemur*) in Ranomafana National Park, Madagascar [PhD diss.]. State University of New York, Stony Brook.

Tattersall, I. (1976). Group structure and activity rhythm in *Lemur mongoz* (Primates, Lemuriformes) on Anjouan and Mohéli Islands, Comoro Archipelago. *Anthropol. Papers Am. Mus. Nat. Hist*. 53:257–261.

Tattersall, I. (1977a). Distribution of the Malagasy lemurs, part 1. The lemurs of northern Madagascar. *Ann. N.Y. Acad. Sci*. 293:160–169.

Tattersall, I. (1977b). The lemurs of the Comoro Islands. *Oryx* 13:445–448.

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

Tattersall, I. (2004). Comments and conclusions. The historical biogeography of the strepsirhini: understanding the colonization of Madagascar. 2004 IPS Symposium. *Folia Primatol*. 75(suppl. 1):120.

Terranova, C. J., and Coffman, B. S. (1997). Body weights of wild and captive lemurs. *Zoo Biol.* 16:17–30.

Thalmann, U. (2001). Food resource characteristics in two nocturnal lemurs with different social behaviour: *Avahi occidentalis* and *Lepilemur edwardsi*. *Int. J. Primatol.* 22:287–324.

Thalmann, U., and Geissmann, T. (2000). Distributions and geographic variation in the western woolly lemur (*Avahi occidentalis*) with description of a new species (*A. unicolor*). *Int. J. Primatol.* 21:915–941.

Van Schaik, C. P., and Kappeler, P. M. (1996). The social systems of gregarious lemurs: lack of convergence with anthropoids due to evolutionary disequilibrium? *Ethology* 102:915–941.

Vargas, A., Jimenez I., Palomares, F. and Palacios, M. J. (2002). Distribution, status, and conservation needs of the golden-crowned sifaka (*Propithecus tattersalli*). *Biol. Conserv.* 108:325–334.

Vasey, N. (2000). Niche separation in *Varecia variegata rubra* and *Eulemur fulvus albifrons*: I. Interspecific patterns. *Am. J. Phys. Anthropol.* 112:411–431.

Vasey, N. (2002). Niche separation in *Varecia variegata rubra* and *Eulemur fulvus albifrons*: II. Intraspecific patterns. *Am. J. Phys. Anthropol.* 118:169–183.

Walker A. (1967). Patterns of extinction among the subfossil Madagascan lemuroids. In: Martin, P. S., and Wright, H. E., Jr. (eds.), *Pleistocene Extinctions: The Search for a Cause*. Yale University Press, New Haven, CT. pp. 425–432.

Warren, R. (1994). Lazy leapers: a study of the locomotor ecology of two species of saltatory nocturnal lemur in sympatry at Ampijoroa, Madagascar [PhD thesis]. University of Liverpool, Liverpool.

Weidt, A., Hagenah, N., Randrianambinina, B., Radespiel, U., and Zimmermann, E. (2004). Social organization of the golden brown mouse lemur (*Microcebus ravelobensis*). *Am. J. Phys. Anthropol.* 123:40–51.

White, F. J. (1989). Diet, ranging behavior and social organization of the black and white ruffed lemur, *Varecia variegata variegata*, in southeastern Madagascar [Abstract]. *Am. J. Phys. Anthropol.* 78:323.

Wilson, J. M., Stewart, P. D., Ramangason, G. S., Denning, A. M., and Hutchings, M. S. (1989). Ecology and conservation of the crowned lemur, *Lemur coronatus*, at Ankarana, N. Madagascar. *Folia Primatol.* 53:1–26.

Winn, R. M. (1989). The aye-ayes, *Daubentonia madagascariensis*, at the Paris Zoological Gardens: maintenance and preliminary behavioural observations. *Folia Primatol.* 52:109–123.

Wright, P. C. (1993). The evolution of female dominance and biparental care among non-human primates. In: Miller, B. (ed.), *Sex and Gender Hierarchies*. Cambridge University Press, Cambridge. pp. 127–147.

Wright, P. C. (1995). Demography and life history of free-ranging *Propithecus diadema edwardsi* in Ranomafana National Park, Madagascar. *Int. J. Primatol.* 16:835–854.

Wright, P. C. (1999). Lemur traits and Madagascar ecology: coping with an island environment. *Ybk. Phys. Anthropol.* 42:31–72.

Wright, P. C., Daniels, P. S., Meyers, D. M., Overdorff, D. J., and Rabesoa, J. (1987). A census and study of *Hapalemur* and *Propithecus* in southeastern Madagascar. *Primate Conserv.* 8:84–88.

Wright, P. C., Heckscher, S. K., and Dunham, A. E. (1997). Predation on Milne-Edwards' sifaka (*Propithecus diadema edwardsi*) by the fossa (*Cryptoprocta ferox*) in the rain forest of southeastern Madagascar. *Folia primatol.* 68:34–43.

Wright, P. C., and Martin, L. B. (1995). Predation, pollination and torpor in two nocturnal prosimians: *Cheirogaleus major* and *Microcebus rufus* in the rain forest of Madagascar. In: Alterman, L., Doyle, G. A., and Izard, M. K. (eds.), *Creatures of the Dark: The Nocturnal Prosimians*. Plenum Press, New York. pp. 45–60.

Wroegemann, D., and Zimmermann, E. (2001). Aspects of reproduction in the eastern rufous mouse lemur (*Microcebus rufus*) and their implications for captive management. *Zoo Biol.* 20:157–167.

Yoder, A. D., Burns, M. M., Zehr, S., Delefosse, T. Veron, G., Goodman, S. M., and Flynn, J. J. (2003). Single origin of Malagasy carnivora from an African ancestor. *Nature* 421:734–737.

Yoder, A. D., Rasoloarison, R. M., Goodman, S. M., Irwin, J. A., Atsalis, S., Ravosa, M. J., and Ganzhorn, J. U. (2000). Remarkable species diversity in Malagasy mouse lemurs (Primates, *Microcebus*). *Proc. Natl. Acad. Sci. USA* 97:11325–11330.

Young, A. L., Richard, A. F., and Aiello, L. C. (1990). Female dominance and maternal investment in strepsirhine primates. *Am. Nat.* 135:473–488.

Zimmermann, E. (1998). Nachtgeister im Tropenwald: die nachtaktiven Lemuren Madagaskars. *Biol. Zeit.* 28:294–303.

Zimmerman, E., Cepok, S., Rakotoarison, N., Zietemann, V., and Radespiel, U. (1998). Sympatric mouse lemurs in north-west Madagascar: a new rufous mouse lemur species. *Folia Primatol.* 69:106–114.