

Chapter 6

Life History Variation in Madagascar's Giant Extinct Lemurs

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

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

L.R. Godfrey (✉)

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

G.T. Schwartz • K.K. Catlett

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

W.L. Jungers

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

K.E. Samonds

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

M.T. Irwin

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

S.J. King

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

K.M. Muldoon

Department of Anatomy, The Geisel School of Medicine at Dartmouth, Hanover, NH 03755, USA

Department of Anthropology, Dartmouth College, Hanover, NH 03755, USA

e-mail: kathleen.m.muldoon@dartmouth.edu

D.A. Burney

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

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

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

Introduction

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

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

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

Estimating Reproductive Rates in Extinct Species

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

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

Table 6.1 Life history parameters of extinct lemurs

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

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

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

Results

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

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

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

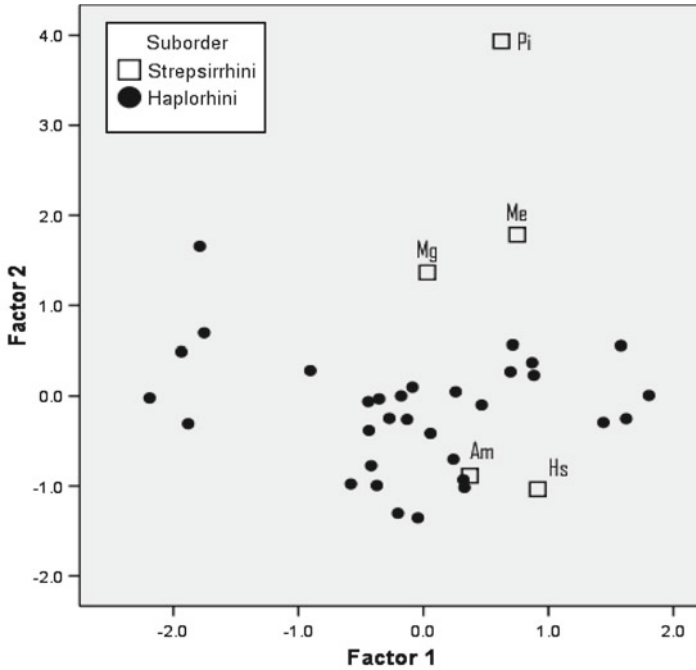


Fig. 6.1 Principal component analysis of life history characteristics of giant lemurs (*open squares*) and representative haplorhines (*solid circles*). Data sources available on request. Am = *Archaeolemur majori*; Hs = *Hadropithecus stenognathus*; Me = *Megaladapis edwardsi*; Mg = *Mesopropithecus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

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

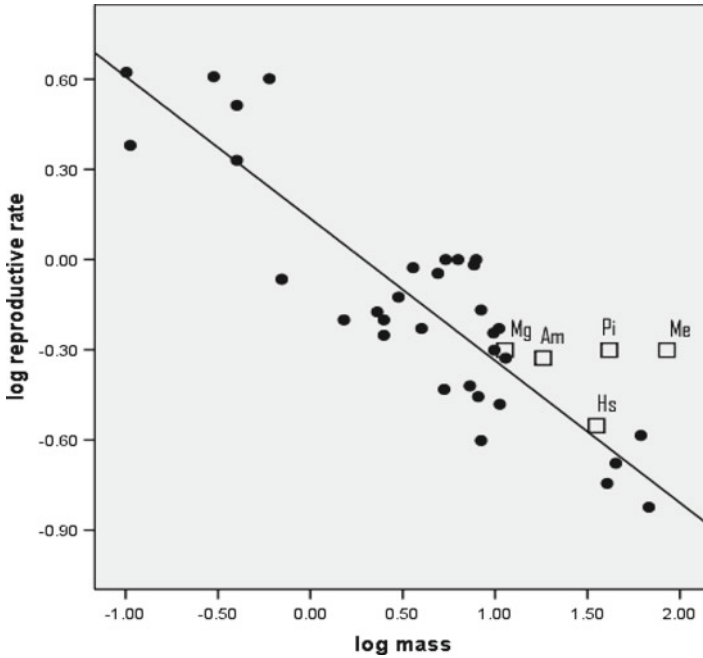


Fig. 6.2 Log reproductive rate (Y) vs. Log body mass (X) for extant haplorhine primates (*solid circles*) and extinct lemurs (*open squares*). The least squares fit for haplorhines only is shown. Note that all of the extinct lemurs fall above the line. $R^2=0.775$. Am = *Archaeolemur majori*; Hs = *Hadropithecus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

Discussion

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

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

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

References

- Allman J (1995) Brain and life span in catarrhine primates. In: Butler R, Brody J (eds) *Delaying the onset of late-life dysfunction*. Springer, New York, pp 221–241
- Barrickman NJ, Bastian ML, Isler K, van Schaik CP (2008) Life history costs and benefits of encephalization: a comparative test using data from long-term studies of primates in the wild. *J Hum Evol* 54:568–590
- Burney DA, Burney LP, Godfrey LR, Jungers WL, Goodman SM, Wright HT, Jull AJT (2004) A chronology for late prehistoric Madagascar. *J Hum Evol* 47:25–63
- Catlett KK, Schwartz GT, Godfrey LR, Jungers WL (2010) “Life history space”: a multivariate analysis of life history variation in extinct and extant Malagasy lemurs. *Am J Phys Anthropol* 143:391–404
- Crowley BE, Godfrey LR, Irwin MT (2011) A glance to the past: subfossils, stable isotopes, seed dispersal, and lemur species loss in southern Madagascar. *Am J Primatol* 73:25–37
- Feistner ATC, Ashbourne CJ (1994) Infant development in a captive-bred aye-aye (*Daubentonia madagascariensis*) over the first year of life. *Folia Primatol* 62:74–92
- Gibson K (1986) Cognition, brain size and the extraction of embedded food resources. In: Else J, Lee P (eds) *Primate ontogeny, cognition, and social behavior*. Cambridge University Press, New York, pp 93–103
- Godfrey LR, Samonds KE, Jungers WL, Sutherland MR (2001) Teeth, brains, and primate life histories. *Am J Phys Anthropol* 114:192–214
- Godfrey LR, Petto AJ, Sutherland MR (2002) Dental ontogeny and life history strategies: the case of the giant extinct indroids of Madagascar. In: Plavcan JM, Kay R, Jungers WL, van Schaik C (eds) *Reconstructing behavior in the primate fossil record*. Kluwer/Plenum, New York, pp 113–157
- Godfrey LR, Semperebon GM, Jungers WL, Sutherland MR, Simons EL, Solounias N (2004) Dental use wear in extinct lemurs: evidence of diet and niche differentiation. *J Hum Evol* 47:145–169

- Godfrey LR, Semperebon GM, Schwartz GT, Burney DA, Jungers WL, Flanagan EK, Cuzzo FP, King SJ (2005) New insights into old lemurs: the trophic adaptations of the Archaeolemuridae. *Int J Primatol* 26:825–854
- Godfrey LR, Jungers WL, Schwartz GT (2006a) Ecology and extinction of Madagascar's subfossil lemurs. In: Gould L, Sauther M (eds) *Lemurs: ecology and adaptation*. Springer, New York, pp 41–64
- Godfrey LR, Schwartz GT, Samonds KE, Jungers WL, Catlett KK (2006b) The secrets of lemur teeth. *Evol Anthropol* 15:142–154
- Godfrey LR, Jungers WL, Schwartz GT, Irwin MT (2008) Ghosts and orphans: Madagascar's vanishing ecosystems. In: Fleagle JG, Gilbert CC (eds) *Elwyn Simons, a search for origins*. Springer, New York, pp 361–395
- Harvey P, Clutton-Brock T (1985) Life history variation in primates. *Evolution* 39:559–581
- Johnson CN (2002) Determinants of loss of mammal species during the Late Quaternary 'mega-fauna' extinctions: life history and ecology, but not body size. *Proc R Soc Lond B* 269:2221–2227
- Jungers WL, Demes B, Godfrey LR (2008) How big were the "giant" extinct lemurs of Madagascar? In: Fleagle JG, Gilbert CC (eds) *Elwyn Simons, a search for origins*. Springer, New York, pp 343–360
- Leigh SR, Terranova CJ (1998) Comparative perspectives on bimaturism, ontogeny, and dimorphism in lemurid primates. *Int J Primatol* 19:723–749
- Pochron ST, Tucker WT, Wright PC (2004) Demography, life history, and social structure in *Propithecus diadema edwardsi* from 1986–2000 in Ranomafana National Park, Madagascar. *Am J Phys Anthropol* 125:61–72
- Rafferty KL, Teaford MF, Jungers WL (2002) Molar microwear of subfossil lemurs: improving the resolution of dietary inferences. *J Hum Evol* 43:645–657
- Richard AF, Dewar RE, Schwartz M, Ratsirarson J (2002) Life in the slow lane? Demography and life histories of male and female sifaka (*Propithecus verreauxi verreauxi*). *J Zool* 256:421–436
- Ross C (1998) Primate life histories. *Evol Anthropol* 6:54–63
- Ryan TM, Burney DA, Godfrey LR, Göhlich U, Jungers WL, Vasey N, Ramilisonina, Walker A, Weber GW (2008) A reconstruction of the Vienna skull of *Hadropithecus stenognathus*. *Proc Natl Acad Sci USA* 105:10698–10701
- Sacher G (1959) Relation of lifespan to brain weight and body weight in mammals. In: Wolstenholme G, O'Connor M (eds) *CIBA foundation symposium on the lifespan of animals*. Little, Brown, and Co., Boston, pp 115–133
- Schwartz GT, Samonds KE, Godfrey LR, Jungers WL, Simons EL (2002) Dental microstructure and life history in subfossil Malagasy lemurs. *Proc Natl Acad Sci USA* 99:6124–6129
- Schwartz GT, Mahoney P, Godfrey LR, Cuzzo FP, Jungers WL, Randria GFN (2005) Dental development in *Megaladapis edwardsi* (Primates, Lemuriformes): implications for understanding life history variation in subfossil lemurs. *J Hum Evol* 49:702–742
- Scott JR, Godfrey LR, Jungers WL, Scott RS, Simons EL, Teaford MF, Ungar PS, Walker A (2009) Dental microwear texture analysis of two families of subfossil lemurs from Madagascar. *J Hum Evol* 56:405–416
- Stephan H, Frahm H, Baron G (1981) New and revised data on volumes of brain structures in insectivores and primates. *Folia Primatol* 35:1–29
- Stephan H, Baron G, Frahm H (1988) Comparative size of brains and brain components. In: Steklis HD, Erwin J (eds) *Comparative primate biology, vol 4, Neurosciences*. Alan R. Liss, New York, pp 1–38
- Sterling EJ (1994) Aye-ayes: specialists on structurally defended resources. *Folia Primatol* 62:142–154
- Tilden C (2008) Low fetal energy deposition rates in lemurs: another energy conservation strategy. In: Fleagle JG, Gilbert CG (eds) *Elwyn Simons, a search for origins*. Springer, New York, pp 311–318
- Wright PC (1999) Lemur traits and Madagascar ecology: coping with an island environment. *Yearb Phys Anthropol* 42:31–72