

Ontogenetic Correlates of Diet in Malagasy Lemurs

L.R. Godfrey,^{1*} K.E. Samonds,² W.L. Jungers,² M.R. Sutherland,³ and M.T. Irwin⁴

¹*Department of Anthropology, University of Massachusetts at Amherst, Amherst, Massachusetts 01003-9278*

²*Department of Anatomical Sciences, School of Medicine, Stony Brook University, Stony Brook, New York 11794-8081*

³*Statistical Consulting Center, University of Massachusetts at Amherst, Amherst, Massachusetts 01003-9337*

⁴*Interdepartmental Doctoral Program in Anthropological Sciences, Stony Brook University, Stony Brook, New York 11794-4364*

KEY WORDS Indriidae; Lemuridae; ecological risk aversion hypothesis; Madagascar; dental development; unpredictable environments; environmental disturbances; life history

ABSTRACT There is a well-documented relationship between development and other life-history parameters among anthropoid primates. Smaller-bodied anthropoids tend to mature more rapidly than do larger-bodied species. Among anthropoids of similar body sizes, folivorous species tend to grow and mature more quickly than do frugivorous species, thus attaining adult body size at an earlier age. This pattern conforms to the expectations of Janson and van Schaik's "ecological risk aversion hypothesis," which predicts that rates of growth and maturation should vary in inverse relation to the intensity of intraspecific feeding competition. According to the ecological risk aversion hypothesis (RAH), species experiencing high intraspecific feeding competition will grow and mature slowly to reduce the risk of mortality due to food shortages. Species experiencing low levels of intraspecific feeding competition will shorten the juvenile period to reduce the overall duration of this high-risk portion of the life cycle. This paper focuses on development and maturation in lemurs. We show that folivorous lemurs (such as indri-

ids) grow and mature more slowly than like-sized frugivorous lemurs (e.g., most lemurids), but tend to exhibit faster dental development. Their dental developmental schedules are accelerated on an absolute scale, relative to craniofacial growth, and relative to particular life-history landmarks, such as weaning. Dental development has a strong phylogenetic component: even those lemurids that consume substantial amounts of foliage have slower dental development than those indriids that consume substantial amounts of fruit. Implications of these results for the RAH are discussed, and an explanation for this hypothesis' failure to predict lemur growth schedules is offered. We propose that the differing developmental schedules of folivorous and frugivorous lemurs may reflect different solutions to the ecological problem of environmental instability: some rely on a strategy of low maternal input and slow returns, while others rely on a strategy of high maternal input and fast returns. *Am J Phys Anthropol* 123:250–276, 2004. © 2004 Wiley-Liss, Inc.

Leigh (1994) observed that folivorous anthropoids have higher growth rates than comparably sized frugivorous anthropoids. Leigh (1994) interpreted this difference within the framework of the "ecological risk aversion hypothesis" of Janson and van Schaik (1993). Accordingly, folivorous anthropoids experience accelerated growth because they have relatively low intraspecific competition for resources. Leigh (1994) thus linked differences in rates of growth directly to the spatial distribution and abundance of preferred food resources.

According to Janson and van Schaik (1993), two factors strongly affect juvenile mortality: 1) the risk of starvation (induced by competition for food with larger and more competent adult foragers), and 2) the risk of predation. Because of their lower competence in foraging, juveniles tend to spend more time feeding than adults, and they tend to be less vigilant when feeding. Because frugivores experience high intraspecific competition for foods distributed in rare (but locally rich) patches, juvenile frugivores face particularly high risks of starvation during ep-

isodes of critically low food abundance. Janson and van Schaik (1993) argued that, were it not for such risks, it should be adaptively advantageous for juveniles to grow as fast as is physiologically possible. This is because predation pressure tends to favor rapid growth and maturation (smaller individuals are generally at higher risk of predation). However, the risk of mortality due to starvation sets an upper

Grant sponsor: NSF; Grant numbers: GER-9450175, SBR-9630350; Grant sponsor: Statistical Consulting Center of the University of Massachusetts; Grant sponsor: Laboratory of Lawrence B. Martin at, Stony Brook University.

*Correspondence to: Laurie Godfrey, Department of Anthropology, Machmer Hall, 240 Hicks Way, University of Massachusetts, Amherst, MA 01003-9278.

Received 9 August 2002; accepted 7 March 2003.

DOI 10.1002/ajpa.10315

TABLE 1. Dietary data from the literature, with sources

Species	Leaves, shoots, and stems	Fruit and/or seeds	Other	Sources
<i>Indri indri</i>	75%	25%		Pollock (1975a)
	75%	16%	8% flowers, galls	Powzyk (1997)
	81.9%	8.2%	9.8% bark, flowers	Britt et al. (2002)
<i>Avahi laniger</i>	90.7%	Some	9.3% flowers	Ganzhorn et al. (1985)
	100%			Harcourt (1991)
<i>Propithecus verreauxi</i>	25%	65%	10% flowers	Jolly (1966)
	39%	48%		Richard (1978), South
	46%	33%	9% flowers	Richard (1978), North
<i>P. tattersalli</i>	39%	46%	13% flowers	Meyers (1993), Meyers and Wright (1993)
				Hemingway (1996)
<i>P. diadema</i>	28%	65%		Meyers and Wright (1993)
	41%	55%	3% flowers	Wright (1987)
	53%	22%	25% flowers	Overdorff and Strait (1998)
	Some	48%	Some	Powzyk (1997)
<i>Lepilemur ruficaudatus</i>	43%	38%	16% flowers, galls	Hladik et al. (1980)
	75%	25%	Coprophagy	Russell (1977)
<i>L. leucopus</i>	91%	6% (including flowers)	Bark, latex	Rigamonti (1993)
<i>Varecia variegata</i>	20.9%	73.9%	5.3% flowers, 2% other	Morland (1991)
	5.1%	74%	21.5% nectar, 1.8% other	White (1991)
	8%	70.8%	15.3% nectar, 2% flowers	Balko (1995)
	6%	90%	4% nectar	Vasey (1997)
	4%	86%	8% nectar, 1% flowers	Ratsimbazafy (2002)
	17%	73.3%	5.3% nectar, 2.8% other	Sussman (1974), West
	89%	11%	4% flowers	Overdorff (1993), East
	23.4%	66.8%	10.8%	Overdorff (1988, July 1986)
	10%	10%	80% flowers	Overdorff (1988, June 1986)
		100%		Overdorff (1993)
<i>E. macaco</i>	13.6%	80.6%	5.8%	Colquhoun (1993)
<i>E. mongoz</i>	Some	Dominant	Some	Curtis (1997)
<i>E. coronatus</i>	Some	Dominant	Some	Tattersall and Sussman (1975)
	1.5%	17.5%	81% flowers and nectar	Freed (1999)
<i>Hapalemur griseus</i>	Some	70%+	10–25% flowers	Overdorff et al. (1997)
	90%	1.2%	Some	Tan (1999a, 2000)
	92%	5%	3% soil and fungi	Wright (1986)
	>90%	4%		Grassi (2001)
	82.7%	13.8%	3.5% flowers, dirt, mushrooms	
<i>H. g. alaotrensis</i>	100%			Randrianarisoa (1999)
<i>Lemur catta</i>	58%	34%	8% flowers	Sussman (1974), West
	34%	60%	6% flowers	Sussman (1974), South
	47%	44%	2% flowers, 7% other	Rasamimanana and Ratidinarivo (1993)
	25%	70%	5% flowers	Jolly (1966)

limit for the rate of growth. Developmental prolongation reduces the energy devoted to growth at any point in time, and thus reduces the risk of starvation under periodic food shortages. Species that are more susceptible to predation will tend to grow fast so as to not delay maturation; those that are more susceptible to starvation would tend to slow down growth so as to reduce the risk of starvation. Slow growth and development are selectively advantageous whenever intraspecific competition for resources is high. The juvenile risk aversion model assumes that selection operates on the interplay between rates and durations of growth and development, slowing the rate but prolonging the duration of growth and development in frugivores.

The notion that diet affects primate life histories in the manner predicted by Janson and van Schaik (1993), or indeed in any important way (Ross, 1998), recently came under criticism (e.g., see Garber and Leigh, 1997, on small-bodied platyrrhines). Nevertheless, with the exceptions described by Garber and Leigh (1997), the growth rates of like-sized anthro-

poid frugivores and folivores do seem to conform to the expectations of the risk aversion hypothesis of Janson and van Schaik (1993). In this paper, we test the hypothesis of Janson and van Schaik (1993) for the larger-bodied prosimians of Madagascar. We show that dental development does tend to be accelerated in folivorous lemurs, but that these species neither grow nor mature more rapidly than their frugivorous cousins. It is therefore difficult to describe folivorous lemurs as having “faster” life histories.

We recognize, of course, that the diets of lemurs do not sort easily into the pigeonholes of folivore and frugivore. Most folivorous lemurs consume some fruit, and frugivorous lemurs consume foliage to varying degrees (Table 1). Behaviorally, the only unequivocally folivorous lemurs are *Lepilemur*, *Avahi*, *Indri*, and *Hapalemur*. Of these, *Lepilemur* and *Avahi* are tree-foliage browsers, while *Hapalemur* relies primarily on grasses (bamboo), and *Indri* supplements tree-foliage with seeds. *Propithecus* and most lemurids (except *Hapalemur*) are appropriately called mixed (fruit and tree-foliage) feeders.

Table 1 summarizes published field data on the diets of the living lemurs considered in this analysis (see also Muchlinski and Overdorff, 2001).

These percentages, taken alone, are poor indicators of some fundamental differences in the diets of lemurs. The resources consumed by lemurs differ in their material properties and chemistry (e.g., Yamashita, 1996, 1998b; Ganzhorn, 1992, 2002; Strait, 1997), as well as their spatial and temporal availability. All species of the genus *Lepilemur* as well as all Indriidae thrive on fibrous foods which require processing specializations to deal with structural carbohydrates, high fiber to protein ratios, and generally high levels of toxic tannins and alkaloids. Of these, *Lepilemur* has the lowest-quality diet (measured in terms of protein to fiber ratios; see Ganzhorn, 1988, 1993; Warren and Crompton, 1997a,b). Indriids, like lemurids, consume a variety of leaves and fruit, but they also consume seeds to varying degrees (Pollock, 1975a; Meyers 1993; Meyers and Wright, 1993; Scharfe and Schlund, 1996; Hemingway, 1996, 1998; Yamashita, 1996, 1998a,b; Dew and Wright, 1998). Most lemurids seek higher-energy foods (including more ripe fruit) than do indriids, but they do not process seeds, preferring to discard or swallow seeds whole (Ganzhorn and Kappeler, 1996; Overdorff and Strait, 1998; Ganzhorn et al., 1999; Freed, 1999). Indriids and sportive lemurs also tend to spend more time resting and less time feeding than do lemurids (Richard, 1978; Nash, 1998; Mutschler, 1999).

All lemurs have simple stomachs and expanded cecums and/or colons. The colon and cecum are particularly enlarged in indriids and in *Lepilemur* (family Lepilemuridae), and the cecum is the primary site of microbial breakdown of the structural cell-wall component of leaves in most lemurs. *Lepilemur* is apparently alone among lemurs in having caecotrophy (Charles-Dominique and Hladik, 1971; but see Russell, 1977) and adaptations for colonic separation of digesta and selective retention of fine particles in the hindgut (Cork, 1996). Indriids also have clear digestive adaptations for folivory, differing from lemurids in their 1) higher ratios of intestine to body length; 2) greater sacculation of the cecum; 3) relatively longer and more coiled proximal colons; and 4) greater vascularization of the cecum and colon (Milne Edwards and Grandidier, 1875; Hill, 1953, 1958; Hladik, 1967; Chivers and Hladik, 1980; Campbell et al., 2000). Campbell et al. (2000) maintained that the most behaviorally folivorous lemurid, *Hapalemur*, converges little with *Lepilemur* or with indriids in its digestive adaptations. These authors studied *Hapalemur griseus*, which deliberately selects only the bases of leaves. It is possible that the high-protein shoots and culms of bamboo on which *Hapalemur griseus* depends are not as difficult to digest as the tree-foilage staples of indriids and *Lepilemur* (although the same may not hold for other species of *Hapalemur*). High food intake may also help all *Hapalemur* survive on a diet consisting largely of grasses (see Randrianarisoa, 1999, on *H. griseus alaotrensis*; Tan, 2000, on all *Hapalemur*). Leaving aside the question of *Ha-*

palemur, indriids and sportive lemurs can be considered more specialized than lemurids for folivory, both ecologically and anatomically.

This paper tests the ecological risk aversion hypothesis against patterns of growth and development of folivorous and frugivorous lemurs of Madagascar. Specifically, we ask: does the pattern of variation in rates of 1) dental development, 2) somatic growth, and 3) reproductive maturation conform to expectations of the RAH? We examine these data for lemurs, and reevaluate the risk aversion hypothesis in light of these data. Excluded from this analysis are members of the families Cheirogaleidae and Daubentoniidae, because of the abundance of animal matter in their diets.

MATERIALS AND METHODS

Developmental data were collected for 778 specimens of lemurs belonging to 22 species (Table 2). All species are represented by dentally immature individuals as well as dental adults (some of which are known to be postcranially immature). We were able to collect data on near-term fetuses or neonates (here defined as individuals that are 5 days old or younger) for 14 of the 22 species. Younger fetuses of *Propithecus* and *Lepilemur* were also available. For each skull, we measured the mesiodistal and buccolingual diameters of the milk and permanent post-canine teeth as well as skull length (prosthion-opisthocranium) and bizygomatic breadth. Skull dimensions were also averaged for adults with complete permanent dentitions and fused or fusing basioccipital sutures. It should be noted that, in lemurs, the dentition sometimes matures *well*-prior to the completion of skeletal growth. Thus, some individuals considered immature here had full adult dentitions, but open cranial sutures and incomplete epiphyseal fusion of the long bones.

Species values for maternal body masses, gestation length, birth seasonality, age at weaning, and age at female first reproduction were compiled from the primary literature. Neonatal masses were compiled largely from the primary literature, although a few were reconstructed from neonatal skull size when no mass values were available in the literature. We estimated neonatal "skull size" using " $\pi * 0.5$ maximum cranial length * 0.5 bizygomatic breadth," i.e., the area of an ellipse with major and minor axes equal to the length and width of the neonatal skulls. We regressed the log of our mean values for neonatal mass on the log of our mean values for neonatal skull size to obtain estimates of neonatal mass for species whose neonatal mass is unknown. Weanling masses were read from published growth curves (e.g., Leigh and Terranova, 1998) or taken from the unpublished growth records of species at the Duke University Primate Center. Occasionally, they were estimated using reports in the primary literature of body masses of immature individuals of known age, or unpublished records obtained through personal communications.

TABLE 2. Ontogenetic database (including skeletal materials and wet specimens)¹

Family	Genus and species	Neonates (0–5 days old)	Other immature individuals	Adult individuals	
Lemuridae	<i>Lemur catta</i>	11	42	20	
	<i>Varecia variegata</i>	1	35	35	
	<i>Eulemur fulvus</i>	2	45	50	
	<i>E. albocollaris</i>	0	3	2	
	<i>E. collaris</i>	1	11	10	
	<i>E. macaco</i>	1	13	12	
	<i>E. mongoz</i>	4	12	15	
	<i>E. rubriventer</i>	1	6	12	
	<i>Haplemur griseus</i>	4	17	14	
	<i>H. simus</i>	0	1	10	
	Indriidae	<i>Propithecus diadema</i>	1 ¹	25	37
		<i>P. verreauxi</i>	6	43	87
<i>P. tattersalli</i>		0	1	1	
<i>Avahi occidentalis</i>		0	1	7	
<i>A. laniger</i>		2 ¹	7	23	
<i>Indri indri</i>		1 ¹	5	19	
Lepilemuridae	<i>Lepilemur ruficaudatus</i>	1 ¹	9	29	
	<i>L. dorsalis</i>	0	3	6	
	<i>L. edwardsi</i>	0	4	15	
	<i>L. leucopus</i>	2 ²	3	18	
	<i>L. mustelinus</i>	0	3	4	
	<i>L. microdon</i>	0	3	14	
Totals		38	292	440	

¹ Museums and primate facilities at which these specimens are housed are listed in Acknowledgments.

² Ages uncertain, probably neonatal or near-term fetus. 770 + 7 fetuses of *Propithecus verreauxi* and 1 fetus of *Lepilemur* sp. Total (including fetuses) = 778.

Because there is little published information on the dental eruption schedules of lemurs, we used a variety of means to reconstruct schedules of dental eruption. We compiled known ages for zoo- or facility-raised individuals in our database, whenever available. We recorded collection dates for wild-caught immature lemurs in museum collections, because reproductive synchrony allows biological age to be estimated for immature individuals with known death dates (Godfrey et al., 2001). Body masses of wild-caught and captive individuals belonging to species whose growth trajectories (mass increase over time) have been published were occasionally useful. Also considered were the cranial dimensions of individuals of known ages and dental eruption stages. Combining these data and published data on dental eruption schedules, we were able to reconstruct at least partial dental eruption schedules for each of the species in our database, and generate growth curves for cranial length and bizygomatic breadth. Full adults (with fused basioccipital sutures) were used to derive adult mean trait values.

Growth curves for cranial length and bizygomatic breadth were generated using the program ORIGIN version 6.1 (Originlabs, Northampton, MA). We used Originlabs's non-linear least squares curve-fitting module to fit a four-parameter logistic curve to each species' bizygomatic breadth and cranial length trajectories. Several conditions were set during the curve-fitting process. We used gestation length to help visualize the full form of each growth curve. Assuming a sigmoidal growth curve with a short left-tail during the embryonic phase of early gestation, we targeted a point one-third of the way

through gestation for an "effective 0-value" for our traits.¹ Adult mean trait values were used to obtain the ceilings of growth curves, and each curve was forced to flat-line at the appropriate mean adult value. All known-age immature individuals in our sample were younger than 36 months. For the purposes of curve-fitting, adults of unknown age were assigned "ages" greater than 3 years.

Using the fitted growth curves, we calculated "instantaneous" growth rates for bizygomatic breadth and maximum cranial length for each species at birth. These were defined as the slopes of the bizygomatic and maximum cranial length growth curves over a 20-day period bracketing birth. We also calculated mean daily prenatal and early-postnatal growth rates for each species in our sample whose neonatal and weaning masses were known. Our "mean prenatal daily growth rate" was defined as neonatal mass in grams divided by gestation length in days. Our "mean early-postnatal growth rate" is the difference between weaning mass and neonatal mass (in grams), divided by age at weaning in days. On an absolute scale, larger-bodied species tend to grow faster than closely related smaller-bodied species (see Leigh, 1994; Leigh and Terranova, 1998). Thus, in comparing taxa of diverse body sizes, we benchmarked growth rates against adult body mass.

To compare schedules for dental development across species, we constructed a variable called

¹Histological and ultrasound data on fetal growth in nonhuman primates demonstrate little increase in fetal mass during the first trimester (e.g., see Schultz, 1937; Hendrickx and Houston, 1971; Brizzee and Dunlap, 1986; Jaquish et al., 1995).

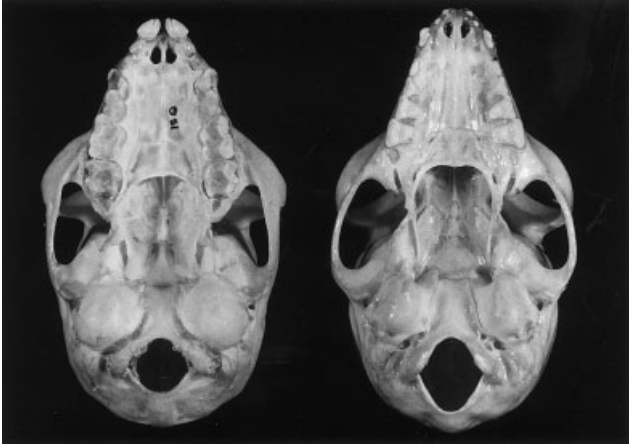


Fig. 1. Comparison of an indriid and lemurid of roughly comparable age. **Left:** DPC 1593f. **Right:** DPC 5854m. For scale, Phaon's bizygomatic breadth is 42.5 mm. *Propithecus verreauxi* becomes a dental adult long before it reaches physical maturation, and well ahead of *Varecia*. Even *Lemur catta*, whose dental developmental schedule is accelerated in comparison to that of *Varecia* or *Eulemur*, lags well behind all indriid species.

“dental developmental stage.” This is roughly equivalent to the proportion of the species-typical number of deciduous and permanent teeth that have erupted. Individual values were calculated by scoring each tooth on a scale from 0–2 (where 0 = unerupted, 1 = erupting, and 2 = fully erupted), and summing the scores. Replaced deciduous teeth were scored as 2. The sum of scores was then divided by 2 times the species-typical total number of teeth (including the deciduous teeth). “Dental developmental stage” thus ranged from 0–1, where 0 represents no teeth erupted, and 1 represents completion of species-typical adult dentition. Mean adult values for cranial length and bizygomatic breadth were calculated separately for distinct subspecies, and the appropriate values were used to assess the somatic maturation of each immature individual. Thus, “percent completion of bizygomatic growth” was constructed as the ratio of the observed bizygomatic diameter to the bizygomatic diameter expected (on the basis of observed means) for adult individuals of the same species or subspecies. “Percent completion of cranial length” was calculated on the basis of observed to expected adult cranial length. Ratios of occlusal area of the maxillary and mandibular last deciduous premolar to first permanent molar (dp4/M1 occlusal area indices) were also calculated. Occlusal areas were estimated on the basis of mesiodistal times buccolingual diameters of the crowns of teeth.

RESULTS

Pace of dental development

Among the frugivorous and folivorous lemurs considered here, the extremes for dental developmental rate occur within the Indriidae and the Lemuridae. Figure 1 shows two individuals in our

sample (a *Propithecus verreauxi coquereli* and a *Lemur catta*) of roughly comparable ages. Both were at or near weaning at the time of death (ca. 6 months, Godfrey et al., 2001, Appendix A). The sifaka (“Erme,” DPC 1593f, Fig. 1 at left) was born in captivity at the Duke University Primate Center and died at 165 days (5.5 months). At death, this individual had I_1^1 , I_2^2 , dc^1 , dp^3 , dp_2 , P_4^4 , M_1^1 , and M_2 in place. M_2 was erupting, and P^3 was beginning to emerge. Most of Erme’s deciduous teeth (including the vestigial dc_1 and dp_3 ; see below) were shed. The ringtailed lemur (“Phaon,” DPC 5854m, Fig. 1. at right) was born in captivity at the Duke University Primate Center and died at 204 days (or 6.8 months). At death, Phaon still possessed all of his deciduous teeth (including the deciduous toothcomb), plus M_1^1 .

Dental developmental differences between lemurs and indriids begin very early. They are manifested in all fetal and neonatal specimens that we examined. The dental developmental schedules of *Propithecus* spp. are better known than those of *Indri* or *Avahi* (Godfrey et al., 2001), but there is good evidence that all indriids are born with their milk teeth virtually fully erupted, their first and second permanent molars in advanced states of crown calcification, the crypts for the third molars open, and the M_3 crown initiated, whereas lemurs are born with only the anteriormost milk teeth erupting and permanent M1 formation just beginning (Schwartz et al., 2002). In *Propithecus*, the first permanent molars begin crown formation at the end of the first trimester of gestation or the beginning of the second (Schwartz et al., 2002). The rapid pace of dental development in indriids has consequences for the relative sizes of the deciduous and permanent teeth and the pattern of dental loss. The space allocated to the developing deciduous premolar buds is reduced, apparently to accommodate the rapidly developing and large permanent molar crowns. The dp4/M1 occlusal area ratios of indriids are exceedingly low (Table 3); the developing crowns of the first and second molars as well as the deciduous teeth are crowded into the small jaws of indriid fetuses.

The deciduous teeth begin to erupt in *Propithecus verreauxi* when fetal head length is less than three-quarters (i.e., ca. 30 mm) of the mean skull length at birth (generally >40 mm).² There is no fixed erup-

²Luckett (1984) conducted a histological study of dental development in even younger fetal *Propithecus verreauxi*. At 25-mm head length (little over half of head length at birth), the deciduous teeth are already well-developed, but unerupted. The vestigial third and fifth mandibular deciduous teeth (dc_1 and dp_3) are the least developed (i.e., in the middle-late bell stage, still lacking dentin and enamel); the crowns of all other deciduous teeth are well calcified. Luckett (1984, p. 187) calls the third and fifth mandibular deciduous teeth “retarded developmentally.” More precisely, they are developmentally *eclipsed* by the faster-developing milk teeth on either side. The developing roots of di_2 , dp_2 , and dp_4 are in close apposition and extend deep within the jaw, providing little space for the growth of dc_1 and dp_3 .

TABLE 3. Mean dp_4/m_1 occlusal area indices in Malagasy lemurs, expressed as %

Family	Genus and species	I. Maxillary dp_4/M^1 occlusal area index	II. Mandibular dp_4/M_1 occlusal area index
Indriidae	<i>Indri indri</i>	26.2	14.5
	<i>Avahi laniger</i>	24.7	16.6
	<i>Propithecus verreauxi</i>	25.5	18.7
	<i>P. diadema</i>	25.5	18.3
Lepilemuridae	<i>Lepilemur ruficaudatus</i>	47.6	34.9
Lemuridae	<i>Hapalemur griseus</i>	98.7	101.0
	<i>Eulemur fulvus</i>	77.1	79.1
	<i>E. macaco</i>	89.5	86.5
	<i>E. mongoz</i>	88.3	86.4
	<i>Lemur catta</i>	72.8	76.5
	<i>Varecia variegata</i>	64.8	75.1

TABLE 4. Dental eruption in fetal *Propithecus verreauxi*

Specimen number	Head length (in mm)	Mandibular teeth erupting	Maxillary teeth erupting
BMNH 95.308	20.5	None	None
BMNH 95.309	31.0	di1, di2, dc1	None
BMNH 95.306	31.4	di1, di2, dp4	di1
BMNH 95.312	32.6	dp4	None
BMNH 95.310	33.6	di1, di2, dc1, dp2, dp4	di1, di2, dc1, dp3, dp4
BMNH 95.311	33.7	di1, di2, dp4	di1, dp4
BMNH 95.307	35.3	di1, di2, dp4	di1, dc1, dp4
BMNH 67.1365	42.3	di1, di2, dc1, dp2, dp3; dp4 fully erupted	di1, di2, dc1, dp3; dp4 fully erupted

tion order: in some individuals, the anterior teeth emerge first, while in others, the opposite is true (Table 4). Most, if not all, of the deciduous teeth erupt before birth. The developmentally eclipsed dc_1 and dp_3 pierce the gumline last because of the very small height of their crowns. dp_3 in particular may be difficult to palpate in living neonates, because it is snuggled against the lingual face of the trigonid of the larger dp_4 , and may not achieve full gingival eruption at birth. Thus it is not surprising that Eaglen (1985; see also Smith et al., 1994) reported relatively late (i.e., postnatal) eruption of dp_3 in *Propithecus*.

More research is required to ascertain the precise degree to which permanent molar crowns are formed at birth in all frugivorous and folivorous lemurs. The dental microstructural data collected to date corroborate the observation drawn largely from radiographs of neonates that indriids are universally ahead of lemuriids in this regard. Milne Edwards and Grandidier (1875, Plate 35) illustrated a fetal (near term) *Indri indri* with fully erupted deciduous teeth and the crowns of the first two partially calcified permanent molars dissected out. Very young *Avahi* are more precocious dentally than are either *Propithecus* or *Indri*

(see Milne Edwards and Grandidier, 1875; Godfrey et al., 2001).

In sharp contrast to those of indriids, lemuriid permanent molar crowns calcify largely after birth. Only the cusps of the anteriormost molars are characteristically visible in radiographs of neonates or very young individuals (Samonds et al., 1999; Schwartz et al., 2002). Generally, the crypts for M_2 open during the second month, when M_1 is still only partially calcified. At a comparable age in *Propithecus*, the crowns of the first and second molars may be fully developed. By 3 months of age, calcification of the third molar is well underway (Fig. 2); the first molars erupt shortly thereafter.

Lemur teeth erupt in waves (Figs. 3, 4; see also Eaglen, 1985). These are clearly visible when ontogenetic series for any cranial trait (e.g., cranial length or bizygomatic breadth in percent mean species-typical adult value, Y) are plotted against dental developmental stage (X). Figure 3 shows cranial length vs. dental developmental stage for two species (*Lemur catta* and *Propithecus verreauxi*), plotted separately. A step pattern is obvious for each. Waves of dental eruption correspond to the horizontal or oblique platforms between vertical steps; the vertical "steps" are intervals during which cranial growth continues but no (or almost no) dental eruption occurs. Periods in which little or no dental eruption is coupled with little or no cranial growth are invisible. Indicated in Figure 3 is the species-typical timing for birth and weaning in *Lemur catta* and *Propithecus verreauxi*. The timing of wave initiation is much ear-

which are situated close to the oral epithelium. The relative retardation of dc_1 and dp_3 results in their failure to develop successional laminae and in the agenesis of successional teeth. In the maxilla, the anteriormost deciduous premolar never develops. Adult indriids lack the maxillary P^2 and the mandibular canine and P_3 . In contrast, four fetal *Lemur* examined by Luckett (1984) showed no relative retardation of dc_1 or dp_3 ; all deciduous teeth develop normally and are evenly spaced, and lemuriids retain the full primitive complement of permanent teeth.

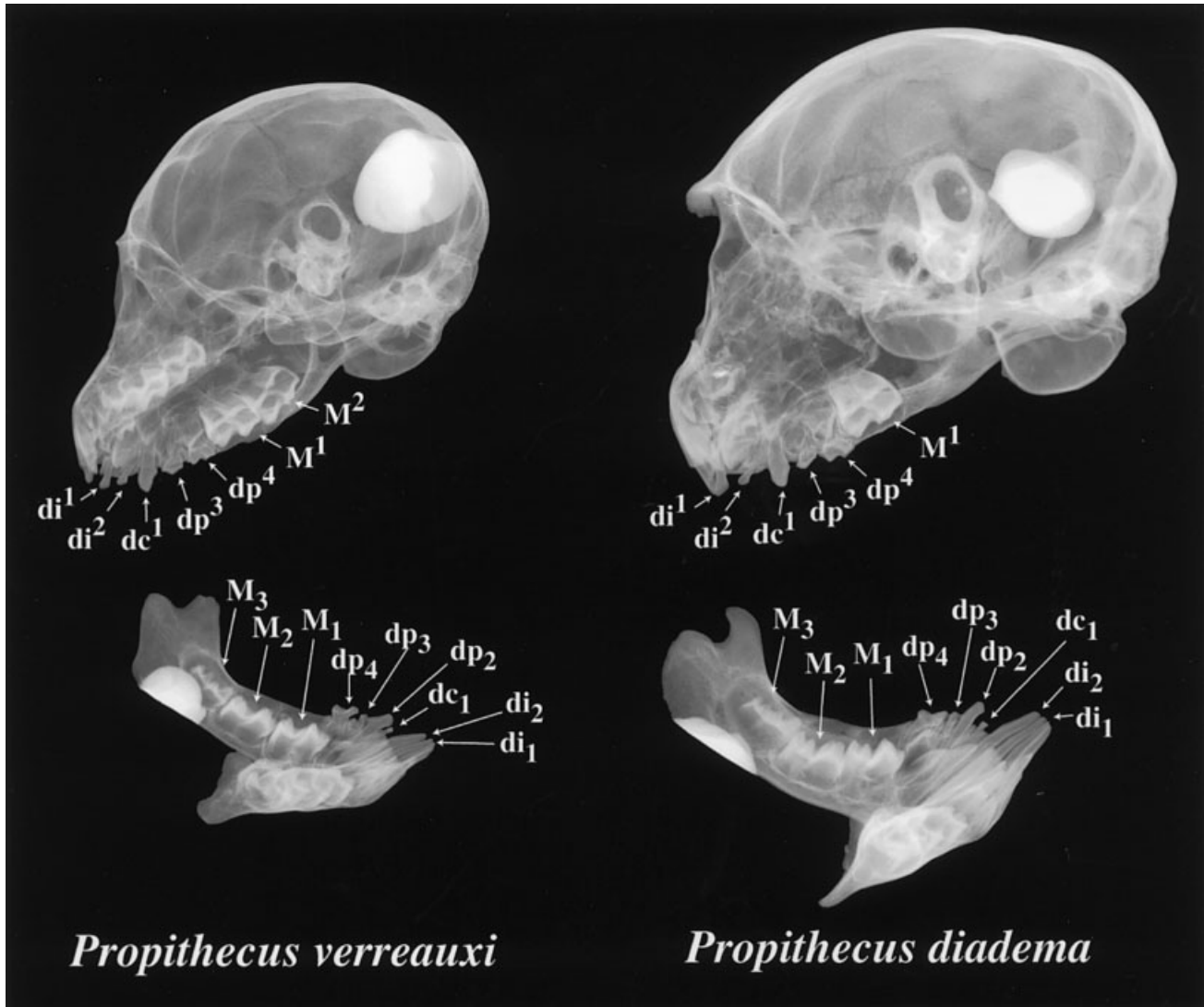


Fig. 2. Radiographs of young sifakas, showing complete deciduous dentitions. **Left:** Natural History Museum (London) ZD 1930.3.15.1, infant male *Propithecus verreauxi verreauxi* collected by E.I. White at Ampoza near Ankazoabo in August 1929. Estimated age, ca. 2 months. **Right:** Natural History Museum (London) ZD 1935.1.8.8a, infant male *P. diadema* collected "1 day west of Andapa" on August 29, 1930. Estimated age: almost 3 months. In this specimen, crypts for M² and M³ are visible, but crowns are missing. Note relatively small size of all milk teeth in *Propithecus*, vestigial nature of dc₁ and dp₃, and advanced state of calcification of permanent molars in very young individuals.

lier relative to birth and weaning in *Propithecus* than in *Lemur catta*.

Figure 4 shows cranial length and bizygomatic breadth for all species of lemurids and indriids in our database. The step pattern is only slightly obscured by this superimposition. Relative to craniofacial growth, dental development is faster in indriids than in lemurids. Thus, at any given dental developmental stage, craniofacial growth is more advanced in young lemurids than in young indriids. Dental development is faster in indriids than in lemurids on absolute as well as relative scales. Figure 5 illustrates this for one lemurid species (*Eulemur fulvus*) and one indriid species (*Propithecus verreauxi*); see also Schwartz et al. (2002).

Pace of somatic growth

Like-sized indriids and lemurids exhibit dramatic differences in pre- and postnatal growth rates. A comparison of trait-growth curves generated by fitting four-parameter logistic curves to the data derived from our samples of immature indriids and lemurids of known or estimated age demonstrates these differences (Fig. 6). Figure 7 shows the entire suite of fitted curves for bizygomatic breadth. Other traits give parallel results; in all cases, lemurids attain their asymptotic adult values more rapidly than do indriids of similar body mass.

Figure 8 compares the mean values for growth in mass prenatally (over gestation) and during

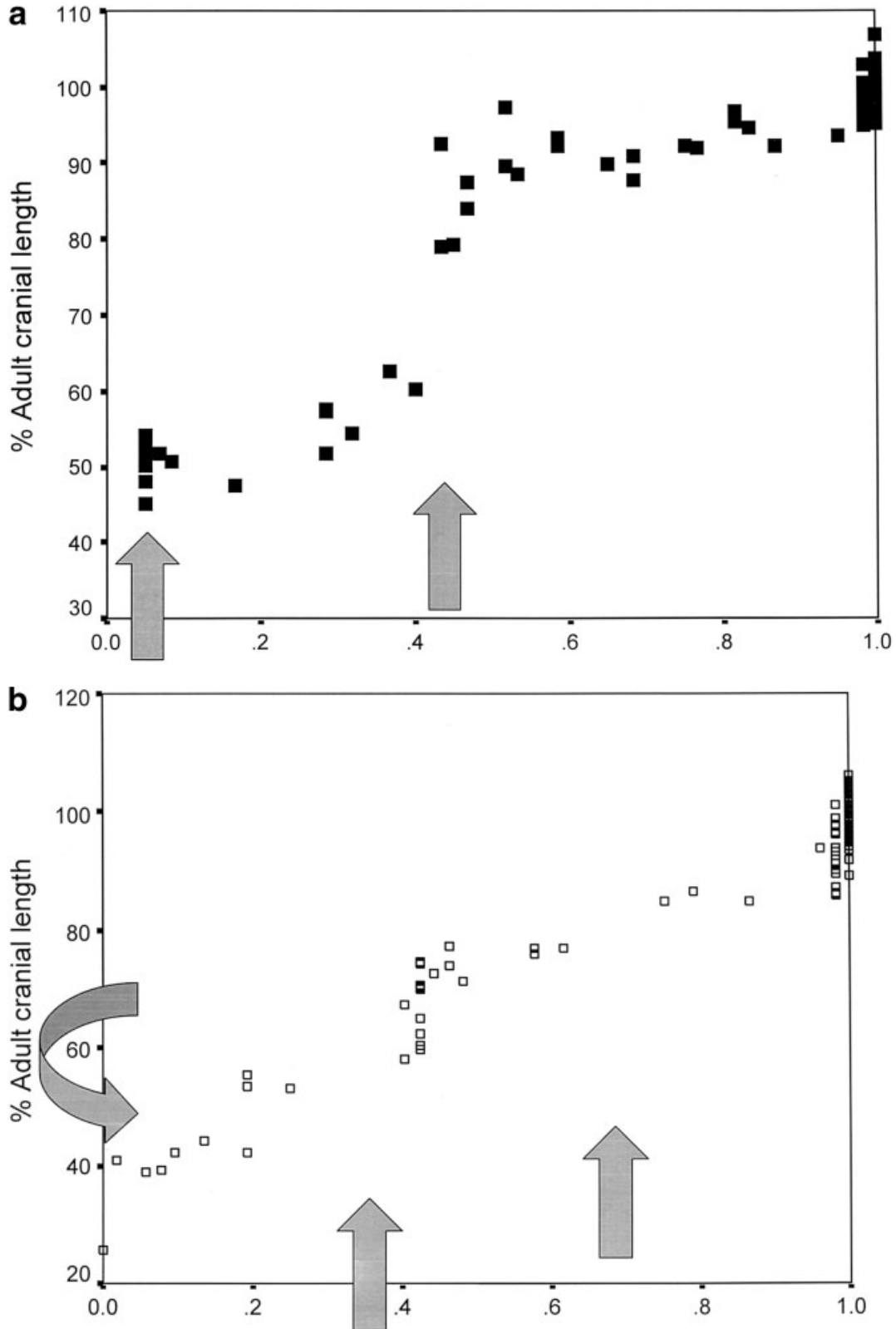


Fig. 3. **a:** Percent adult cranial length vs. dental developmental stage in *Lemur catta*. In lemurids, birth characteristically occurs between dental developmental stages 0.04–0.2, and weaning occurs at 0.38–0.53. **b:** Percent adult cranial length vs. dental developmental stage in *Propithecus verreauxi*. Birth characteristically occurs between dental developmental stages 0.31–0.43, and weaning typically occurs between dental developmental stages 0.56–0.8. Straight arrows indicate approximate timing of birth and weaning, respectively, in *Lemur catta* and in *Propithecus verreauxi*. Sifaka fetuses are indicated by curved arrow.

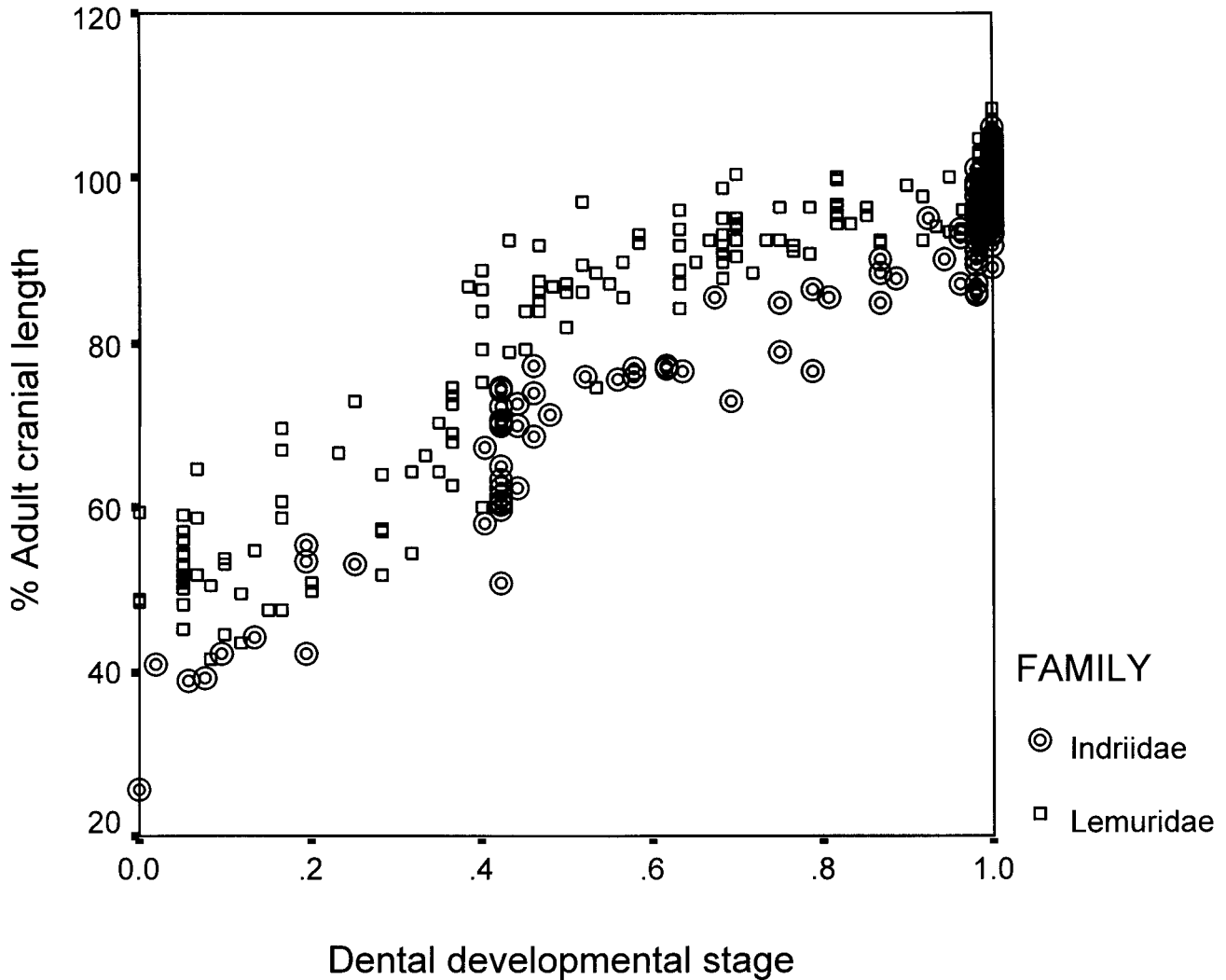


Fig. 4. Percent adult mean cranial length vs. dental developmental stage in families Indriidae and Lemuridae.

infancy (between birth and weaning) (for the data and their sources, see Tables 5 and 6). These mean values are plotted against adult female body mass. In all cases, indriids grow slowly in comparison to lemurs. Instantaneous growth rates at birth show the same contrast (Fig. 9; Table 7).

Several important inferences can be drawn from these data. First, for both indriids and lemurs, there is a very strong correlation between adult body mass and growth rates (either prenatal or postnatal). Second, the strength of the correlation weakens considerably when viewed across families. Third and most importantly, indriids and lemurs exhibit different growth patterns: both before and after birth (and before and after weaning), lemurs grow considerably faster than do indriids of similar adult body mass. In sharp contrast to the pattern for dental development, it is the indriids that lag behind like-sized lemurs in their rates of somatic growth.

Reproductive maturation and age at first reproduction

Female age at first reproduction and other reproductive parameters are poorly known for wild lemurs, with the exception of species studied over extended periods of time.³ Those data that do exist

³Age at first reproduction is better known for captive than for wild samples, but these cannot be compared because wild individuals usually begin to reproduce at an older age than their conspecifics in captivity. Nevertheless, it is noteworthy that the pattern we observe for wild indriids and lemurs is mirrored by the pattern exhibited by captive populations. A number of lemurs were reported to reach sexual maturity and conceive in captivity during the second breeding season after birth (i.e., prior to their second birthday; Boskoff, 1977; Klopfer and Boskoff, 1979; Van Horn and Eaton, 1979; Izard et al., 1993; Digby, 1999). This includes *Lemur catta* (Van Horn and Eaton, 1979), *Eulemur collaris* (Izard et al., 1993), and *Eulemur macaco* (Digby, 1999). Even the largest-bodied extant lemurid, *Varecia variegata*, regularly conceives in captivity during the second breeding season after birth (at ca. 20 months), although early conceptions

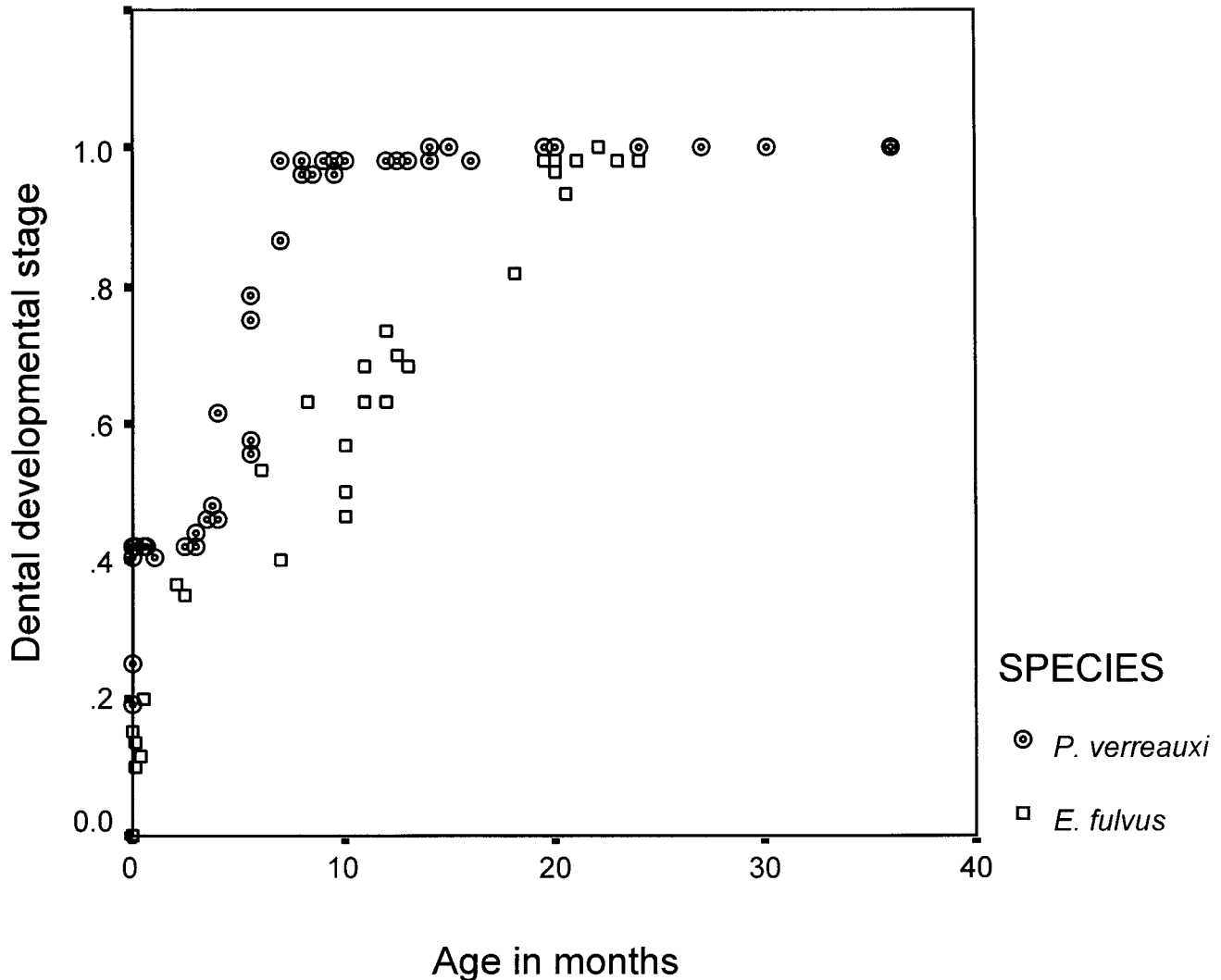


Fig. 5. Dental developmental stage vs. age in months for *Propithecus verreauxi* and *Eulemur fulvus*.

suggest earlier ages at first reproduction in lemurs than in like-sized indriids. Occasionally in lemurs, 2-year-old females give birth in the wild (see Colquhoun, 1993, on *Eulemur macaco macaco*; Overdorff et al., 1999, on *Eulemur fulvus rufus*; Cur-

generally produce low-weight singletons with a high probability of mortality (Boskoff, 1977), and infants conceived in the third breeding season or later are more likely to belong to larger litters (twins or triplets, or even quadruplets), to have higher neonatal masses (ca. 100 g each), and to survive (see also Klopfer and Boskoff, 1979; Foerg, 1982). Captive *Propithecus* tend to reach sexual maturity in the third breeding season after birth (Tattersall, 1982; Duke University Primate Center records), and to give birth at 3 years (and thus later than in lemurs). Often the very upper end of the range for first breeding in captivity is the lower end of the range for first breeding in the wild. Life spans are also better known for captive than for wild lemurs. Both lemurs and indriids can live long in captivity. Clotho (a female *Varecia variegata* at the Duke University Primate Center) died at age 36 or older; Nigel (a male *Propithecus verreauxi*, also at the Duke University Primate Center) was over 30 years old when he died. Better data from long-term field studies will be required to test possible differences in the life spans of lemurs and indriids.

and Zaramody, Colquhoun, 1999, on *Eulemur mongoz*; Morland, Colquhoun, 1991, on *Varecia variegata*; and Koyama et al., 2001, on *Lemur catta*). However, the norm for first successful births, even among small-bodied lemurs (see Tan, 1999b, on *Haplemur griseus*), is 3 years or older, as infants born to 2-year-old mothers tend not to survive. Wild ringtail females tend to give birth for the first time at age 3 or 4 years (for ringtails at Berenty, see Jolly, 1966; Koyama et al., 2001; for ringtails at Beza Mahafaly, see Sussman, 1992; Gould et al., 1999).

It is unlikely that any wild indriid reproduces at age 2 years. The data for *Avahi* are poor, but Albignac (1981) described *Avahi* as living in social groups of up to five individuals with an adult male and female and offspring up to 2 years of age. If offspring generally leave their parents at sexual maturity and take up to a year to find a mate (as is usual for monogamous species; see Wright, 1990), then first reproduction in *Avahi* should occur at 3 years or later.

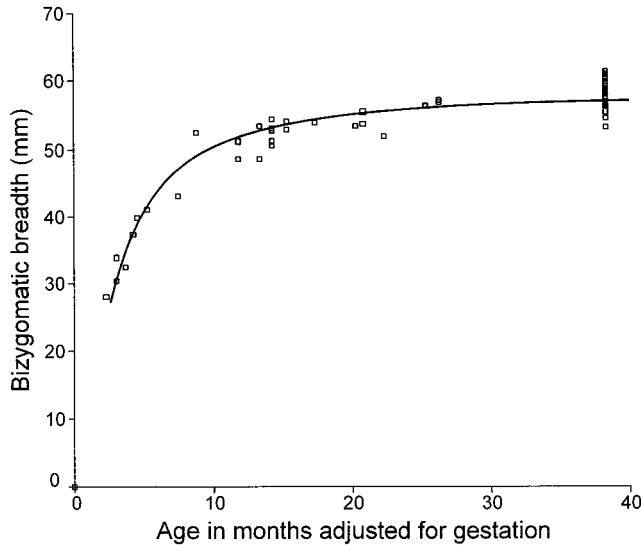


Fig. 6. Four-parameter logistic curve fit to data for bizygomatic breadth (Y) by age in months (X) in *Varecia variegata*, shown to illustrate our curve-fitting procedure. “Zero” value for bizygomatic breadth was set at one-third of the way through gestation. Equation for logistic curve is $A_2 + (A_1 + A_2)/(1 + (X/X_0)^P)$, where A_1 (27.55 ± 1.87 mm) is initial Y value at birth (or $X = 0$), and A_2 (62.0 ± 1.56 mm) is adult ceiling for Y. Chi-square degrees of freedom = 3.69; $R^2 = 0.94$.

Excellent data now exist for age at first reproduction in wild sifakas (Richard et al., 1991, 1993, 2002; Wright, 1995; Pochron et al., in press). Occasionally, 3-year-old *Propithecus verreauxi* give birth in the wild, but more often sifakas do not give birth until they are older (sometimes considerably older). It is not uncommon for female *P. verreauxi* to reproduce for the first time at 6 years; 50% of females at Beza Mahafaly have not given birth by the time they are 6. Females can give birth in consecutive years (Richard et al., 2002). Whereas the death of an infant does not increase the probability that females will successfully raise the next year’s infant, there is quite a bit of variance in female reproductive success, depending on each individual’s ability to regain body mass and thereby store resources prior to the breeding season (Richard et al., 2000). In *Propithecus diadema edwardsi* at Ranomafana (Wright, 1995; Pochron et al., in press), females tend to leave their groups and breed for the first time at between 3–5 years. Most females give birth every other year (Pochron et al., in press). First reproduction in female *Indri indri* does not occur until even later. Mittermeier et al. (1994) recorded ages at first reproduction from 7–9 years, on the basis of an unpublished report to the WWF-US Primate Program by J. Pollock. *Indri* do not reproduce every year; they often reproduce only every third year (Powzyk, 1997). Table 8 summarizes data from the literature on age at first reproduction in females of folivorous and frugivorous species. Clearly, folivorous species (e.g., indriids) do not experience early sexual maturation or first reproduction in comparison to like-sized, more frugivorous lemurs.

A second difference between the more frugivorous and more folivorous lemur species is litter size. Twinning occurs in many lemurs, including *Varecia*, *Eulemur*, and *Lemur*; we are unaware of reports of twinning in any indriid, either in the wild or in captivity. Table 9 provides data compiled from published and unpublished sources on litter size in folivorous and frugivorous lemurs.

DISCUSSION

That lemurs grow more rapidly than indriids of like-body mass has obvious implications for the risk aversion hypothesis. Lemurs are more “frugivorous” than indriids: they prefer higher-quality but presumably less predictable resources. According to the RAH, lemurs should be more vulnerable to starvation than indriids, and would therefore be expected to grow more slowly than indriids of comparable body size. However, the data show that the opposite is true. Contrary to the expectations of the RAH, frugivorous lemurs tend to grow faster than like-sized folivorous species, have relatively larger weanlings, and reproduce earlier. It is only in their pace of dental development that folivorous and frugivorous lemurs conform to the expectations of the risk aversion hypothesis.

Indriids are unique in having rapid dental development superimposed on a matrix of slow overall growth and reproductive maturation. Because the RAH posits that adjustments in the speed of development serve to counter varying degrees of starvation risk, it is the rate of growth that seems most relevant, and the RAH seems ill-suited to explain the developmental differences between indriids and lemurs. The apparent conformity of the pace of dental development to the predictions of the RAH seems coincidental. Alternative ecological pressures might better explain the differences between indriids and lemurs in somatic development and age at maturation, as well as the “decoupling” of dental and somatic development seen in indriids.

Adaptive significance of variation in rates of dental development

We suggest, following Eaglen (1985), that variation in the timing of dental development is tied to variation in the behavioral ontogeny of food processing. Many lemur species, including all indriids and most lemurs, exhibit reproductive synchrony. Indeed, reproductive synchrony may characterize all lemurs except *Daubentonia* and possibly *Haplemur*, whose specialized diets may be less subject to seasonal changes (Glander et al., 1989; Sterling, 1994; Tan, 1999a,b; Mutschler, 1999). Because of reproductive synchrony, lemurs grow in cohorts, and natural selection can mold dental eruption schedules to anticipate specific seasonal phenological events. In fact, it was shown that phenological changes are closely monitored by lemur species (Sauther, 1991, 1998; Meyers and Wright, 1993),

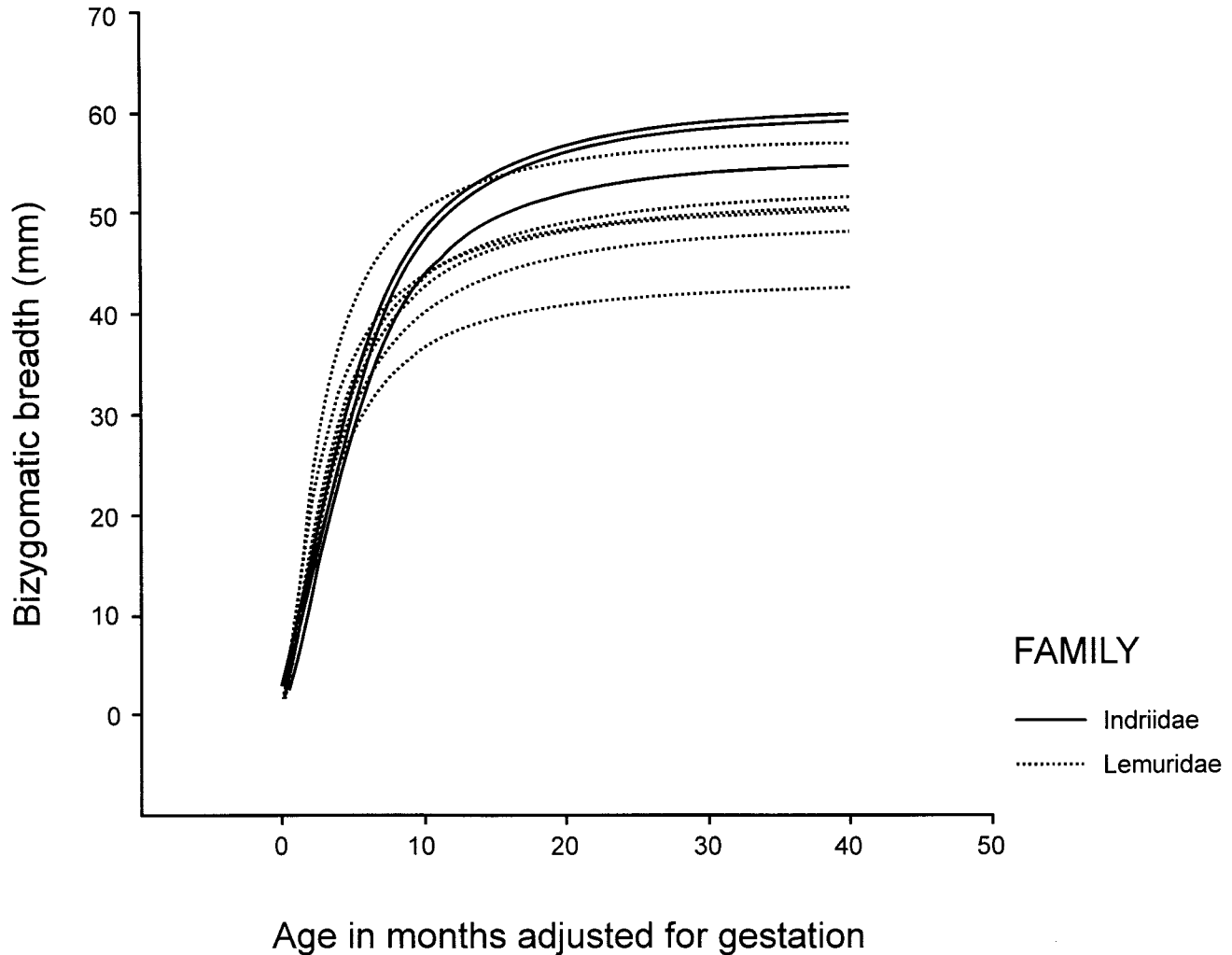


Fig. 7. Bizygomatic breadth vs. age in months (adjusted for gestation length) in indriids vs. lemurs. Each curve was generated using Originlabs curvilinear regression algorithm for a four-parameter logistic curve, with “zero” value for bizygomatic breadth set at beginning of gestational growth phase, about one-third of the way through gestation period. Note that indriids reach adult values for bizygomatic breadth more slowly than like-sized lemurs.

and that weaning itself is timed to correspond to the season of greatest availability of young leaves in many species (Wright, 1997, 1999). It was also shown that late-cycle infants may be at a distinct selective disadvantage despite the possibility of catch-up growth (Sauter, 1991, 1998; Pereira, 1993). Eaglen (1985) linked the timing of dental eruption in lemurs to plant phenology, by suggesting that the state of the dentition at weaning (or during the first postweaning dry season) may be a critical target of selection. Reproductive synchrony may allow the pace of dental development to undergo selective fine-tuning, possibly independent of somatic growth, in accordance with the leafing and fruiting schedules of important plant resources.

The first dental eruption wave (comprising the emergence of the deciduous dentition) begins just prior to birth in lemurs, and extends over the first several months of infancy. In contrast, it begins well prior to birth in indriids, and extends only into the

first few weeks after birth if at all. Solid foods are tasted or mouthed exceptionally early in indriids. Richard (1976) reported such behavior in wild Verreaux's sifakas at about 2 weeks of age. *Propithecus diadema edwardsi* begin to play-bite twigs and leaves at about 3 weeks, and actually ingest solid foods at 4–6 weeks of age; young leaves are ingested at 2–3 months, and fruits are added at about 2–4 months prior to the onset of weaning (Pat Wright, personal communication; see also Grieser, 1992). *Indri* infants start feeding on solid food at 8 weeks of age, long before weaning at ca. 8 months (Pollock, 1975b).

The second dental eruption wave involves the eruption of the anterior permanent molars and permanent incisors (plus the lower canine, when this tooth is part of the tooth comb). It begins at or shortly after the onset of weaning, which occurs between 4–6 months in most lemurs, and during the wet season. *Haplemur simus* is an exception in

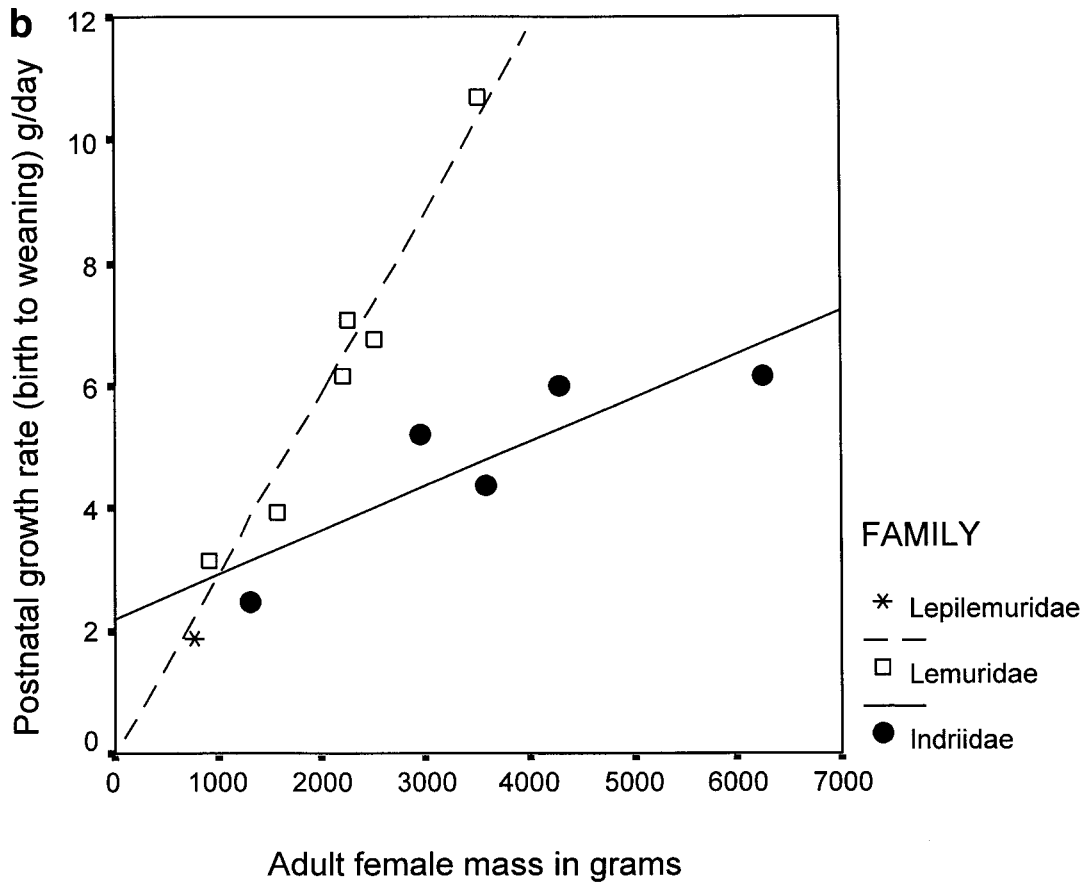
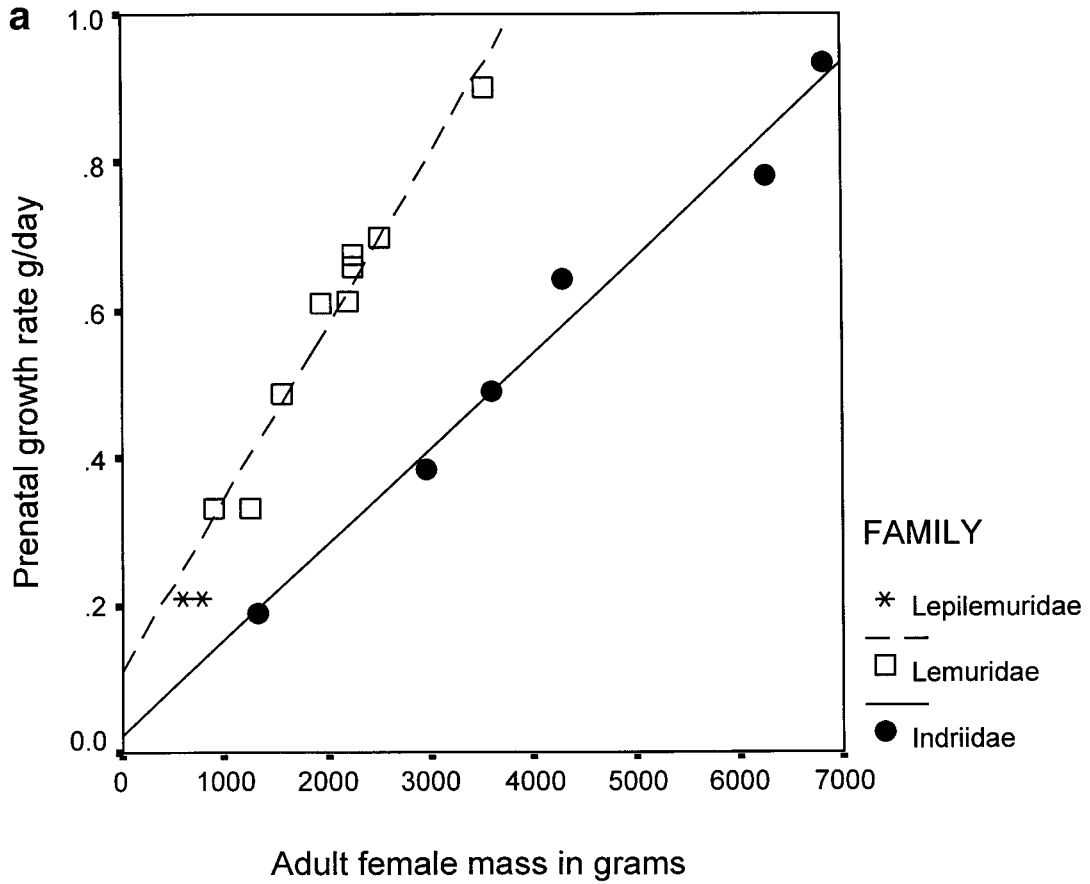


Fig. 8.

that it delays weaning until about 8 months of age (Tan, 1999b) (well after the initiation of the second wave of eruption), so that new weanlings are well-endowed dentally and can process the tough, fibrous stems of giant bamboos. In most lemurids, eruption of the second wave of teeth extends through the wet season and well into the first half of the dry season. During the 6-month period of fruit scarcity (particularly the latter half), growth slows dramatically and dental eruption halts for a period of about 3 months, until the rains come again and the third wave of dental eruption (the premolars, third molars, and upper canines) begins (Eaglen, 1985; Pereira, 1993, 1995).

The second wave of dental eruption begins well prior to weaning in indriids (which similarly occurs during the wet season), and there is no extended break in time between the second and third waves. For example, M1 erupts at age 12–14 weeks (3 months) in *Propithecus verreauxi*, when this species regularly samples solid foods (Eaglen and Boskoff, 1978). Weaning begins in sifakas at about 5–6 months (Meyers and Wright, 1993). At weaning, their dentition includes the first two molars, the last permanent premolar, the full battery of adult upper incisors, and the adult mandibular toothcomb (Godfrey et al., 2001). During the wet season, the availability of young leaves increases, as does the availability of fruit (including unripe fruit) and seeds.

By the beginning of the first postweaning season of scarce resources, sifakas are 8 or 9 months old and still small in comparison to adults (about a third of adult mass or slightly more). In the early dry season, adult sifakas process very hard fruits, which are cracked open by the postcanine teeth (N. Yamashita, personal communication). Characteristically in *Propithecus*, the mandibular dentition is complete (or virtually so) at around 8 months, and the maxillary dentition except the canine is complete around 1 year. The upper canine continues to erupt slowly after all postcanine teeth have fully erupted. Thus, 8-or-9-month-old sifakas have their full battery of adult teeth except the upper canines and, perhaps, the maxillary third molars (which are erupting at this age). During their first postweaning season of scarce resources, sifakas are capable of processing the foods eaten by full adults.

One might wonder whether enlargement of the posteriormost deciduous premolar might not be a viable alternative to dental developmental acceleration, especially since delaying molar eruption would

prolong the overall life span of the dentition. At least with respect to primates, we suggest that no degree of enlargement of the molarlike posterior deciduous premolar can rival the masticatory efficiency of the first and second permanent molars combined, particularly when the latter are large in adults. There is a strong correlation among primates between the percentage of teeth that have erupted at weaning and the postcanine occlusal area at weaning (expressed as a percentage of the species-typical adult postcanine occlusal area; see Godfrey et al., 2001). Among primate species with no permanent molars or replacement teeth at weaning, weanling postcanine occlusal area is generally 20–30% of the species-typical adult value. Very few such species (indeed, only callitrichines) display values in excess of 40%, and none display values in excess of 50% (Godfrey and Samonds, unpublished data). In contrast, values over 50% are common for species with at least some permanent teeth erupted at weaning. For indriids, postcanine occlusal area at weaning always exceeds 60% of the corresponding species-typical adult value (sometimes well over 60%).

Molars with large crushing basins and high shearing quotients are ideal for breaking down unripe fruit, hard or tough seeds, and mature leaves. The megadont and cresty molars that indriids possess help them to do just that (Table 10; see also Godfrey et al., 2002; Jungers et al., 2002). If recent weanlings must process the same foods as adults, and if those foods include unripe fruit, hard or tough seeds, and mature leaves, there should be a strong selective pressure to accelerate molar eruption or to delay weaning until the first several permanent molars have erupted. Delaying weaning requires prolonged lactation. Indriids appear to have accelerated dental development without prolonging lactation.

Dental development can be accelerated through earlier initiation of crown formation, faster enamel accretion (shortening the crown formation time), or both. Eruption can follow quickly after crown mineralization is complete. Schwartz et al. (2002) showed that *Propithecus* has rapid molar crown formation time, very early molar crown initiation (the first permanent molar crown initiates soon after the end of the first trimester of gestation, and all three molar crowns initiate prior to birth), and rapid molar eruption following crown completion. The small size of indriid deciduous teeth is a clear consequence of this adaptive strategy, as the permanent molar crowns must occupy most of the space available for developing teeth in the jaws of fetuses (Godfrey et al., 2002; Schwartz et al., 2002).

The upshot is that, at weaning, dental endowment (i.e., percent species-typical postcanine occlusal area at weaning) is considerably greater in indriids than in their more frugivorous relatives (Godfrey et al., 2001). The same is true at the onset of the first season of scarce resources following weaning. Selection seems to have operated on dental development (independent of the growth and development of the

Fig. 8. a: Prenatal growth rates for lemurids and indriids, benchmarked against maternal body mass. **b:** Postnatal growth rates for lemurids and indriids benchmarked against maternal body mass. For lemurids: regression of prenatal growth rate on adult female mass, $r = 0.979$ ($N = 9$, $P < 0.001$); regression of postnatal growth rate on adult female mass, $r = 0.977$ ($N = 7$, $P < 0.001$). For indriids: regression of prenatal growth rate on adult female mass, $r = 0.990$ ($N = 6$, $P < 0.001$); regression of postnatal growth rate on adult female mass, $r = 0.869$ ($N = 5$, $P < 0.05$, one-tailed).

TABLE 5. Lemur gestation lengths, neonatal mass, maternal mass, age at weaning, and sources

Genus and species	Gestation length (years)	Neonatal mass (kg)	Weanling mass (kg)	Maternal mass (kg)	Age at weaning (years)	References
<i>Avahi laniger laniger</i>	0.42	0.029	0.5	1.32	0.41	Tattersall (1982), Petter-Rousseaux (1962), Glander et al. (1992), Goodman et al. (1993). Weaning may occur prior to 4-months (P. Wright, personal communication). Wean mass is probably overestimated (see Table 6).
<i>Propithecus verreauxi verreauxi</i>	0.43	0.063	1.0	2.95	0.5	Haring (1990), Garbutt (1999), Richard and Dewar (1991), Kappeler and Ganzhorn (1993), Roberts (1994), Ravosa et al. (1993), and records of Duke University Primate Center, Beza Mahafaly Special Reserve, and S. O'Connor (personal communication)
<i>P. v. coquereli</i>	0.43	0.1	1.18	4.28	0.5	Records of Duke University Primate Center.
<i>P. tattersalli</i>	0.5	0.088	0.741	3.59	0.42	Meyers and Wright (1993), Ravosa et al. (1993), and records of Duke University Primate Center. Weanling mass taken from growth records at Duke University Primate Center.
<i>P. diadema</i>	0.49	0.145	1.25	6.26	0.5	Glander et al. (1992), Meyers and Wright (1993), Powzyk (1996), Wright (1995, 1999), and Smith and Jungers (1997). We used Glander et al.'s (1992) sample of individuals 5 days or younger in calculation of neonatal mass. Wright (1999) reported a 153-day-old weanling at 1.10 g.
<i>Indri indri</i>	0.42	0.14		6.84	0.67	Bauchot and Stephan (1966), Powzyk (1996), and Pollock (1975a, 1977).
<i>Lepilemur ruficaudatus</i>	0.38	0.027	0.25	0.78	0.33	Doyle (1979), Bauchot and Stephan (1966), Schmid and Ganzhorn (1996), Smith and Jungers (1997), Garbutt (1999), Petter et al. (1977), and Drack et al. (1999). Wean mass was reconstructed using a growth curve based on estimated birth mass and field records for immature individuals ca. 9.5 months old.
<i>Varecia variegata</i>	0.28	0.092	2.5	3.52	0.4	Foerg (1982), Cartmill et al. (1979), Brockman et al. (1987), Rogers (1988), Ruempler (1993), Terranova and Coffman (1997), and Morland (1990), records of San Diego Zoo, and the Duke Primate Center.
<i>Eulemur fulvus</i>	0.34	0.079	1.35	2.25	0.5	Glander et al. (1992), Leutenegger (1973), Eisenberg (1981), Roberts (1994), Izard et al. (1993), Frazier and Hunt (1994), and Kappeler and Ganzhorn (1993), and records of Duke University Primate Center.
<i>E. macaco</i>	0.34	0.088	1.00	2.51	0.37	Prescott (1980), Ruempler (1993), Smith and Jungers (1997), Colquhoun (1993), and Roberts (1994), and records of Duke University Primate Center. Birth mass for individuals in our database.
<i>E. mongoz</i>	0.35	0.063	0.65	1.56	0.42	Smith and Leigh (1998), Terranova and Coffman (1997), Doyle (1979), and Wright (1990), and records of Duke University Primate Center, Leigh and Terranova (1998).
<i>Hapalemur griseus</i>	0.38	0.045	0.42	0.9	0.33	Wright (1990), Terranova and Coffman (1997), Smith and Jungers (1997), Kappeler (1991), Tan (1999b), Leigh and Terranova (1998).
<i>Lemur catta</i>	0.37	0.083	1.08	2.21	0.49	Hick (1976), Ruempler (1993), Leutenegger (1973), Sussman (1991), Mittermeier et al. (1994), Roberts (1994), and Ross and Jones (1999), and records of Lowry Park Zoo and Duke University Primate Center.

TABLE 6. Prenatal and postnatal growth rates in lemurs

Genus and species	Prenatal growth in mass, conception to birth (g/day)	Postnatal growth in mass, birth to weaning (g/day)	Notes
<i>Avahi laniger</i>	0.19 g/day	3.14 g/day	Gestation length was taken from Tattersall (1982). Neonatal mass for <i>Avahi</i> was estimated on basis of regression analysis of neonatal mass on neonatal skull size, using skulls of very young <i>Avahi</i> in collections of the Muséum National d'Histoire Naturelle, Paris. These skulls may belong to individuals that were more than 5 days old; thus, our estimate for neonatal mass may be too high. A recently weaned several-month-old <i>Avahi laniger</i> that was captured at Ranomafana weighed under 500 g (Wright, personal communication). Goodman et al. (1993) weighed a lone "juvenile" after it was killed by a hawk. Given its isolation from other group members, it is likely that this individual had been weaned. With its head missing, this individual weighed 500 g (thus its mass was >500 g). We take 500 g as a conservatively high estimate for wean mass in <i>Avahi laniger</i> .
<i>Propithecus verreauxi coquereli</i>	0.64 g/day	6.00 g/day	Gestation length, neonatal mass, and growth in mass to weaning based on records of Duke University Primate Center.
<i>P. v. verreauxi</i>	0.40 g/day	5.21 g/day	Gestation length, neonatal mass, and growth in mass to weaning based on records of Duke University Primate Center and Beza Mahafaly Special Reserve.
<i>P. tattersalli</i>	0.49 g/day	4.35 g/day	Gestation length, neonatal mass, and growth in mass to weaning based on records of Duke University Primate Center and Meyers (1993).
<i>P. diadema</i>	0.81 g/day	6.14 g/day	Neonatal mass estimated on basis of published data on wild-caught week-old <i>P. diadema</i> , adjusted on basis of first-week growth curves for captive <i>P. verreauxi</i> . For postnatal growth rates, Wright (1999) reports an even lower value of 5.5 g/day for birth to weaning in <i>P. d. edwardsi</i> .
<i>Indri indri</i>	0.93 g/day		Neonatal mass for <i>Indri</i> estimated on basis of regression analysis of neonatal mass on neonatal skull size, using skull of neonatal <i>Indri</i> depicted in Milne Edwards and Grandidier (1875). Skulls of newborn indris are similar in size to those of newborn <i>P. diadema</i> .
<i>Lepilemur ruficaudatus</i>	0.21 g/day	1.86 g/day	Estimate by Doyle (1979) of neonatal mass for <i>Lepilemur</i> was based on unspecified <i>L. mustelinus</i> . In 1979, all currently recognized species of <i>Lepilemur</i> were considered conspecific. Drack et al. (1999) collected <i>Lepilemur ruficaudatus</i> during July and August 1996 at Kirindy Forest. All were adults save two youngsters, ca. 9–10 months old, one 470 g, and the other 513 g. Mean mass for two juveniles was 491.8 g, or 61% of adult female weight. Full adults in population ranged in mass between 660–940 g, with a mean of 785.6 g. Mean mass for nine adult females in study group was 803.9 g, close to value reported by Smith and Jungers (1997) of 779 g.
<i>Varecia variegata</i>	0.90 g/day	10.67 g/day	Duke Primate Center. Pereira et al. (1987): ruffed lemurs may attain 70% of average adult body weight by age 4 months Cartmill et al. (1979), Kappeler (1996), and Kirkwood and Strathatos (1992).
<i>Eulemur fulvus</i>	0.66 g/day	7.06 g/day	Duke Primate Center, Zürich
<i>E. macaco</i>	0.70 g/day	6.75 g/day	Duke Primate Center, Leigh and Terranova (1998)
<i>E. mongoz</i>	0.49 g/day	3.93 g/day	Duke Primate Center, Leigh and Terranova (1998)
<i>Haplemur griseus</i>	0.33 g/day	3.12 g/day	Duke Primate Center, Leigh and Terranova (1998)
<i>Lemur catta</i>	0.61 g/day	6.15 g/day	Duke Primate Center, Zürich

rest of the skeleton) so as to guarantee masticatory proficiency at weaning and during the first postweaning "dry" season. Dissociation of dental development and overall somatic growth allows young indriids to become ecological "adults" while they are still immature by all other standards, i.e., long before they reach sexual maturation or adult body mass.

Adaptive significance of variation in somatic growth rates

Janson and van Schaik (1993) posited a relationship between juvenile (postweaning) growth rates and resource predictability. Our data for infant growth are more complete than those for juveniles. However, we can assert on the basis of growth

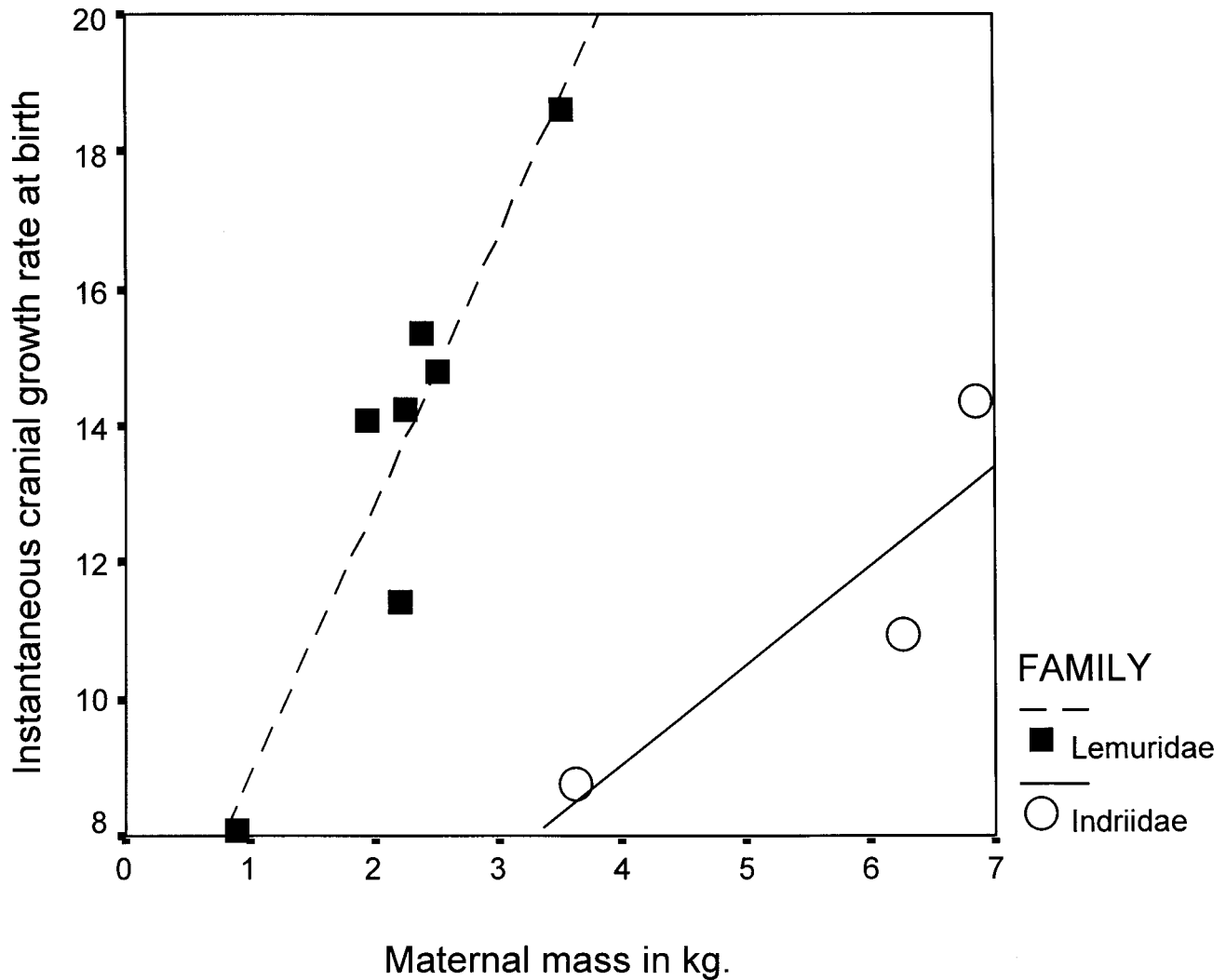


Fig. 9. Lemurid vs. indriid species values for instantaneous growth in cranial length at birth, benchmarked against maternal body mass.

TABLE 7. "Instantaneous" growth rates at birth, calculated for 20-day period before and after birth

Species	Maternal mass in kg	Mean daily rate of increase in cranial length averaged for 20-day interval surrounding and including birth (mm/20 days)
<i>Varecia variegata</i>	3.52	18.62
<i>Eulemur macaco</i>	2.51	14.79
<i>Eulemur fulvus</i>	2.25	14.25
<i>Eulemur collaris</i>	2.38	15.34
<i>Lemur catta</i>	2.21	11.43
<i>Eulemur rubriventer</i>	1.94	14.06
<i>Hapalemur griseus</i>	0.9	8.07
<i>Indri indri</i>	6.84	14.34
<i>Propithecus diadema</i>	6.26	10.94
<i>Propithecus verreauxi</i>	3.62	8.75

curves that those species that grow rapidly during infancy also attain adult size relatively early. These are the more frugivorous (not the more folivorous) lemur species.

How can this variation in growth rates be explained? An extensive literature relates fetal and infant growth rates to maternal investment. Indeed, rates of fetal and infant growth are sometimes taken as *measures* of maternal investment, particularly when benchmarked against maternal mass. Thus, for example, the "prenatal maternal investment rate" might be measured as the average daily maternal energy output during gestation (litter weight divided by gestation length), and this in turn is plotted against maternal mass or basal metabolic rate in species comparisons. Ideally, when measuring maternal investment, energy expenditure should be benchmarked against the energy available to the mother, and thus against basal metabolism (oxygen consumed per unit time) and not maternal mass. Young et al. (1990) suggested that the cost of reproduction is high in many lemur species relative to the available energy, and therefore female lemurs are energetically stressed during gestation and lactation. They took sifakas to be a prime example. How-

TABLE 8. Maternal age at first reproduction in the wild

Genus and species	Maternal age at first reproduction in the wild (years)	Sources and notes
<i>Indri indri</i>	7–9	Pollock (1977); Mittermeier et al. (1994) on basis of 1984 unpublished report by J. Pollock to WWF-US Primate Program
<i>Avahi laniger</i>	3	Albignac (1981)
<i>Propithecus verreauxi</i>	5–6	Richard et al. (1993, 2002)
<i>P. diadema</i>	3–5	Meyers and Wright (1993); Wright (1995, personal communication)
<i>Lepilemur ruficaudatus</i>	2?	Petter-Rousseaux (1964); Nash (1993) ¹
<i>Varecia variegata</i>	2–3	Morland (1991)
<i>Eulemur fulvus</i>	2–4	Overdorff et al. (1999)
<i>E. macaco</i>	2	Colquhoun (1993)
<i>E. mongoz</i>	3	Curtis and Zaramody (1999)
<i>Hapalemur griseus</i>	3	Tan (1999b)
<i>Lemur catta</i>	3–4	Jolly (1966); Sussman (1992); Gould et al. (1999)

¹ Information on *Lepilemur* is scanty. Petter-Rousseaux (1964) reported that young *L. ruficaudatus* stay with their mothers for a year after birth. Thus, they cannot give birth to their first young until age 2. Leanne Nash observed *L. leucopus*, not *L. ruficaudatus*. Year-old *Lepilemur* are not fully grown (unpublished observations on museum specimens, L.R.G.).

ever, Kappeler (1996) showed that the cost of reproduction, benchmarked against either maternal mass or metabolic rate, is not unusually high in lemurs (including sifakas) when compared to other groups of primates. He also showed that metabolic rate does not vary independently of body size in lemurs and is not correlated with measures of maternal investment (prenatal and postnatal infant or litter growth rates).

Of course, the rate of infant growth can be a poor proxy for maternal investment (Whitten and Brockman, 2001). It does not take into account contributions to infant growth from sources other than mother's milk; early ingestion of solid food, for example, may ease the burden on the mother. It does not take into account contributions to infant care from other group members or behavioral modifications on the part of the mother (e.g., parking vs. carrying infants) that may positively or negatively impact energy expenditure. It does not take into account variation in the relative proportions of cheap vs. expensive tissue. For example, it may cost more to raise an infant with a relatively large brain than an infant with a relatively small brain because of the high expense of brain tissue.⁴ If the species compared have markedly different tissue proportions, maternal investment is not well-captured by overall rates of growth.

We have shown that fetal and infant growth rates are higher in lemurs than in indriids of similar body size, and that lemurs attain adult values for cranial traits at a relatively earlier age. To the extent that these differences reflect variation in maternal investment, adult female lemurs invest more in their young than do adult female indriids. The upper extreme for lemurs is occupied by the highly frugivorous *Varecia* (the largest living le-

murid), which regularly gives birth to multiple offspring, each of which grows rapidly during infancy to gain as much as 70% of its mother's mass by the time it reaches 4 months of age, when weaning occurs (Cartmill et al., 1979; Pereira et al., 1987; Kirkwood and Stathatos, 1992; Kappeler, 1996). This contrasts sharply with the condition in *Propithecus*, which regularly gives birth to a single young that grows slowly throughout infancy and afterward (Wright, 1999; Richard et al., 2002). Wright (1999) reported an infant growth rate to weaning for wild *Propithecus diadema* of 5.5 g/day. Our data suggest a similarly low preweaning growth rate for *P. diadema* (6.14 g/day), as for other species or subspecies of *Propithecus* (4.35–6.0 g/day), even when raised in captivity. When a young sifaka is weaned at 5–6 months, it may weigh only 20–25% of its adult mass (Wright, 1999).

Other factors do not alter the conclusion that maternal investment is lower in indriids than in lemurs. Early ingestion of solid food in indriids would function to further reduce maternal investment in indriids. All indriids and most lemurs carry their young (except *Varecia*, which uses infant parking and biparental guarding to ease the maternal cost of raising multiple, extremely rapidly growing infants; see Pereira et al., 1987). Relative brain size is not higher in indriids than in lemurs; to the contrary, indriids have significantly *smaller* brains relative to body mass ($t = 3.83$ with 12 degrees of freedom, two-tailed $P = 0.002$; W.L.J., unpublished data). This difference is not a simple function of brain/body allometry, as like-sized indriids and lemurs show consistent differences in their relative brain size. It is likely that indriid weanlings have small bodies with relatively small brains.

The basic premise of Young et al. (1990) is that energy is limiting in reproductive female lemurs. Pereira et al. (1999) argued that this premise may be correct, even if maternal reproductive effort is not particularly high in these species (see review by Whitten and Brockman, 2001). The critical factor is

⁴Teeth, like brains, may be an expensive tissue; unfortunately, little is known about the relative "cost" of raising infants with precocious vs. retarded dental development. Studies of milk composition and lactation rates should be helpful here. However, studies of milk composition in prosimians (e.g., Tilden and Oftedal, 1997) have not included indriids.

TABLE 9. Litter size in wild and captive frugivorous and folivorous lemurs

Taxon	Litter size	Sources
<i>Varecia variegata</i>	Twins are very common in the wild; litters of up to five have been raised under semifree ranging conditions with food supplementation. Both twins and triplets are common in captivity.	For <i>Varecia</i> in the wild, see Morland (1989, 1991); Ratsimbazafy (2002). For <i>Varecia</i> in captivity, see Cartmill et al. (1979), Foerg (1982), Shidler and Lindburg (1982), Brockman et al. (1987), Bollen (1996), Kerridge (1999), and records of Happy Hollow Park and Zoo, Twycross Zoo, Kansas City Zoo, Bristol Zoo Gardens, Pittsburgh Zoo, San Diego Zoo, Zoo Atlanta, Parc Ivoloïna, and Duke University Primate Center.
<i>Eulemur macaco</i>	Twins occasionally occur in captivity.	Records of Henson Robinson Zoo and Duke Primate Center (D. Haring, personal communication).
<i>Eulemur mongoz</i>	Twins occur in low frequency in captivity, and possibly in the wild.	For possible twinning of <i>Eulemur mongoz</i> in the wild, see Tattersall (1977), Petter and van der Sloot (2000), D.J. Curtis (personal communication). For twinning in mongoose lemurs at Duke Primate Center, see Perry et al. (1992).
<i>Eulemur coronatus</i>	Twins and singletons are equally common, both in the wild (e.g., Ankarana) and in captivity.	For twinning in <i>Eulemur coronatus</i> in the wild, see Freed (1996); Petter and van der Sloot (2000). Twinning has been recorded for <i>Eulemur coronatus</i> in captivity; see Kappeler (1987), and records of the Duke Primate Center.
<i>Eulemur fulvus</i>	Twins occur occasionally in the wild (e.g., Ranomafana, Mt. d'Ambre, Berenty) and in captivity.	Overdorff et al. (1999) do not observe twinning in <i>Eulemur fulvus rufus</i> at Ranomafana. However, several pairs of twin <i>E. fulvus rufus</i> were recently observed at Ranomafana by D. Durham (personal communication). Twinning also occurs in <i>E. fulvus rufus</i> at Berenty (Berenty web site, 2002) and in <i>Eulemur fulvus sanfordi</i> at Mt. d'Ambre (Freed, 1996). For twinning in <i>Eulemur fulvus</i> in captivity, see Izard et al. (1994), and records of Duke Primate Center.
<i>Eulemur collaris</i> <i>Eulemur rubriventer</i>	Twins occur in captivity. Twins are born in the wild (e.g., Ranomafana) and in captivity.	Izard et al. (1994); see records of Duke Primate Center. For twinning in <i>Eulemur rubriventer</i> in the wild, see Overdorff (1996). For twinning in <i>E. rubriventer</i> in captivity, see Petter and van der Sloot (2000), and records of Duke Primate Center.
<i>Lemur catta</i>	Twins and occasionally triplets are born in the wild (e.g., Berenty) and in captivity.	For <i>Lemur catta</i> in the wild, see Koyama et al. (2001), and Jolly et al. (2002). For twinning in <i>Lemur</i> in captivity, see Van Horn and Eaton (1979), Pereira and Weiss (1991), Petter and van der Sloot (2000), records of Indianapolis Zoo, Hongshan Forestry Zoo (Nanjing, China), and Duke Primate Center.
<i>Hapalemur griseus</i>	In the wild, singletons are usually born. Twins sometimes occur in captivity.	For singleton births of <i>Hapalemur griseus</i> in the wild, see Tan (1999a). For twinning in captive <i>Hapalemur</i> , see Taylor and Feistner (1996, on <i>H. griseus alaotrensis</i>), records of Myakka City Free-Ranging Reserve, Florida (on <i>H. griseus griseus</i>), and records of Duke Primate Center.
<i>Hapalemur aureus</i> <i>Propithecus verreauxi</i>	In the wild, singletons are the norm. Singletons are born in the wild and in captivity.	See Norosoarainivo and Tan (1998). No twinning has been observed in <i>Propithecus</i> at Kirindy (P. Kappeler, personal communication), Beza Mahafaly (A. Richard and M. Schwartz, personal communication). No twinning has occurred in <i>Propithecus verreauxi</i> at Duke Primate Center (D. Haring, personal communication).
<i>Propithecus diadema</i>	Singletons are born in the wild.	No twinning has been observed for <i>Propithecus diadema</i> at Ranomafana, P. Wright (personal communication). This species has not reproduced in captivity.
<i>Propithecus tattersalli</i>	Singletons are born in the wild and in captivity.	No twinning has been observed for <i>Propithecus tattersalli</i> at Duke Primate Center (D. Haring, personal communication).
<i>Indri indri</i>	Singletons are born in the wild. <i>Indri</i> does not reproduce in captivity.	<i>Indri indri</i> twins have never been recorded in the wild. For reproduction in the wild, see Pollock (1975a), Petter et al. (1977), Thalmann et al. (1993), Petter and van der Sloot (2000), J. Powzyk (personal communication).
<i>Avahi laniger</i>	Singletons are born in the wild. <i>Avahi</i> does not reproduce in captivity.	Ganzhorn et al. (1985, personal communication) and Petter and van der Sloot (2000) report no twinning in wild <i>Avahi</i> .

the precarious nature of food resources in highly unpredictable climates (Wright, 1999; Richard et al., 2000, 2002). The climate of Madagascar is unusually unpredictable (Ganzhorn, 1995; Dewar and Wallis, 1999). Reproductive stress is a product of both energy availability and the competitive regime. Le-

murs are energy conservers apparently because energy availability is unreliable. Reducing maternal investment is one way to minimize reproductive costs and conserve energy. Our hypothesis is that the relatively low fetal and infant growth rates manifested in indriids do indeed reflect reduced mater-

TABLE 10. ANOVA for mean molar megadonty index in extant lemurs¹

Family ²	N of species	Mean molar megadonty index	Standard deviation
Indriidae	5	4.32	0.22
Lemuridae	6	3.67	0.28
Lepilemuridae	1	3.73	
Total	12	3.94	0.40

F = 9.34 (df 2, 9), $P < 0.01$

¹ Molar megadonty is measured here as: molar occlusal area (mesiodistal * buccolingual diameters for three upper and three lower molars, summed) divided by skull cross-sectional area (cranial length * bizygomatic breadth), and expressed as percentage.

² Taxa sampled here are, for Indriidae: *Indri indri*, *Propithecus verreauxi*, *Propithecus diadema*, *Propithecus tattersalli*, and *Avahi laniger*; for Lemuridae: *Lemur catta*, *Eulemur fulvus*, *Eulemur mongoz*, *Eulemur macaco*, *Varecia variegata*, and *Haplemur griseus*; and for Lepilemuridae: *Lepilemur ruficaudatus*.

nal investment, and their adaptive value lies in the energy they save for indriid mothers.

Juvenile growth rates are apparently correlated with infant growth rates among lemurs. Slow rates of growth continue in indriids after weaning. Glander et al. (1992) reported a mass of 43% of the mean adult value in a year-old wild *Propithecus diadema*, 58% of the adult value at age 2 years, and 78–90% of the adult value at age 3. In contrast, Leigh and Teranova (1998) showed that most lemurs achieve full adult mass at or around 2 years of age. Richard et al. (2002) reported that wild *Propithecus verreauxi* require 5 years to reach adult values for thigh length. Using skeletons of known or estimated age, King (2003) reported that the humeri and femora of *Propithecus verreauxi* attain near-adult values between 2–3 years, although the epiphyses do not fully fuse for years thereafter. King et al. (2001) also reported skeletal size in juvenile *Propithecus verreauxi* lagging well behind *Eulemur fulvus* and *Lemur catta* at standardized stages of (postweaning) dental development.

Adaptive significance of variation in age at first reproduction

As might be expected, those lemur species that exhibit relatively slow somatic growth tend to have relatively late first reproduction. Conversely, species with relatively rapid somatic growth tend to have relatively early first reproduction. However, in the case of lemurs, it is the more *frugivorous* (not folivorous) species that display the combination of more rapid growth and earlier reproductive maturation. Our hypothesis is that these differences reflect fundamentally different strategies for population maintenance. Of particular importance are responses to environmental catastrophes: cyclones, droughts, and the like.

In the life-history literature, variation in age at first reproduction is generally interpreted within the context of mortality schedules and life-history strategies. Comparative data on lemur mortality sched-

ules are limited. Those that exist do not offer strong support for the hypothesis that juvenile mortality from starvation is reduced in the more folivorous species (as predicted by the RAH). Indeed, among lemurs, juvenile mortality is often high for both leaf- and fruit-eaters. Infants are particularly vulnerable: typical values are 35.7–50% in *Eulemur fulvus rufus* (Overdorff et al., 1999); about 50% in *Eulemur rubriventer* (Overdorff, 1991; Mittermeier et al., 1994); 30–52% in *Lemur catta* (Sussman, 1991, 1992); 43% in *Propithecus diadema* (Wright, 1995); and 48% in *Propithecus verreauxi* (Richard et al., 2002). *P. verreauxi* infant mortality appears to peak shortly after birth and again around weaning (i.e., during the wet season; Richard et al., 2002). Juvenile mortality rates are not often reported. In three well-studied ringtail groups, juvenile mortality during a non-drought year was only 6% (Gould et al., 1999).

An interesting comparison can be made of sympatric *Lemur catta* and *Propithecus verreauxi* during a prolonged period of increasing aridity at Beza Mahafaly in southwest Madagascar (3 successive years of diminishing rainfall, culminating in a catastrophic drought during the years 1991–1992; Sauter, 1998; Gould et al., 1999; Richard et al., 2002). Ringtail lemur mortality was high across all life-cycle stages in 1992–1993. During the 1992–1993 birth and rearing season, infant mortality in *Lemur catta* was 80%, and more than half of the juveniles (57%) in three well-studied groups died during that time. Adults in the whole study population (nine groups) declined from a high of 85 in 1991 to a low of 51 in 1994 (a 27% loss), and the number of adult females fell from 48 to 27 (a 30% loss; see Gould et al., 1999). Lactating females were particularly vulnerable. An incredible 89% of the adult males disappeared in the 2 immediate postdrought years (either due to mortality or migration to another area). However, by 1995–1996, a population recovery was well underway. Infant mortality during the 1993–1994 resource-recovery year dropped precipitously (to 18%), and infants that survived the 1993 birth season reached sexual maturity in 1996. High annual birth rates (0.80–0.86), and a string of good years for fruit production, contributed to the population recovery.

Propithecus verreauxi reacted differently to the same drought (Richard et al., 2002). During the 1992 dry season, the proportion of adult females who gave birth dropped to 11% (well below the mean of 30%), and infant mortality during the 1992–1993 birth and rearing season rose to 66%. Adult female mortality also rose, primarily during the late dry season of 1992, to 20% from a “normal” level of around 10%, but rapidly fell back to around 10% in succeeding years. Survival among all age classes during the peak of the drought was higher in *Propithecus verreauxi* than in sympatric *Lemur catta*. The greatest impact of the drought on the *Propithecus* population at Beza was a dearth of infants born during its peak, and a doubling of the typically low level of adult

TABLE 11. Differing reproductive strategies in response to differing intensity of disturbance

Family	Low-intensity disturbance	Medium-intensity disturbance	High-intensity disturbance
Indriidae	Continue to produce low-cost offspring through period of disturbance.	Continue to produce low-cost offspring through period of disturbance.	Stop reproducing during period of disturbance; replenish population slowly through normal reproduction after habitat recovers.
Lemuridae	Continue to produce high-cost offspring through period of disturbance.	Stop reproducing during period of disturbance; replenish population through rapid reproduction after habitat recovers.	Stop reproducing during period of disturbance; replenish population through rapid reproduction after habitat recovers.

female mortality. Despite this drought-induced mortality spike, Richard et al. (2002) reported no significant correlation over the period from 1986–1999 between adult female (or male) mortality and rainfall.

A more intense climatic disturbance impacted a population of *Varecia variegata* at Manombo Forest in Eastern Madagascar. Cyclone Gretelle hit Manombo in January 1997, wiping out over half of the population's preferred food trees (Ratsimbazafy, 2002). *Varecia* seems to have survived this disaster, despite heavy losses, by dramatically decreasing activity levels and foraging opportunistically on shrub fruit. About half of the population of *Varecia* was lost in the immediate aftermath of the cyclone (Ratsimbazafy, personal communication). Reproduction was halted entirely for 5 years, after which, with the recovery of food resources, some infants were born (Ratsimbazafy, 2002). If, in the future, the population fully recovers, it will owe that recovery to an ability to replenish its population before the next intense disturbance, a task made easier by this species' extraordinarily high reproductive rates.

Strategies for population maintenance in indriids and lemurs

Indriids and lemurs appear to follow different strategies for population maintenance in an unpredictable environment. Indriids become ecological adults quickly: able to subsist on young leaves, and then unripe fruit, seeds, and mature leaves, at a relatively early age. Fibrous and hard-to-process (i.e., low "quality") foods are the mainstay of indriid diets, and young indriids rapidly become efficient food processors, with tiny jaws full of teeth. During resource crunches, the relatively low growth rates of young indriids may reduce the risk that they will starve. More importantly, slow infant growth coupled with relatively early weaning may reduce the burden on the mother during lactation. If population stability (or recovery after a disturbance) depends on a high probability of *adult* survival, then early reproductive maturation is not necessary. Indeed, female *Propithecus* are "bet-hedgers par excellence" (Richard et al., 2002, p. 431): trading the ability to grow and mature rapidly for reduced maternal cost

of reproduction, and long reproductive life spans (see also Wright, 1995).

Among lemurs, adults as well as juveniles may be at a greater risk of mortality under food crunches, due to their frugivorous diet. They appear to compensate for this increased risk by the ability to rebound quickly, through early reproductive maturation and a high reproductive recovery rate during good times. Lemurs grow and mature rapidly, but their dentitions develop on a slower schedule, because their preferred food resources can be processed by weanlings possessing little more than their milk dentitions.

We propose that the differing developmental schedules of indriids and lemurs may be different solutions to the ecological problem of environmental instability (periodically stressful environments). Year-to-year variation in climate and the fairly regular occurrence of catastrophes such as cyclones and droughts have led to reproductive adaptations to confront temporary dietary stress. Indriids appear to have evolved a "low maternal input, slow returns" strategy whereby fewer infants are produced, infants grow slowly, and the ability to survive on tough and fibrous foods is quickly achieved (due in part to rapid dental development). In contrast, lemurs appear to have evolved a "high maternal input, fast returns" strategy whereby more and faster-growing infants are produced, but adults require foods that provide more "ready" energy if they are to reproduce.

In order to understand the efficacy of each strategy in times of disturbance and resource scarcity, it is important to consider various intensities of disturbance (Table 11). Both strategies will have a "critical threshold" of resource availability, below which reproduction is not possible. However, one would expect this threshold to be reached much sooner for lemurs, given 1) the higher rate at which resources are invested in offspring, and 2) the higher reliance on reproductive plant parts which may be virtually or totally unavailable in times of environmental stress. Conversely, the indriid's threshold will be reached much later (i.e., they are more tolerant of environmental stress), as a result of 1) the lower resource input required by each off-

spring, and 2) their ability to consume high quantities of nonreproductive plant parts (leaves), which are less likely to be affected by environmental stress. Given these differences, one might predict that during a “medium-intensity” disturbance, indriids would implement a “slow and steady” strategy, continuing to reproduce at the normal rate. Lemurids, on the other hand, would implement a “catch-up” strategy, foregoing reproduction during the period of disturbance and capitalizing on their high potential reproductive rate to rapidly replenish populations once the environment recovered. Part of the catch-up strategy in lemurids may be their ability to twin. The “slow and steady” and “catch-up” strategies of indriids and lemurids, respectively, both seem to be adequate solutions to the problem of temporary, medium-intensity disturbance (as might occur frequently in an unpredictable environment). One would only predict significant differences between them in the highly unlikely situation of extremely prolonged medium-intensity disturbance (in which case, lemurids would perish, while indriids persisted).

It is interesting to note that, as the intensity of disturbance increases, these two strategies would tend to converge: under a “high-intensity” disturbance, one would expect both indriids and lemurids to experience reproductive failure. In this case, populations would be forced to wait until the environment had recovered sufficiently to allow normal reproduction. Indriids would be expected to begin their recovery sooner, given their different response threshold, while lemurids would be forced to wait longer before resuming reproduction, but would replenish populations at a faster rate. Due to the fact that it is the most intense disturbances which have warranted study as “disturbances” per se (Gould et al., 1999; Richard et al., 2002; Ratsimbazafy, 2002), one might not appreciate the true differences between the two strategies by considering these cases alone. Consequently, evidence for or against the existence of these strategies will not be found by considering only intense disturbances, but by examining variability in reproductive output over time. Two important predictions follow from these hypothesized strategies, that could be easily tested given long-term birth-rate data accompanied by climatic data. First, indriids should exhibit lower coefficients of variation in annual reproductive output (infants per female) than lemurids. Second, and more importantly, reproductive output (infants per female) should be more strongly correlated with climatic variables (e.g., total rainfall, diversity in monthly rainfall, or dry season length) for lemurids than for indriids. A tighter linkage between climate and reproduction in lemurids would imply that they tend to limit their reproduction to years with higher resource availability, effectively “waiting out” the bad times and “catching up” in the good times.

CONCLUSIONS

When tested for lemurs, the predictions of the risk aversion hypothesis regarding differences in growth rates of folivorous and frugivorous species do not hold. Whereas it is true that folivorous, seed-crunching anthropoids (such as colobus and leaf monkeys) grow and develop faster than like-sized anthropoid frugivores (such as macaques), the same is not the case for folivorous, seed-crunching lemurs. Indriids grow and develop less quickly than lemurids. Because the more frugivorous lemurids do not grow slowly, one cannot maintain that slow growth reduces the risk of juvenile mortality through starvation in these species. Folivory is not associated with rapid reproductive maturation or early age at first reproduction in lemurs. To the contrary, frugivorous lemurids tend to reproduce at a relatively earlier age.

Rapid dental development does characterize indriids, but it is superimposed on a matrix of relatively slow overall growth and development, and delayed female age at first reproduction. We suggest that dental development is more rapid in indriids than in lemurids because of the mechanical requirements of processing high-fiber foods.

In summary, notwithstanding its apparent success in explaining variation in rates of growth and development among many anthropoids, the ecological risk aversion hypothesis fares poorly when applied to lemurs. Frugivorous lemurs do not grow more slowly than like-sized folivorous lemurs. Reproductive maturation is not slower in frugivorous than folivorous lemurs. Infant and juvenile mortality may be high in fruit-eaters, but it is also elevated in leaf-eaters in times of food shortage. Lemurs might be said to conform to the expectations of the RAH only in that folivores exhibit more rapid dental development. But the risk aversion hypothesis does not single out *teeth* for rapid development, and other hypotheses are superior in accounting for unusually rapid dental development in folivorous lemur species. Instead, differences in the behavioral ontogeny of food processing and of food-processing requirements can better explain the observed differences between indriid and lemurid dental developmental schedules.

We believe that the key to understanding the differences in growth rates and age at first reproduction of lemurids vs. indriids may lie not in a comparison of the mortality rates of immature individuals alone, but in an examination of mortality rates across all life-cycle stages. Specifically, we propose that this variation reflects varying strategies for population maintenance in the face of frequent environmental disturbance, and is closely tied to the trade-off between adult female survival and reproductive effort. We suggest that indriids exhibit a “slow and steady” life-history strategy, continuing to produce offspring during medium-intensity disturbances, whereas lemurids exhibit a “catch-up”

strategy, forgoing reproduction during medium-intensity disturbances and relying on reproductive resilience in good years. These "slow and steady" and "catch-up" strategies both seem to be adequate solutions to the problem of temporary, medium-intensity disturbances.

Our research emphasizes the importance of phylogeny to life-history strategies: the alternative adaptive solutions described here are clade-specific, and very different from those observed in anthropoids. Diet *does* influence life-history strategies (contra Ross, 1998), as the indriid and lemurid developmental strategies are responses to the manner in which preferred resources are likely to behave under environmental stress. Ultimately, both indriids and lemurids may thrive under the same environmental stresses, but those stresses have very different effects on their preferred food resources, and seem to have led to divergent life-history strategies. Diet *does not* influence life-history strategies in lemurs in the manner predicted by the ecological risk aversion hypothesis.

ACKNOWLEDGMENTS

This project would not have been possible without the assistance of numerous people, for which we are grateful. For special help in supplying specimens or unpublished data, we are indebted to G. Gray Eaton, Kenneth Glander, D. Haring, Claire Hemingway, Stephen King, Steve Leigh, Lawrence B. Martin, Sheila O'Connor, Jonah Ratsimbazafy, Alison Richard, Gary Schwartz, Elwyn Simons, and Patricia C. Wright. This paper benefited from our discussions of life histories or various aspects of primate ontogeny with Ann Grady, Jukka Jernvall, Stephen King, Lawrence Martin, Andrew Petto, Alison Richard, Frank Williams, and Patricia Wright. Captive, semi-captive, and wild animal birth records, as well as other archival data on known-aged individuals, were compiled from the records of the following zoos, museums, and research facilities: American Museum of Natural History, New York; Duke University Primate Center; Field Museum of Natural History; Laboratoire de Paléontologie des Vertébrés, Université d'Antananarivo, Madagascar; Laboratoire de Zoologie, Muséum National d'Histoire Naturelle, Paris; Lowry Park Zoological Garden; Museum of Comparative Zoology at Harvard University; Muséum National d'Histoire Naturelle; Nationaal Natuurhistorisch Museum (formerly, the Rijksmuseum van Natuurlijke Historie), Leiden; Natural History Museum, London (formerly the British Museum (Natural History)); Oregon Regional Primate Center; Parc Ivoloina; Parc Tsimbazaza; Ranomafana National Park; San Diego Zoo; State University of New York at Stony Brook; United States National Museum, Smithsonian Institution; and the University of Massachusetts at Amherst. Specimens under the care of the following institutions were measured for this study: American Museum of Nat-

ural History, New York, NY; Duke University Primate Center, Durham, NC; Field Museum of Natural History, Chicago, IL; Laboratoire de Paléontologie des Vertébrés, Université d'Antananarivo, Madagascar; Museum of Comparative Zoology, Harvard University, Cambridge, MA; Muséum National d'Histoire Naturelle, Laboratoire de Zoologie (Mammifères et Oiseaux), Paris, France; Nationaal Natuurhistorisch Museum, Leiden, The Netherlands; Natural History Museum, Zoology Department, London, UK; Naturhistoriska Riksmuseet, Stockholm, Sweden; Mammals Department; Parc Tsimbazaza, Antananarivo, Madagascar; United States National Museum, Smithsonian Institution, Washington, DC; Department of Anthropology, University of Massachusetts, Amherst, MA; and the Zoologische Museum, University of Zürich, Zürich, Switzerland. We extend special thanks to the caretakers of the collections listed above, as well as to our many colleagues and friends in Madagascar (Berthe Rakotosamimanana, Gisèle Randria, Armand Rasoamiaramanana, Benjamin Andriamihaja, Albert Randrianjafy, and Gilbert Rakotoarisoa, among others) for their hospitality, assistance, and access to specimens at the Université d'Antananarivo and the Parc Tsimbazaza. For help with the generation of growth curves, we thank Abby Grace Drake (University of Massachusetts at Amherst) and Scott Bertrand (Originlabs, Northampton, MA). Peter Andrews generously supplied the radiographs of sifaka skulls that Luci Bettinash translated into the final version of Figure 2. Darren Godfrey helped with the generation of the final versions of Figures 6 and 7. Dental and morphometric data for this study were collected by K.E.S. and L.R.G.

LITERATURE CITED

- Albignac R. 1981. Variabilité dans l'organisation territoriale et l'écologie de *Avahi laniger* (Lémurien nocturne de Madagascar). C R Acad Sci [III] 292:331–334.
- Balko EA. 1995. Preliminary report on the ecological behavior of *Varecia variegata variegata* in Ranomafana National Park, Madagascar. Unpublished report.
- Bauchot R, Stephan H. 1966. Données nouvelles sur l'encéphalisation des insectivores et des prosimiens. Mammalia 30:160–196.
- Bollen K. 1996. The birth of ruffed lemur (*Varecia variegata*) triplets in a newly formed mixed species exhibit with ringtail lemurs (*Lemur catta*). Proc Natl Conf AAZK 22:1–11.
- Boskoff KJ. 1977. Aspects of reproduction in ruffed lemurs (*Lemur variegata*). Folia Primatol (Basel) 28:241–250.
- Britt A, Randriamandraronirina NJ, Glasscock KD, Iambana BR. 2002. Diet and feeding behaviour of *Indri indri* in a low-altitude rain forest. Folia Primatol 73:225–239.
- Brizzee KR, Dunlap WP. 1986. Growth. In: Dukelow WR, Erwin J, editors. Comparative primate biology, volume 3: reproduction and development. New York: Alan R. Liss, Inc. p 363–413.
- Brockman DK, Willis MS, Karesh WB. 1987. Management and husbandry of ruffed lemurs, *Varecia variegata*, at the San Diego Zoo. II. Reproduction, pregnancy, parturition, litter size, infant care and reintroduction of hand-raised infants. Zoo Biol 6:343–369.
- Campbell JL, Eisemann JH, Williams CV, Glenn KM. 2000. Description of the gastrointestinal tract of five lemur species: *Propithecus tattersalli*, *Propithecus verreauxi coquereli*, *Varecia variegata*, *Haplemur griseus*, and *Lemur catta*. Am J Primatol 52:133–142.

- Cartmill M, Brown K, Eaglen R, Anderson DE. 1979. Hand-rearing twin ruffed lemurs *Lemur variegatus* at the Duke University Primate Center. *Int Zoo Yrbk* 19:258–261.
- Charles-Dominique P, Hladik CM. 1971. *Le Lepilemur* du sud de Madagascar: écologie, alimentation et vie sociale. *Terre Vie* 25:3–66.
- Chivers DJ, Hladik CM. 1980. Morphology of the gastrointestinal tract in primates: comparisons with other mammals in relation to diet. *J Morphol* 166:337–386.
- Colquhoun IC. 1993. The socioecology of *Eulemur macaco*: a preliminary report. In: Kappeler PM, Ganzhorn JU, editors. *Lemur social systems and their ecological basis*. New York: Plenum. p 11–24.
- Cork SJ. 1996. Optimal digestive strategies for arboreal herbivorous mammals in contrasting forest types: why koalas and colobines are different. *Aust J Ecol* 21:10–20.
- Curtis DJ. 1997. The mongoose lemur (*Eulemur mongoz*): a study in behavior and ecology. Ph.D. dissertation, Universität Zürich, Zürich, Switzerland.
- Curtis DJ, Zaramody A. 1999. Social structure and seasonal variation in the behaviour of *Eulemur mongoz*. *Folia Primatol* (Basel) 70:79–96.
- Dew JL, Wright P. 1998. Frugivory and seed dispersal by four species of primates in Madagascar's eastern rain forest. *Biotropica* 30:425–437.
- Dewar RE, Wallis JR. 1999. Geographical patterning of interannual rainfall variability in the tropics and near tropics: an L-moments approach. *J Climate* 12:3457–3466.
- Digby LJ. 1999. Targeting aggression in blue-eyed black lemurs (*Eulemur macaco flavifrons*). *Primates* 40:613–617.
- Doyle GA. 1979. Development of behavior in prosimians with special reference to the lesser bushbaby, *Galago senegalensis moholi*. In: Doyle GA, Martin RD, editors. *The study of prosimian behavior*. New York: Academic Press. p 158–206.
- Drack S, Ortmann S, Bührmann N, Schmid J, Warren RD, Heldmeier G, Ganzhorn J. 1999. Field metabolic rate and the cost of ranging of the red-tailed sportive lemur (*Lepilemur ruficaudatus*). In: Rakotosamimanana B, Rasamimanana H, Ganzhorn JU, Goodman SM, editors. *New directions in lemur studies*. New York: Kluwer Academic/Plenum Publishers. p 83–91.
- Eaglen RH. 1985. Behavioral correlates of tooth eruption in Madagascar lemurs. *Am J Phys Anthropol* 66:307–315.
- Eaglen RH, Boskoff KJ. 1978. The birth and early development of a captive sifaka, *Propithecus verreauxi coquereli*. *Folia Primatol* (Basel) 30:206–219.
- Eisenberg JF. 1981. *The mammalian radiations: an analysis of trends in evolution, adaptation, and behavior*. Chicago: University of Chicago Press.
- Foerg R. 1982. Reproductive behaviour in *Varecia variegata*. *Folia Primatol* (Basel) 38:108–121.
- Frazier H, Hunt K. 1994. *Zoo infant development notebook, volume 1*. Topeka, KS: American Association of Zoo Keepers.
- Freed BZ. 1996. Co-occurrence among crowned lemurs (*Lemur coronatus*) and Sanford's lemurs (*Lemur fulvus sanfordi*) of Madagascar. Ph.D. dissertation, Washington University, St. Louis, MO.
- Freed BZ. 1999. An introduction to the ecology of daylight-active lemurs. In: Dolhinow P, Fuentes A, editors. *The nonhuman primates*. Mountain View, CA: Mayfield Publishing Co. p 123–132.
- Ganzhorn JU. 1988. Food partitioning among Malagasy primates. *Oecologia* 75:436–450.
- Ganzhorn JU. 1992. Leaf chemistry and the biomass of folivorous primates in tropical forests. *Oecologia* 91:540–547.
- Ganzhorn JU. 1993. Flexibility and constraints of *Lepilemur* ecology. In: Kappeler PM, Ganzhorn JU, editors. *Lemur social systems and their ecological basis*. New York: Plenum Press. p 153–165.
- Ganzhorn JU. 1995. Cyclones over Madagascar: fate or fortune? *Ambio* 24:124–125.
- Ganzhorn JU. 2002. Distribution of a folivorous lemur in relation to seasonally varying food resources: integrating quantitative and qualitative aspects of food characteristics. *Oecologia* 131: 427–435.
- Ganzhorn JU, Kappeler PM. 1996. Lemurs of the Kirindy Forest. In: Ganzhorn JU, Sorg JP, editors. *Ecology and economy of a tropical dry forest in Madagascar*. Primate report 46-1. Göttingen: E. Goltze. p 257–274.
- Ganzhorn JU, Abraham JP, Razanahoera-Rakotomalala M. 1985. Some aspects of the natural history and food selection of *Avahi laniger*. *Primates* 26:452–463.
- Ganzhorn JU, Fietz J, Rakotovoao E, Schwab D, Zinner D. 1999. Lemurs and the regeneration of dry deciduous forest in Madagascar. *Conserv Biol* 13:794–804.
- Garber PA, Leigh SR. 1997. Ontogenetic variation in small-bodied New World primates: implications for patterns of reproduction and infant care. *Folia Primatol* (Basel) 68:1–22.
- Garbutt N. 1999. *Mammals of Madagascar*. New Haven: Yale University Press.
- Glander KE, Wright PC, Seigler DS, Randrianasolo V, Randrianasolo B. 1989. Consumption of cyanogenic bamboo by a newly discovered species of bamboo lemur. *Am J Primatol* 19:119–124.
- Glander KE, Wright PC, Daniels PS, Merenlender AM. 1992. Morphometrics and testicle size of rain forest lemur species from southeastern Madagascar. *J Hum Evol* 22:1–17.
- 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 RF, Jungers WL, van Schaik CP, editors. *Reconstructing behavior in the primate fossil record*. New York: Kluwer Academic/Plenum Publishers. p 113–157.
- Goodman SM, O'Connor S, Langrand O. 1993. A review of predation on lemurs: implications for the evolution of social behavior in small, nocturnal primates. In: Kappeler PM, Ganzhorn JU, editors. *Lemur social systems and their ecological basis*. New York: Plenum. p 51–66.
- Gould L, Sussman RW, Sauther ML. 1999. Natural disasters and primate populations: the effects of a 2-year drought on a naturally occurring population of ring-tailed lemurs (*Lemur catta*) in southwestern Madagascar. *Int J Primatol* 20:69–84.
- Grassi C. 2001. The behavioral ecology of *Hapalemur griseus griseus*: The influences of microhabitat and population density on this small-bodied prosimian folivore (Madagascar). PhD dissertation. University of Texas, Austin, TX.
- Grieser B. 1992. Infant development and parental care in two species of sifakas. *Primates* 33:305–314.
- Harcourt C. 1991. Diet and behaviour of a nocturnal lemur, *Avahi laniger*, in the wild. *J Zool Lond* 223:667–674.
- Haring DM. 1990. Leaves and light: diet, housing, and reproduction in captive sifakas, *Propithecus verreauxi*. In: American Association of Zoological Parks and Aquariums, Wheeling, WV. 1990 Regional Proceedings. p 404–413.
- Hemingway CA. 1996. Morphology and phenology of seeds and whole fruit eaten by Milne-Edwards' sifaka, *Propithecus diadema edwardsi*, in Ranomafana National Park, Madagascar. *Int J Primatol* 17:637–659.
- Hemingway CA. 1998. Selectivity and variability in the diet of Milne-Edwards' sifakas (*Propithecus diadema edwardsi*). Implications for folivory and seed-eating. *Int J Primatol* 19:355–377.
- Hendrickx AG, Houston ML. 1971. Appendix: fetal growth. In: Hendrickx AG, editor. *Embryology of the baboon*. Chicago: University of Chicago Press. p 173–196.
- Hick U. 1976. Hand-rearing a ring-tailed lemur *Lemur catta* and a crowned lemur *Lemur mongoz coronatus* at Cologne Zoo. *Int ZooYrbk* 16:187–189.
- Hill WCO. 1953. *Primates—Strepsirhini*. Edinburgh: Edinburgh Press.
- Hill WCO. 1958. Pharynx, oesophagus, stomach, small and large intestine: form and position. *Primatologia* 3:139–147.
- Hladik CM. 1967. Surface relative du tractus digestif de quelques primates. Morphologie des villosités intestinales et corrélations avec le régime alimentaire. *Mammalia* 31:120–146.

- Hladik CM, Charles-Dominique P, Petter JJ. 1980. Feeding strategies of five nocturnal prosimians in the dry forest of the west coast of Madagascar. In: Charles-Dominique P, Cooper HM, Hladik A, Hladik CM, Pages E, Pariente GF, Petter-Rousseaux A, Schilling A, Petter JJ, editors. Nocturnal Malagasy primates: ecology, physiology, and behavior. New York: Academic Press. p 41–73.
- Izard MK, Coffman B, Katz A, Simons EL. 1993. Reproduction in the collared lemur (*Eulemur fulvus collaris*). *Am J Primatol* 30:320.
- Izard K, Savage C, Simons E. 1994. Reproduction in Sanford's lemur (*Eulemur fulvus sanfordi*). *Am J Primatol* 33:217.
- Janson C, van Schaik C. 1993. Ecological risk aversion in juvenile primates: slow and steady wins the race. In: Pereira ME, Fairbanks LA, editors. Juvenile primates: life history, development and behavior. New York: Oxford University Press. p 57–76.
- Jaquish CE, Toal RL, Tardif SD, Carson RL. 1995. Use of ultrasound to monitor prenatal growth and development in the common marmoset (*Callithrix jacchus*). *Am J Primatol* 36:259–275.
- Jolly AB. 1966. Lemur behavior. Chicago: University of Chicago Press.
- Jolly AB, Dobson A, Rasamimanana HM, Walker J, O'Connor S, Solberg M, Perel V. 2002. Demography of *Lemur catta* at Berenty Reserve, Madagascar: effects of troop size, habitat and rainfall. *Int J Primatol* 23:327–353.
- Jungers WL, Godfrey LR, Simons EL, Wunderlich RE, Richmond BG, Chatrath PS. 2002. Ecomorphology and behavior of giant extinct lemurs from Madagascar. In: Plavcan JM, Kay RF, Jungers WL, van Schaik CP, editors. Reconstructing behavior in the primate fossil record. New York: Kluwer Academic/Plenum Publishers. p 371–411.
- Kappeler PM. 1987. Reproduction in the crowned lemur (*Lemur coronatus*) in captivity. *Am J Primatol* 12:497–503.
- Kappeler PM. 1991. Patterns of sexual dimorphism in body weight among prosimian primates. *Folia Primatol (Basel)* 57: 132–146.
- Kappeler PM. 1996. Causes and consequences of life history variation among strepsirhine primates. *Am Nat* 148:868–891.
- Kappeler PM, Ganzhorn JU. 1993. The evolution of primate communities and societies in Madagascar. *Evol Anthropol* 2:159–171.
- Kerridge FJ. 1999. Part-time fostering by a pair of black and white ruffed lemurs (*Varecia variegata variegata*). *Anim Welfare* 8:35–42.
- Kirkwood JK, Stathatos K. 1992. Biology, rearing, and care of young primates. Oxford: Oxford University Press.
- King SJ. 2003. An evolutionary perspective on differential craniodental and postcranial growth and development in primates. Ph.D. dissertation, University of Massachusetts, Amherst.
- King SJ, Godfrey LR, Simons EL. 2001. Adaptive and phylogenetic significance of ontogenetic sequences in *Archaeolemur*, subfossil lemur from Madagascar. *J Hum Evol* 41:545–576.
- Klopfer PH, Boskoff KJ. 1979. Maternal behavior in prosimians. In: Doyle GA, Martin RD, editors. The study of prosimian behavior. New York: Academic Press. p 123–156.
- Koyama N, Nakamichi M, Oda R, Miyamoto N, Ichino S, Takahata Y. 2001. A ten-year summary of reproductive parameters for ring-tailed lemurs at Berenty, Madagascar. *Primates* 42:1–14.
- Leigh SR. 1994. Ontogenetic correlates of diet in anthropoid primates. *Am J Phys Anthropol* 94:499–522.
- Leigh SR, Terranova CJ. 1998. Comparative perspectives in bimaturism, ontogeny, and dimorphism in lemurid primates. *Int J Primatol* 19:723–749.
- Leutenegger W. 1973. Maternal fetal weight relationships in primates. *Folia Primatol (Basel)* 20:280–293.
- Luckett WP. 1984. Developmental evidence for toothcomb homology in the lemuriform primates *Propithecus* and *Lemur*. *Am J Phys Anthropol* 63:187–188.
- Meyers DM. 1993. The effects of resource seasonality on behavior and reproduction in the golden-crowned sifaka (*Propithecus tattersalli*, Simons, 1988) in three Malagasy forests. Ph.D. dissertation, Duke University, Durham, NC.
- Meyers DM, Wright PC. 1993. Resource tracking: food availability and *Propithecus* seasonal reproduction. In: Kappeler PM, Ganzhorn JU, editors. Lemur social systems and their ecological basis. New York: Plenum. p 179–192.
- Milne Edwards A, Grandidier G. 1875. Histoire physique, naturelle et politique de Madagascar: histoire naturelle des mammifères. Volume 9. Tome 4, atlas 1. Paris: Imprimerie Nationale.
- Mittermeier RA, Tattersall I, Konstant B, Meyers DM, Mast RB, editors. 1994. Lemurs of Madagascar. Washington, DC: Conservation International.
- Morland HS. 1989. Infant survival and parental care in ruffed lemurs (*Varecia variegata*) in the wild. *Am J Primatol* 18:157.
- Morland HS. 1990. Parental behavior and infant development in ruffed lemurs (*Varecia variegata*) in a northeast Madagascar rain forest. *Am J Primatol* 20:253–265.
- Morland HS. 1991. Social organization and ecology of black-and-white ruffed lemurs (*Varecia variegata variegata*) in a lowland rain forest, Nosy Mangabe, Eastern Madagascar. Ph.D. dissertation, Yale University, New Haven, CT.
- Muchlinski M, Overdorff DJ. 2001. Flowers and foliage: how important are these to lemurs? *Am J Primatol [Suppl]* 54:39.
- Mutschler T. 1999. Folivory in a small-bodied lemur: the nutrition of the Alaotran gentle lemur (*Hapalemur griseus alaotrensis*). In: Rakotosamimanana B, Rasamimanana H, Ganzhorn JU, Goodman SM, editors. New directions in lemur studies. New York: Kluwer Academic/Plenum Publishers. p 221–239.
- Nash LT. 1993. Juveniles in nongregarious primates. In: Pereira ME, Fairbanks LA, editors. Juvenile primates: life history, development, and behavior. Oxford: Oxford University Press. p 119–137.
- Nash LT. 1998. Vertical clingers and sleepers: seasonal influences on the activities and substrate use of *Lepilemur leucopus* at Beza Mahafaly Special Reserve, Madagascar. *Folia Primatol [Suppl] (Basel)* 69:204–217.
- Norosoarainivo JA, Tan CL. 1998. Infant care in *Hapalemur aureus*, Ranomafana National Park, Madagascar [abstract]. Congress of the International Primatological Society. Antananarivo, Madagascar: University of Antananarivo.
- Overdorff DJ. 1988. Preliminary report on the activity cycle and diet of the red-bellied lemur (*Lemur rubriventer*) in Madagascar. *Am J Primatol* 16:143–153.
- Overdorff DJ. 1991. Ecological correlates of social structure in two prosimian primates: *Eulemur fulvus rufus* and *Eulemur rubriventer* in Madagascar. Ph.D. thesis, Duke University, Durham, NC.
- Overdorff DJ. 1993. Similarities, differences, and seasonal patterns in the diets of *E. rubriventer* and *E. fulvus rufus* in Ranomafana National Park, Madagascar. *Int J Primatol* 14: 721–752.
- Overdorff DJ. 1996. Ecological correlates to activity and habitat use of two prosimian primates: *Eulemur rubriventer* and *Eulemur fulvus rufus* in Madagascar. *Am J Primatol* 40:327–342.
- Overdorff DJ, Strait SG. 1998. Seed handling by three prosimian primates in southeastern Madagascar: implications for seed dispersal. *Am J Primatol* 45:69–82.
- Overdorff DJ, Strait SG, Telo A. 1997. Seasonal variation in activity and diet in a small-bodied folivorous primate, *Hapalemur griseus*, in southeastern Madagascar. *Am J Primatol* 43: 211–223.
- Overdorff DJ, Merenlender AM, Talata P, Telo A, Forward ZA. 1999. Life history of *Eulemur fulvus rufus* from 1988–1992 in Southeastern Madagascar. *Am J Phys Anthropol* 108:295–310.
- Pereira ME. 1993. Seasonal adjustment of growth rate and adult body weight in ringtailed lemurs. In: Kappeler PM, Ganzhorn JU, editors. Lemur social systems and their ecological basis. New York: Plenum Press. p 205–221.
- Pereira ME. 1995. Development and social dominance among group-living primates. *Am J Primatol* 37:143–175.
- Pereira ME, Weiss ML. 1991. Female mate choice, male migration, and the threat of infanticide in ringtailed lemurs. *Behav Ecol Sociobiol* 28:141–152.
- Pereira ME, Klepper A, Simons EL. 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.
- Pereira ME, Strohecker RA, Cavigelli SA, Hughes CL, Pearson DD. 1999. Metabolic strategy and social behavior in Lemuridae. In: Rakotosamimanana B, Rasamimanana H, Ganzhorn JU, Goodman SM, editors. *New directions in lemur studies*. New York: Kluwer Academic/Plenum Publishers. p 93–118.
- Perry JM, Izard MK, Fail PA. 1992. Observations on reproduction, hormones, copulatory behavior, and neonatal mortality in captive *Lemur mongoz* (mongoose lemur). *Zoo Biol* 11:81–97.
- Petter J-J, van der Sloot J-H. 2000. Lemurs of Madagascar and the Comoros. World biodiversity database (CD-ROM series), Expert Center for Taxonomic Identification. Paris: UNESCO-Publishing.
- Petter J-J, Albignac R, Rumpler Y. 1977. Faune de Madagascar 44: Mammifères Lémuriens (Primates Prosimiens). Paris: Orstom.
- Petter-Rousseaux A. 1962. Recherches sur la biologie de la reproduction des primates inférieurs. *Mammalia [Suppl]* 26:1–88.
- Petter-Rousseaux A. 1964. Reproductive physiology and behavior of the Lemuroidea. In: Buettner-Janusch J, editor. *Evolutionary and genetic biology of primates*. Volume 2. London: Academic Press. p 91–132.
- Pochron ST, Tucker WT, Wright PC. In press. Demography, life history and social structure in *Propithecus diadema edwardsi* from 1986 to 2000 of Ranomafana National Park, Madagascar. *Am J Phys Anthropol*.
- Pollock JI. 1975a. The social behaviour and ecology of *Indri indri*. Ph.D. dissertation, University of London, London, UK.
- Pollock JI. 1975b. Field observations on *Indri indri*: a preliminary report. In: Tattersall I, Sussman RW, editors. *Lemur biology*. New York: Plenum. p 287–311.
- Pollock JI. 1977. The ecology and sociology of feeding in *Indri indri*. In: Clutton-Brock TH, editor. *Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys, and apes*. New York: Academic Press. p 38–71.
- Powzyk JA. 1996. A comparison of feeding strategies between the sympatric *Indri indri* and *Propithecus diadema diadema* in primary rain forest. *Am J Phys Anthropol [Suppl]* 22:190.
- Powzyk JA. 1997. The socio-ecology of two sympatric indriids: *Propithecus diadema diadema* and *Indri indri*. A comparison of feeding strategies and their possible repercussions on species-specific behaviors. Ph.D. dissertation, Duke University, Durham, NC.
- Prescott J. 1980. Breeding the brown lemur (*Lemur macaco fulvus*) at the Quebec Zoo. *Int Zoo Yrbk* 20:215–218.
- Randrianarisoa AJ. 1999. Estimation of food intake in wild Alaotran gentle lemurs *Hapalemur griseus alaotrensis*. *Dodo* 35: 171.
- Rasamimanana HR, Rafidinarivo E. 1993. Feeding behavior of *Lemur catta* in relation to their physiological state. In: Kappeler PM, Ganzhorn JU, editors. *Lemur social systems and their ecological basis*. New York: Plenum. p 123–134.
- Ratsimbazafy JH. 2002. On the brink of extinction and the process of recovery: responses of black-and-white ruffed lemurs (*Varecia variegata variegata*) to habitat disturbance in Manombo. Ph.D. dissertation, Stony Brook University, Stony Brook, NY.
- Ravosa MJ, Meyers DM, Glander KE. 1993. Relative growth of the limbs and trunk in sifakas: heterochronic, ecological, and functional considerations. *Am J Phys Anthropol* 92:499–520.
- Richard AF. 1976. Preliminary observations on the birth and development of *Propithecus verreauxi* to the age of six months. *Primates* 17:357–366.
- Richard AF. 1978. Behavioral variation: case study of a Malagasy lemur. Lewisburg, PA: Bucknell University Press.
- Richard AF, Dewar RE. 1991. Lemur ecology. *Annu Rev Ecol Syst* 22:145–175.
- Richard AF, Rakotomanga P, Schwartz M. 1991. Demography of *Propithecus verreauxi* at Beza Mahafaly: sex ratio, survival and fertility, 1984–1989. *Am J Phys Anthropol* 84:307–322.
- Richard AF, Rakotomanga P, Schwartz M. 1993. Dispersal by *Propithecus verreauxi* at Beza Mahafaly, Madagascar: 1984–1991. *Am J Primatol* 30:1–20.
- Richard AF, Dewar RE, Schwartz M, Ratsirarson J. 2000. Mass change, environmental variability and female fertility in wild *Propithecus verreauxi*. *J Hum Evol* 39:381–391.
- 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.
- Rigamonti M. 1993. Home range and diet in red ruffed lemurs (*Varecia variegata rubra*) on the Masoala Peninsula, Madagascar. In: Kappeler PM, Ganzhorn JU, editors. *Lemur social systems and their ecological basis*. New York: Plenum Press. p 25–39.
- Roberts M. 1994. Growth, development, and parental care in the western tarsier (*Tarsius bancanus*) in captivity: evidence for a “slow” life-history and nonmonogamous mating system. *Int J Primatol* 15:1–28.
- Rogers R. 1988. Nestbuilding behavior of the ruffed lemur: a longitudinal study at Miami Metrozoo. *Anim Keepers Forum* 15:483–493.
- Ross C. 1998. Primate life histories. *Evol Anthropol* 6:54–63.
- Ross C, Jones KE. 1999. Socioecology and the evolution of primate reproductive rates. In: Lee PC, editor. *Comparative primate socioecology*. Cambridge: Cambridge University Press. p 73–110.
- Ruempler U. 1993. 20 Jahre Lemurenhaus—30 Jahre Lemurenhaltung im Kölner Zoo. *Z Kolner Zoo* 36:127–155.
- Russell RJ. 1977. The behavior, ecology, and environmental physiology of a nocturnal primate, *Lepilemur mustelinus* (Strepsirhini, Lemuriformes, Lepilemuridae). Ph.D. dissertation, Duke University, Durham, NC.
- Samonds KE, Godfrey LR, Jungers WL, Martin LB. 1999. Primate dental development and the reconstruction of life history strategies in subfossil lemurs. *Am J Phys Anthropol [Suppl]* 28:238–239.
- Sauther ML. 1991. Reproductive behavior of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. *Am J Phys Anthropol* 84:463–477.
- Sauther ML. 1998. Interplay of phenology and reproduction in ring-tailed lemurs: implications for ring-tailed lemur conservation. *Folia Primatol [Suppl]* (Basel) 69:309–320.
- Scharfe F, Schlund W. 1996. Seed removal by lemurs in a dry deciduous forest of western Madagascar. In: Ganzhorn JU, Sorg JP, editors. *Ecology and economy of a tropical dry forest in Madagascar*. Primate report 46-1. Göttingen: E. Goltze. p 295–304.
- Schmid J, Ganzhorn JU. 1996. Resting metabolic rates of *Lepilemur ruficaudatus*. *Am J Primatol* 38:169–174.
- Schultz AH. 1937. Fetal growth and development of the rhesus monkey. *Contrib Embryol Carneg Inst* 26:71–97.
- 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.
- Shidler S, Lindburg D. 1982. Select aspects of *Lemur variegatus* reproductive biology. *Zoo Biol* 1:127–134.
- Smith BH, Crummett TL, Brandt KL. 1994. Ages of eruption of primate teeth: a compendium for aging individuals and comparing life histories. *Yrbk Phys Anthropol* 37:177–231.
- Smith RJ, Jungers WL. 1997. Body mass in comparative primatology. *J Hum Evol* 32:523–559.
- Smith RJ, Leigh SR. 1998. Sexual dimorphism in primate neonatal body mass. *J Hum Evol* 34:173–201.
- Sterling EJ. 1994. Evidence for nonseasonal reproduction in wild aye-ayes (*Daubentonia madagascariensis*). *Folia Primatol* (Basel) 62:46–53.
- Strait SG. 1997. Tooth use and the physical properties of food. *Evol Anthropol* 5:199–211.
- Sussman RW. 1974. Ecological distinctions in sympatric species of *Lemur*. In: Martin RD, Doyle GA, Walker AC, editors. *Prosimian biology*. London: Duckworth. p 75–108.
- Sussman RW. 1991. Demography and social organization of free-ranging *Lemur catta* in the Beza Mahafaly Reserve, Madagascar. *Am J Phys Anthropol* 84:43–58.

- Sussman RW. 1992. Male life history and intergroup mobility among ringtailed lemurs (*Lemur catta*). *Int J Primatol* 13:395–414.
- Tan CL. 1999a. Group composition, home range size, and diet of three sympatric bamboo lemur species (genus *Hapalemur*) in Ranomafana National Park, Madagascar. *Int J Primatol* 20: 547–566.
- Tan CL. 1999b. Life history and infant rearing strategies of three *Hapalemur* species. *Primate Rep [Special Issue]* 54–1:33.
- Tan CL. 2000. Behavior and ecology of three sympatric bamboo lemur species (genus *Hapalemur*) in Ranomafana National Park, Madagascar. Ph.D. dissertation, State University of New York at Stony Brook, Stony Brook, NY.
- Tattersall I. 1977. Behavioural variation in *Lemur mongoz* (= *L. m. mongoz*). In: Chivers DJ, Joysey KA, editors. Recent advances in primatology. Volume 3. London: Academic Press. p 127–132.
- Tattersall I. 1982. The primates of Madagascar. New York: Columbia University Press.
- Tattersall I, Sussman RW. 1975. Observations on the ecology and behavior of the mongoose lemur *Lemur mongoz mongoz* (Linnaeus, Primates, Lemuriformes) at Ampijoroa, Madagascar. Anthropological papers of the American Museum of Natural History 52:195–216.
- Taylor TD, Feistner ATC. 1996. Infant rearing in captive *Hapalemur griseus alaotrensis*: singleton versus twins. *Folia Primatol (Basel)* 67:44–51.
- Terranova CJ, Coffman BS. 1997. Body weights of wild and captive lemurs. *Zoo Biol* 16:17–30.
- Thalmann U, Geissmann T, Simona A, Mutschler T. 1993. The indris of Anjanaharibe-Sud, northeastern Madagascar. *Int J Primatol* 14:357–381.
- Tilden CD, Oftedal OT. 1997. Milk composition reflects pattern of maternal care in prosimian primates. *Am J Primatol* 41:195–211.
- Van Horn RN, Eaton GG. 1979. Reproductive physiology and behavior in prosimians. In: Doyle GA, Martin RD, editors. The study of prosimian behavior. New York: Academic Press. p 79–122.
- Vasey N. 1997. Community ecology and behavior of *Varecia variegata rubra* and *Lemur fulvus albifrons* on the Masoala Peninsula, Madagascar. Ph.D. dissertation, Washington University, St. Louis, MO.
- Warren RC, Crompton RH. 1997a. Locomotor ecology of *Lepilemur edwardsi* and *Avahi occidentalis*. *Am J Phys Anthropol* 104:471–486.
- Warren RD, Crompton RH. 1997b. A comparative study of the ranging behaviour, activity rhythms and sociality of *Lepilemur edwardsi* (Primates, Lepilemuridae) and *Avahi occidentalis* (Primates, Indriidae) at Ampijoroa, Madagascar. *J Zool Lond* 243:397–415.
- White FJ. 1991. Social organization, feeding ecology, and reproductive strategy of ruffed lemurs, *Varecia variegata*. In: Ehara A, Kimura T, Takenaka O, Iwamoto M, editors. Primatology today. Amsterdam: Elsevier Science Publishers. p 81–84.
- Whitten PL, Brockman DK. 2001. Strepsirrhine reproductive ecology. In: Ellison PT, editor. Reproductive ecology and human evolution. New York: Aldine de Gruyter. p 321–350.
- Wright PC. 1986. Diet, ranging behavior, and activity patterns of the gentle lemur (*Hapalemur griseus*) in Madagascar. *Am J Phys Anthropol* 69:283.
- Wright PC. 1987. Diet and ranging patterns of *Propithecus diadema edwardsi* in Madagascar. *Am J Phys Anthropol* 72:271.
- Wright PC. 1990. Patterns of parental care in primates. *Int J Primatol* 11:89–102.
- Wright PC. 1995. Demography and life history of free-ranging *Propithecus diadema edwardsi* in Ranomafana National Park, Madagascar. *Int J Primatol* 16:835–854.
- Wright PC. 1997. Behavioral and ecological comparisons of neotropical and Malagasy primates. In: Kinzey WG, editor. New World primates: ecology, evolution, and behavior. New York: Aldine de Gruyter. p 127–141.
- Wright PC. 1999. Lemur traits and Madagascar ecology: coping with an island environment. *Yrbk Phys Anthropol* 42:31–72.
- Yamashita N. 1996. Seasonality and site specificity of mechanical dietary patterns in two Malagasy lemur families (Lemuridae and Indriidae). *Int J Primatol* 17:355–387.
- Yamashita N. 1998a. Molar morphology and variation in two Malagasy lemur families (Lemuridae and Indriidae). *J Hum Evol* 35:137–162.
- Yamashita N. 1998b. Functional dental correlates of food properties in five Malagasy lemur species. *Am J Phys Anthropol* 106:169–188.
- Young AL, Richard AF, Aiello LC. 1990. Female dominance and maternal investment in strepsirrhine primates. *Am Nat* 135: 473–488.