CHAPTER TWENTY

Primate Bioenergetics: An Evolutionary Perspective

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INTRODUCTION

Energy dynamics represent an important interface between an organism and its environment. A variety of factors, including body mass, locomotor strategy, and foraging behavior, determine an animal's energy demands. Body mass is the most important determinant in predicting metabolic costs both for resting metabolic rate (RMR; the amount of energy used by an inactive animal under thermoneutral conditions) (Kleiber, 1961) and total daily energy costs (TEE or FMR) (Nagy, 1987; Nagy et al., 1999). The Kleiber (1961) scaling relationship correlates RMR with adult body mass and demonstrates that RMR scales to the three-quarters power of body mass in mammals, from the very small (e.g., mice) to the very large (e.g., elephants). While most mammals have RMRs predicted by body size, certain groups (e.g., marsupials, edentates) deviate significantly from this relationship.

Primates as a group do not significantly differ from the mammalian scaling relationship, though there exists a great deal of variation within the order. For example, strepsirrhines differ from other primates in having depressed RMRs from those predicted for their size based on the Kleiber

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scaling relationship. Although a number of explanations have been offered to explain hypometabolism[1] in strepsirrhines, the phenomenon remains enigmatic. At least four hypotheses for strepsirrhine hypometabolism have been proposed: (1) adaptation to arboreal folivory, (2) adaptation to a diet deviant for body size, (3) a thermoregulatory adaptation, and (4) phylogenetic inertia (i.e., hypometabolism is a primitive mammalian trait) (Kurland and Pearson, 1986; Ross, 1992). Since Kurland and Pearson's (1986) review of strepsirrhine[2] hypometabolism, RMR has been measured on numerous additional primate species, doubling the available data for strepsirrhines. Additional data are available on diet and ecology in primate species.

In this chapter, we examine data on resting metabolic rates from a large sample of primate species to investigate variation in RMRs within the primate order. First, we explore the nature of metabolic variation in strepsirrhines and haplorhines, specifically focusing on strepsirrhine hypometabolism. We then consider whether specific ecological factors, such as folivory, arboreality, or activity cycle (i.e., diurnal or nocturnal), can explain strepsirrhine hypometabolism. After evaluating these proximate explanations, we then examine whether strepsirrhine hypometabolism may be a primitive characteristic shared with other closely related mammalian species. Finally, the implications of primate metabolic variation and strepsirrhine hypometabolism for early primate evolution are addressed.

SAMPLE AND METHODS

We obtained information on body mass (kg) and RMR (kcal/day) for 41 primate species, including 17 species of strepsirrhine and 24 species of haplorhine from published sources, from which we calculated a single unweighted average for each species (Table 1). All RMR values are expressed as kilocalories per day (kcal/day) and were converted from other units when necessary.

Data on brain mass (g) and body mass (kg) for 15 strepsirrhine species and 21 haplorhines were obtained from Bauchot and Stephan (1969) and Stephan et al. (1981). For each species, we calculated a single unweighted average for both brain mass and body mass (Table 2). Humans were excluded from the

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[1] We follow Kurland and Pearson (1986) in defining hypometabolism as having a RMR more than 20% below that predicted for body size by the Kleiber scaling relationship. This conservative definition is used in order to avoid the misclassification of a species as hypometabolic as a result of measurement error, the measurement of an animal during sleep, or due to lack of standardized procedures.

[2] Kurland and Pearson (1986) used the traditional Prosimii–Anthropoidea taxonomic split but, since they did not include *Tarsius* in their analysis, there is no difference between their use of prosimian and our use of strepsirrhine.

Table 1. Sample information for primate metabolic and ecological data

Species	Metabolic data[a]			Ecological data[b]		
	RMR (kcal/day)	Body mass (kg)	Deviation[c]	DQ[d]	Habitat[e]	Activity cycle[f]
Suborder Strepsirrhini						
Arctocebus calabarensis	15.2	0.206	–28.99	327.5	A	N
Cheirogaleus medius	22.7	0.300	–20.00	–	A	N
Eulemur fulvus	42.0	2.397	–68.85	129.0	A	D
Euoticus elegantulus	25.1	0.260	–1.52	230.0	A	N
Galago moholi	13.9	0.155	–19.62	–	A	N
Galago senegalensis	18.1	0.215	–18.11	278.0	A	N
Galagoides demidoff	6.3	0.058	–23.85	305.0	A	N
Lemur catta	45.1	2.678	–69.22	166.0	A	D
Lepilemur ruficaudatus	27.6	0.682	–47.46	149.0	A	N
Loris tardigradus	14.8	0.284	–45.65	327.5	A	N
Microcebus murinus	4.9	0.054	–37.51	–	A	N
Nycticebus coucang	32.4	1.380	–63.65	–	A	N
Otolemur crassicaudatus	47.6	0.950	–29.33	195.0	A	N
Otolemur garnettii	47.8	1.028	–33.13	275.0	A	N
Perodicticus potto	41.3	1.000	–41.00	190.0	A	N
Propithecus verreauxi	86.8	3.080	–46.67	200.0	A	D
Varecia variegata	69.9	3.512	–61.08	–	A	D
Suborder Haplorhini						
Alouatta palliata	231.9	4.670	+4.28	136.0	A	D
Aotus trivirgatus	52.4	1.020	–26.25	177.5	A	N
Callithrix geoffroyi	27.0	0.225	+18.07	235.0	A	D
Callithrix jacchus	22.8	0.356	–29.23	235.0	A	D
Cebuella pygmaea	10.1	0.105	–21.78	249.5	A	D
Cercopithecus mitis	407.7	8.500	+17.00	201.5	T	D
Cercocebus torquatus	196.2	4.000	–0.90	234.0	A	D
Colobus guereza	357.9	10.450	–12.03	126.0	A	D
Erythrocebus patas	186.9	3.000	+17.13	–	T	D
Homo sapiens	1400.0	53.500	+1.10	–	T	D
Hylobates lar	123.4	1.900	+8.93	181.0	A	D
Leontopithecus rosalia	51.1	0.718	–6.41	–	A	D
Macaca fascicularis	400.9	7.100	+31.67	200.0	T	D
Macaca fuscata	485.4	9.580	+27.34	223.0	T	D
Macaca mulatta	231.9	5.380	–6.22	159.0	T	D
Pan troglodytes	581.9	18.300	–6.05	178.0	T	D
Papio anubis	342.9	9.500	–9.47	207.0	T	D
Papio cynocephalus	668.9	14.300	+29.95	184.0	T	D
Papio papio	297.3	6.230	+7.70	–	T	D
Papio ursinus	589.3	16.620	+2.27	189.5	T	D
Pongo pygmaeus	569.1	16.200	+0.68	172.5	A	D
Saguinus geoffroyi	50.5	0.500	+21.43	263.0	A	D
Saimiri sciureus	68.8	0.850	+11.03	323.0	A	D
Tarsius syrichta	8.9	0.113	–34.80	350.0	A	N

[a] McNab and Wright (1987); Leonard and Robertson (1994); Thompson et al. (1994); Kappeler (1996).

[b] Richard (1985); Sailer et al. (1985); Nowak (1991); Napier and Napier (1994); Rowe (1996).

[c] Metabolic deviation from predicted by Kleiber equation.

[d] Dietary quality.

[e] A = primarily arboreal; T = primarily terrestrial.

[f] D = diurnal; N = nocturnal.

Table 2. Sample information for primate brain data

Species	Brain mass (g)[a]	Body mass (kg)[a]
Suborder Strepsirrhini		
Arctocebus calabarensis	7.2	0.323
Cheirogaleus medius	3.1	0.177
Eulemur fulvus	25.2	2.397
Euoticus elegantulus	7.2	0.274
Galago senegalensis	4.8	0.186
Galagoides demidoff	3.4	0.081
Lemur catta	25.6	2.678
Lepilemur ruficaudatus	7.6	0.682
Loris tardigradus	6.6	0.322
Microcebus murinus	1.8	0.054
Nycticebus coucang	12.5	0.800
Otolemur crassicaudatus	10.3	0.850
Perodicticus potto	14.0	1.150
Propithecus verreauxi	26.7	3.480
Varecia variegata	34.2	3.512
Suborder Haplorhini		
Alouatta palliata	51.0	6.400
Aotus trivirgatus	16.0	0.850
Callithrix geoffroyi	7.6	0.280
Callithrix jacchus	7.6	0.280
Cebuella pygmaea	4.5	0.140
Cercopithecus mitis	76.0	6.500
Cercocebus torquatus	104.0	7.900
Colobus guereza	73.0	7.000
Erythrocebus patas	118.0	8.000
Hylobates lar	102.0	6.000
Macaca fascicularis	74.0	5.500
Macaca fuscata	84.0	5.900
Macaca mulatta	110.0	8.000
Pan troglodytes	420.0	46.000
Papio anubis	205.0	26.000
Papio cynocephalus	195.0	19.000
Papio papio	190.0	18.000
Papio ursinus	190.0	18.000
Pongo pygmaeus	370.0	55.000
Saguinus geoffroyi	10.0	0.380
Saimiri sciureus	22.0	0.680

[a] Bauchot and Stephan (1969); Stephan et al. (1981).

analysis because they are outliers for brain size in relation to body size and consequently substantially alter regressions. Because of differences between the body masses of animals used for brain studies and those for metabolic studies, when comparing metabolic rates to brain size, we calculated an adjusted RMR for each species to account for this difference.

Information on dietary quality (DQ) was obtained for 12 strepsirrhine and 20 haplorhine species (Table 1) from Richard (1985), Rowe (1996) and Sailer et al. (1985). Diet quality was assessed using an index, developed by Sailer et al. (1985), which considers the relative energy and nutrient density of dietary items. The DQ index is a weighted average of the proportions of foliage, reproductive plant material, and animal material. The DQ is calculated as:

$$\mathrm{DQ} = s + 2(r) + 3.5(a).$$

Here s = percent of diet derived from structural plant parts (e.g., leaves, stems, and bark), r = percent of diet derived from reproductive plant parts (e.g., fruits, flowers, nectar, and resin), and a = percent of diet derived from animal parts (including both vertebrates and invertebrates). The DQ ranges from a minimum of 100 (100% foliage) to a maximum of 350 (100% animal material). Humans were excluded from the dietary analysis because the range of possible diets is larger than any nonhuman primate species, and consequently an all-inclusive DQ for the human species is not possible.

To assess functional consequences of substrate and habitat use, we classified species as arboreal or terrestrial based on primary habitat (Table 1); this determination was derived from relevant literature (Nowak, 1991; Rowe, 1996). While this dichotomy is overly simplified, it is used simply to get a general picture of habitat use. Additionally, we obtained information on activity cycle (i.e., nocturnal or diurnal) from published sources for all 17 species of strepsirrhine and all 24 haplorhine species (Rowe, 1996; Table 1).

To examine the evolutionary context of RMR in primates, we compiled metabolic data for closely related mammalian orders. We obtained information on RMR (kcal/day) and body mass (kg) for bats (order Chiroptera) and tree shrews (order Scandentia) from published sources, from which we calculated a single unweighted average for each species (Table 3). No metabolic data were available for colugos (order Dermoptera). All RMR values are expressed as kilocalories per day (kcal/day) and were converted from other units when necessary.

We compiled data on body mass (kg) estimates for 16 species of subfossil Malagasy lemurs from Godfrey et al. (1997; Table 4). Body mass reconstructions, based on regressions of humeral and femoral midshaft circumferences

Table 3. Sample information for RMR and body mass for selected mammalian species

Species	RMR (kcal/day)[a]	Body mass (kg)[a]
Order Chiroptera		
Anoura caudifer	4.07	0.012
Artibeus lituratus	9.82	0.070
Carollia perspicilla	3.64	0.015
Chalinolobus gouldii	2.92	0.018
Chrotopterus auritus	11.80	0.096
Cynopterus brachyotis	5.45	0.037
Desmodus rotundus	3.06	0.029
Diaemus youngi	3.99	0.037
Diphylla ecaudata	3.96	0.028
Dobsonia minor	12.71	0.087
Eonicterus spelaea	5.61	0.052
Glossophaga longirostris	3.07	0.014
Glossophaga soricina	2.50	0.010
Hipposideros galeritus	1.08	0.009
Histiotus velatus	1.16	0.011
Leptonycteris curasoae	3.95	0.024
Leptonycteris sanborni	5.10	0.022
Macroderma gigas	10.94	0.107
Macroglossus minimus	2.39	0.016
Megaloglossus woermanni	2.52	0.012
Miniopterus schreibersii	3.01	0.011
Molossus molossus	4.61	0.056
Noctilio albiventris	2.75	0.027
Noctilio leporinus	5.44	0.061
Nyctimene albiventer	4.64	0.028
Nyctophilus geoffroyi	1.32	0.008
Nyctophilus major	2.36	0.014
Paranyctimene raptor	3.36	0.021
Phyllostomus discolor	4.06	0.034
Phyllostomus elongatus	4.55	0.036
Phyllostomus hastatus	8.18	0.084
Pteropus poliocephalus	36.74	0.598
Pteropus scapulatus	28.12	0.362
Rhinonycteris aurantius	1.88	0.008
Rhinophylla fisherae	1.88	0.010
Rousettus aegyptiacus	14.22	0.146
Sturnira lilium	4.56	0.022
Syconycteris australis	3.92	0.018
Tonatia bidens	4.48	0.027
Uroderma bilobatum	3.08	0.016
Order Scandentia		
Ptilocercus lowii	5.04	0.058
Tupaia glis	10.84	0.123

[a]Bradley and Hudson (1974); Whittow and Gould (1976); McNab (1988); Arends et al. (1995); Geiser et al. (1996); Hosken (1997); Hosken and Withers (1997, 1999); Bartels et al. (1998); Baudinette et al. (2000).

Table 4. Reconstructed body masses (kg) and cranial capacities (cc) for selected subfossil Malagasy lemur species

Species	Body mass (kg)[a]	Cranial capacity (cc)[b]
Family Archaeolemuridae		
Archaeolemur edwardsi	22.0	104[c,d]
Archaeolemur majori	17.0	
Hadropithecus stenognathus	28.0	
Family Daubentoniidae		
Daubentonia robusta	10.0	
Family Lemuridae		
Pachylemur insignis	10.0	
Pachylemur jullyi	12.5	46[c]
Family Megaladapidae		
Megaladapis edwardsi	75.0	
Megaladapis grandidieri	65.0	
Megaladapis madagascariensis	40.0	118[c]
Family Palaeopropithecidae		
Archaeoindris fontoynontii	200.0	
Babakotia radofilai	15.0	49[d]
Mesopropithecus dolichobrachion	12.0	
Mesopropithecus globiceps	10.0	
Mesopropithecus pithecoides	11.0	
Palaeopropithecus ingens	45.0	
Palaeopropithecus maximus	55.0	99[c]

[a]Godfrey et al. (1997).
[b]Ravosa (unpublished data).
[c]British Museum (Natural History).
[d]Duke University Primate Center.

indicate that the subfossil lemurs were all larger than living strepsirrhine primates. Some species had body masses slightly greater than the largest living strepsirrhines (*Indri indri* and *Propithecus diadema*) (Smith and Jungers, 1997); however, all known species appear to have had body masses of at least 10 kg (Godfrey et al., 1997). Numerous species were considerably larger, including *Archaeoindris fontoynontii*, which is estimated to have reached an adult mass of 200 kg. We additionally present data on cranial capacity (cc) for five species of subfossil Malagasy lemur, which were collected by M. Ravosa (unpublished data) (Table 4).

Allometric relationships were determined using ordinary least squares regressions (OLS)[3] of $\log_{10}$-transformed data. Additionally, allometric relationships were calculated using reduced major axis (RMA); however, RMA values are not reported because they were not significantly different from parameters calculated using OLS. Differences in regression parameters were assessed using Student's t-tests. All analyses were performed using SPSS (Version 8.0), except RMA equations, which were calculated using BIOMstat (Version 3.30a).

RESULTS

Metabolic Variation in Strepsirrhines and Haplorhines

Metabolic rates in the strepsirrhines are significantly lower than those predicted by the Kleiber scaling relationship, averaging 38.6 ± 4.7% *below* the norm (Table 1). The range of predicted values for strepsirrhines is from −1.52 to −69.22% below those predicted by the Kleiber scaling relationship, and 14 of the 17 strepsirrhine species are hypometabolic by criteria described above (i.e., >20% below predicted by Kleiber scaling relationship). *Euoticus elegantulus*, *Galago moholi*, and *Galago senegalensis* are the three strepsirrhine species not classified as hypometabolic, with metabolic deviations from those predicted by Kleiber scaling relationship of −1.52, −19.62, and −18.11%, respectively. Within strepsirrhines, lorisiforms (lorises, pottos, and bushbabies) ($n = 10$) have RMRs that average 30.5% below predicted, while the lemuriforms (Malagasy lemurs) ($n=7$) average 50.1% below predicted. Bushbabies (Galagonidae) ($n = 6$) are slightly hypometabolic averaging 20.9% below predicted.

The relationship between RMR and body mass in strepsirrhines significantly differs in both scaling coefficient (slope) and y-intercept from the haplorhine regression ($P < 0.001$) (Figure 1). Differences in metabolic rates are also evident from the standardized residuals (z-scores) of the RMR to body mass regression for the pooled sample. Mean z-scores are significantly lower in strepsirrhines than haplorhines ($P<0.001$). The strepsirrhine regression substantially deviates from the Kleiber scaling relationship. The scaling relationship in the strepsirrhines is: $\mathrm{RMR}=36.3\mathrm{M}^{0.56}$, whereas in haplorhines the relationship is: $\mathrm{RMR}=66.4\mathrm{M}^{0.80}$; the latter is almost identical to the Kleiber scaling relationship prediction (i.e., $\mathrm{RMR}=70\mathrm{M}^{0.75}$). Haplorhines average 1.9 ± 3.8% *above* predicted values and do not significantly differ from Kleiber scaling relationship predictions. The relationship between body mass and RMR for the combined sample of primates ($n=41$) is $\mathrm{RMR}=54.7\mathrm{M}^{0.81}$.

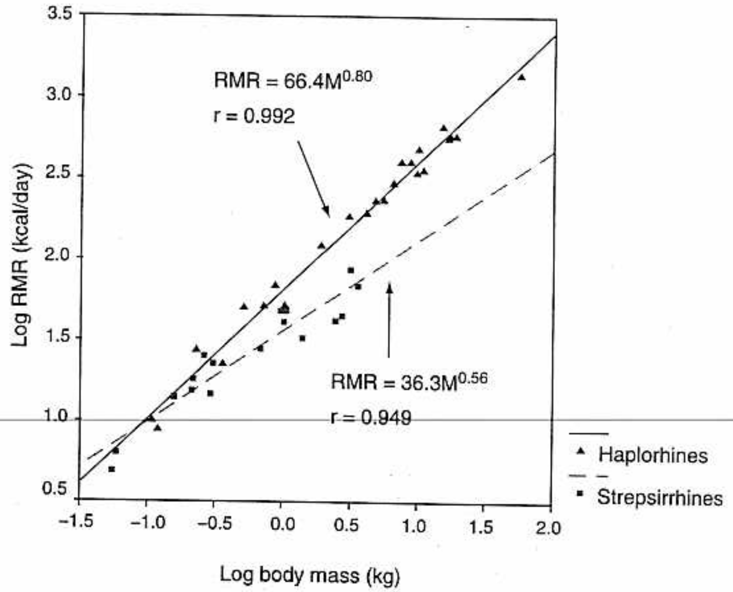

Figure 1. Log_{10} plot of RMR (kcal/day) versus body mass (kg) for strepsirrhine species ($n=17$) and haplorhine species ($n=24$). The strepsirrhine regression has a significantly lower scaling coefficient than predicted by the Kleiber equation ($\mathrm{RMR}=70\mathrm{M}^{0.75}$).

Ecological Correlates of Strepsirrhine Hypometabolism

Hypometabolism is often observed in species consuming a nutrient-poor (low quality) diet (Kurland and Pearson, 1986; McNab, 1986). In the present sample, relatively lower DQ is associated with depressed metabolic rates in both strepsirrhine ($n=12$) and haplorhine primates ($n=20$). However, while variation in DQ helps to explain within-group differences in RMR, the

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[3] There has been debate in the anthropological literature in recent years regarding the most appropriate line fitting technique for describing allometric equations; some favor the use of ordinary least squares regressions (OLS), some the major axis (MA), and others the reduced major axis (RMA). OLS may underestimate the true slope (when the coefficient of determination [r^2] is low) because it does not consider error in the X variable (Harvey and Pagel, 1991). However, the preferable method for accurate and effective controls (especially with high r^2 values) for the effects of body mass is OLS (Harvey and Pagel, 1991), which we use in this study.

metabolic differences between strepsirrhines and haplorhines cannot be explained by dietary differences.

All strepsirrhines are primarily arboreal, including *Lemur catta*, which spends roughly 25% of its time on the ground (Martin, 1990). Across all primates, arboreal species ($n = 30$) have significantly lower metabolic rates than terrestrial species ($n = 11$) (−24.1% versus 10.2%) ($P < 0.001$). However, even after controlling for habitat use, strepsirrhines ($n = 17$) have significantly lower metabolic rates than arboreal haplorhines ($n = 13$) (−38.6 ± 4.7% versus −5.2 ± 5.1%; $P < 0.001$). Both arboreal haplorhines and terrestrial haplorhines ($n = 11$) significantly differ from strepsirrhines ($P < 0.001$).

The relationship between activity cycle (i.e., nocturnal or diurnal) and body mass to deviation from predicted RMR among species demonstrates that the degree of hypometabolism is significantly greater among the larger species. The diurnal[4] strepsirrhine species ($n = 4$), of which all are Malagasy lemurs, have the largest body sizes and have significantly lower metabolic rates than the nocturnal strepsirrhine species ($n = 13$) (61.5% versus −31.5%; $P < 0.01$).

Metabolic Variation and Body Composition

The relationship between brain mass and body mass in strepsirrhine ($n = 15$) and haplorhine species ($n = 21$) demonstrates that strepsirrhines have relatively smaller brains than haplorhine species (Figure 2). The scaling coefficient for strepsirrhine species is significantly lower than that of the haplorhines (0.75 versus 0.64; $P < 0.05$). Additionally, the y-intercept of strepsirrhines is significantly lower than haplorhines ($P < 0.001$). The relative size difference in brain mass of strepsirrhines and haplorhines is also evident from the z-scores of the brain mass to body mass regression for the pooled sample. Mean z-scores are significantly lower in strepsirrhines than haplorhines ($P < 0.001$).

When the relationship of brain size and RMR in strepsirrhines ($n = 15$) and haplorhines ($n = 21$) is examined, the scaling coefficients for the strepsirrhine and haplorhine regressions are comparable and both scale isometrically (1.02 versus 0.96; n.s.). This suggests that both groups spend similar proportions of RMR on brain metabolism and that species with different body sizes have similar relationships between brain size and RMR. The y-intercepts in strepsirrhines and haplorhines are not significantly different. Additionally, strepsirrhines do not significantly differ from haplorhines in mean z-scores of the brain mass to RMR regression for the pooled sample.

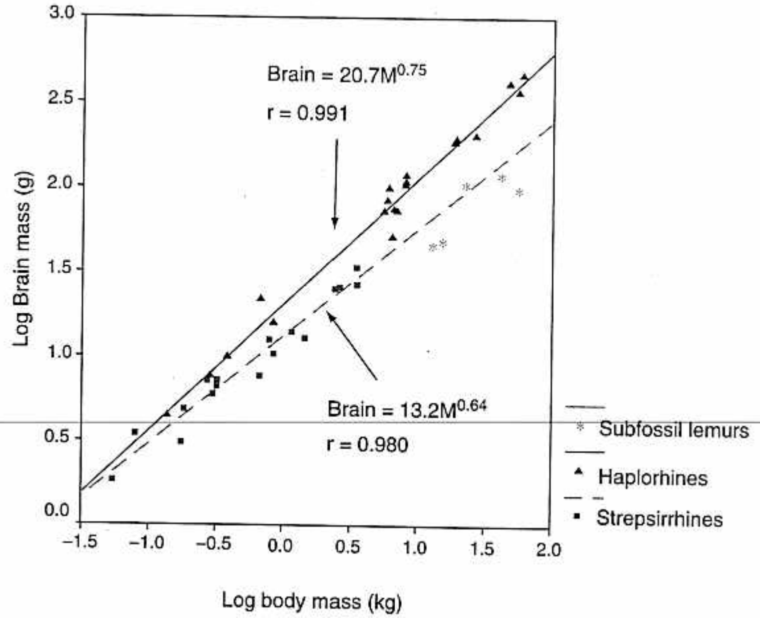

Figure 2. Log_{10} plot of brain mass (kg) versus body mass (kg) for strepsirrhine species ($n = 15$) and haplorhine species ($n = 21$; humans excluded). The scaling coefficient for strepsirrhine species is significantly lower than that of the haplorhines (0.75 versus 0.64; $P < 0.05$). Asterisks represent values for subfossil Malagasy lemurs based on reconstructions (Table 4).

Phylogenetic Influences on Strepsirrhine Hypometabolism: Comparative Metabolic Data

From our previous analyses, it appears that proximate ecological factors do not provide a full explanation for strepsirrhine hypometabolism. Consequently, we next considered whether the distinctive metabolic pattern of strepsirrhines is a primitive trait that is shared with other closely related mammalian species. To evaluate this explanation, we considered metabolic data for selected nonprimate species (Figure 3).

In the two studies of RMR in tree shrews that were conducted under standardized conditions, both species measured were shown to be hypometabolic by above criteria. *Ptilocercus lowii*, the only nocturnal tree shrew species and

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[4] One of these species, *Eulemur fulvus*, is more appropriately classified as "cathemeral," which reflects its activity period both during the day and night (Fleagle, 1999); it has been collapsed into the category "diurnal" to allow statistical treatment.

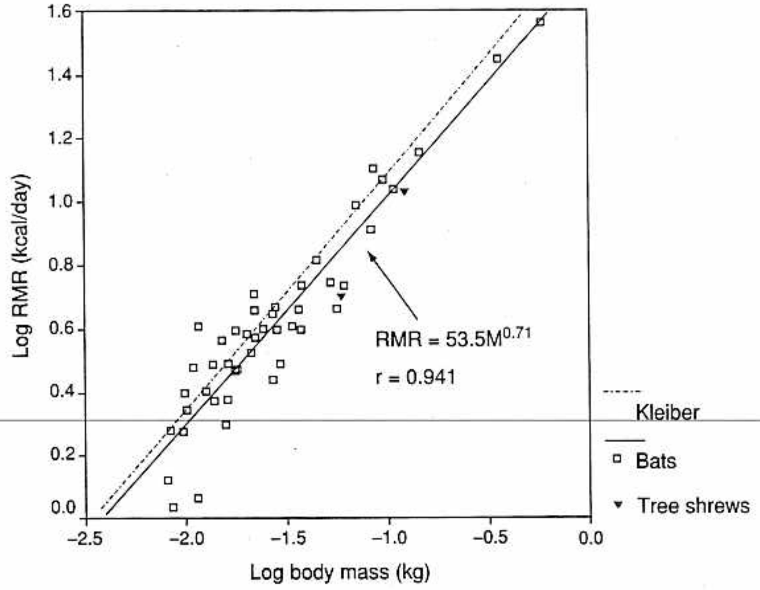

Figure 3. Log_{10} plot of RMR (kcal/day) versus body mass (kg) for selected bat (order Chiroptera; $n=46$) and tree shrew (order Scandentia; $n=2$) species. Also shown is the Kleiber equation ($RMR=70M^{0.75}$).

one of the few that is also predominantly arboreal, has an RMR 39.1% below that predicted by the Kleiber equation (Whittow and Gould, 1976). *Tupaia glis*, which is diurnal and partially terrestrial (Martin, 1990; Nowak, 1991), is also hypometabolic and has an RMR 25.5% below that predicted by the Kleiber equation.[5]

Bats have metabolic rates that average 10% below those predicted by the Kleiber equation, though this masks considerable variation found within the order. Bats are not hypometabolic by previously described criteria. The scaling relationship between RMR and body mass in bats is: $RMR = 53.5M^{0.71}$. Microbats ($n=34$) have metabolic rates nearly identical to megabats (family Pteropodidae; $n=12$) and a similar range of variation in body size is seen within the two groups. Microbats on average deviate from that predicted by the Kleiber equation by −10% and megabats deviate by on average −9%.

[5] The body mass for this species is not given in the original publication (Bradley and Hudson, 1974) and was obtained from McNab (1988).

Phylogenetic Influences on Strepsirrhine Hypometabolism: Implications for Subfossil Lemurs

The extant lemurs of Madagascar are diverse in species number, morphological adaptation, and ecology, but there is evidence that this diversity was much larger in the recent past (Godfrey and Jungers, 2002; Mittermeier et al., 1994; Simons, 1997). Known primarily from recent paleontological sites (i.e., "subfossils"), there is evidence for at least 17 species representing at least five families of extinct lemurs: Archaeolemuridae, Daubentoniidae, Lemuridae, Megaladapidae, and Palaeopropithecidae (Godfrey and Jungers, 2002). Only two of these, Daubentoniidae and Lemuridae, have living representatives. Humans initially colonized Madagascar only about 2000 years ago and are implicated in the extinction event of numerous lemur species, as well as three species of hippopotamus, two species of bibymalagasy, a medium-sized carnivore, two genera of flightless birds, and a species of giant tortoise (Garbutt, 1999). Human activities, such as hunting, habitat alteration, introduction of nonnative species (e.g., wild cattle), and possibly, the introduction of nonnative diseases, likely played a major role in the extinction. There is also some evidence that Late Holocene climatic changes might have contributed to the extinctions. The range of dates for subfossil lemurs runs from about 26,000 years BP (*Megaladapis* from Antsiroandoha Cave in northern Madagascar) to about 500 years BP for *Palaeopropithecus* from Manamby Plateau in southwest Madagascar (Simons, 1997). Additionally, there is a historical report that suggests the presence of a large-bodied lemur in Madagascar in the 17th century (Flacourt, 1658). Ethnographic sources also suggest that a large-bodied lemur might have survived in Madagascar into the 20th century (Burney and Ramilisonina, 1999). By all indication, the subfossil and extant lemurs are part of the same contemporary fauna and the former should not be considered as ancestors of the latter (Mittermeier et al., 1994).

All of the subfossil lemurs, with the exception of *Daubentonia robusta* (a relative of the aye-aye), are thought to have been diurnal, based on relative orbit size and body size (Simons, 1997). An enormous range of locomotor diversity is seen in the subfossil lemurs, but it seems likely that, based on body size and postcranial morphology, most of the subfossil lemurs likely spent at least some time on the ground (Godfrey et al., 1997). Certain groups, such as *Hadropithecus* and *Archaeolemur*, may have spent considerable time on the ground (Godfrey et al., 1997). With the possible exception of *D. robusta*, all extinct lemur species likely included some leaves in their diet, supplementing this diet with fruit, seeds, and possibly fauna. Many of the larger species are inferred to be highly folivorous on the basis of both body size and morphological adaptations.

Body mass reconstructions, based on regressions of humeral and femoral midshaft circumferences indicate that the subfossil lemurs were all larger than living strepsirrhine primates (Godfrey et al., 1997; Table 4). Some species had body masses slightly greater than the largest living strepsirrhines (*Indri indri* and *Propithecus diadema*) (Smith and Jungers, 1997); however, all known species appear to have had body masses of at least 10 kg (Godfrey et al., 1997). Numerous species were considerably larger, including *Archaeoindris fontoynontii*, which is estimated to have reached an adult body mass of about 200 kg.

The RMR predictions for 16 species of subfossil lemur are presented in Figure 4 and are based on body masses reconstructed for subfossil taxa (Table 4). For a given body mass, we calculated RMR based on the Kleiber scaling relationship ($70M^{0.75}$) and a strepsirrhine-only regression from this study ($36.3M^{0.56}$), which assumes that the subfossil lemurs were hypometabolic (based on the retention of the primitive condition). Assuming metabolic rates similar to those seen in living strepsirrhines, there would have been considerable energy savings in all species, which would have been amplified at larger body sizes. For example, in the largest of the subfossil lemurs, *A. fontoynontii*, with an estimated body mass of 200 kg, would have had an RMR (using the strepsirrhine-only regression) of only about 20% of that predicted by Kleiber scaling relationship. This energy savings likely would have been further amplified through low-total energy costs, as is likely based on morphological evidence, which indicates a highly folivorous sloth-like creature that probably spent considerable time on the ground (Simons, 1997). One of the consequences of depressed metabolic rates is that they may have had the effect of limiting competition for resources (McNab, 1980). However, there are also reproductive consequences of depressed metabolic rates as there is some indication that mammalian species with depressed metabolic rates also have low-intrinsic rates of population increase (McNab, 1980, 1986).

Data on cranial capacity for five species of subfossil lemurs (Table 4) demonstrated a similar scaling relationship of brain size and body mass as in extant strepsirrhines (Figure 2). *M. madagascariensis* and *P. maximus* have similar body masses (40 kg and 55 kg, respectively) as common chimpanzees (*P. troglodytes*) though their brain sizes are only about one-quarter the size. However, there is variation in the subfossil lemurs in relative brain size; data from *A. edwardsi* indicate that it was relatively encephalized when compared to the larger subfossil lemurs. These results are in general agreement with Jungers (1999), and demonstrate that strepsirrhines have larger brains than similar-sized mammals but considerably smaller brains than haplorhine primates. This may be the result of physiological limitations in supporting brain metabolism (Armstrong, 1983, 1985).

It seems likely that the earliest strepsirrhine colonizers of Madagascar were hypometabolic and small bodied. Purvis (1995) suggests that mouse and dwarf lemurs of the family Cheirogaleidae are the most ancestral of

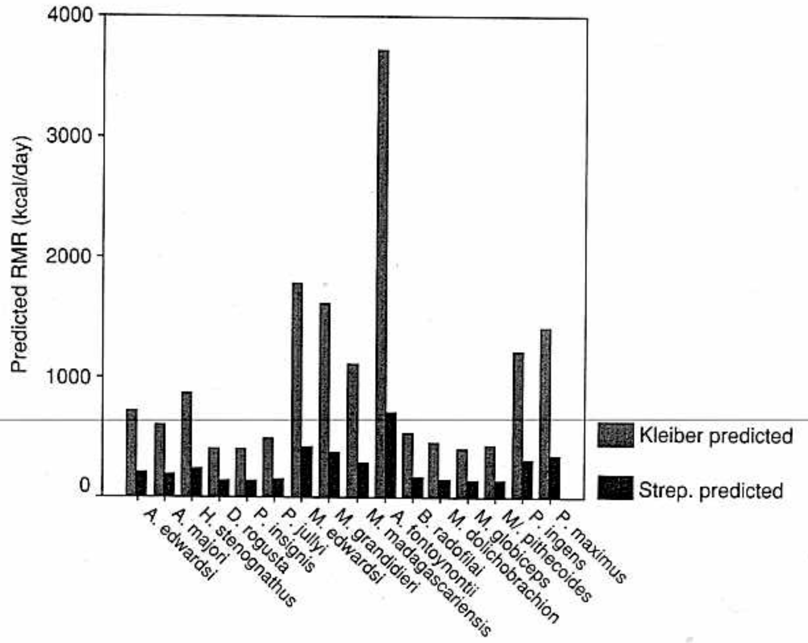

Figure 4. Predicted RMR (kcal/day) for selected subfossil Malagasy lemurs based on reconstructed body weights from Godfrey et al. (1997). Gray bars represent predicted RMRs based on the Kleiber scaling relationship ($70M^{0.75}$) and black bars represent predicted RMRs based on the strepsirrhine regression ($36.3M^{0.56}$).

extant lemurs and, on these grounds, it seems likely that the initial colonizers of Madagascar were small-bodied and later diversified in terms of body size. However, this evidence is currently untestable given the dearth of pre-Holocene primate fossils from Madagascar. Depressed metabolic rates and the ability to enter torpor may also have increased chances of survival during a transoceanic rafting to Madagascar from Africa (Kappeler, 2000; Warren and Crompton, 1996). These low-metabolic rates may have had important consequences for the survival and diversification of Malagasy primates.

DISCUSSION

Ecological Correlates of Primate Metabolic Variation

Although primates do not significantly differ from other mammals in the scaling of body mass and metabolic rate, there is considerable variation within the order. Haplorhines, as a group, have a scaling relationship similar to other mammals. In contrast, strepsirrhines are hypometabolic and have a scaling relationship that markedly deviates from that of haplorhines and other mammals. Indeed, all strepsirrhine species have RMRs lower than those predicted for body mass based on the Kleiber scaling relationship.

A number of ecological factors, such as low-quality diet, arboreality, and nocturnality, have been linked with hypometabolism, both in strepsirrhines and other mammalian groups (Kurland and Pearson, 1986; McNab, 1978, 1980, 1986; Ross, 1992). In these explanations, adaptations to particular ecological factors are postulated to have led to depressed metabolic rates.

Hypometabolism, which slows passage rates to allow increased nutrient extraction, has been linked to low-quality diets associated with the inclusion of large amounts of foliage (McNab, 1978, 1980, 1986). This may be particularly important in the smaller species with folivorous diets. It has also been suggested that depressed metabolic rates allow a species to consume greater quantities of toxic insects without experiencing deleterious effects (Charles-Dominique, 1977; McNab, 1980, 1986; Oates, 1984).

Our examination of the role of low-diet quality in hypometabolism produced mixed results. Strepsirrhine species with low-quality diets for body size tended to have depressed metabolic rates, suggesting that hypometabolism in this group is partially influenced by low-diet quality, particularly in the larger species. Depressed metabolic rates also appear to be associated with low-quality diets in haplorhines; species with lower quality diets than predicted for body size have lower metabolic rates than predicted for body size. However, the regressions describing the relationship for each group are parallel, and thus, dietary differences alone cannot explain the metabolic differences between strepsirrhines and haplorhines.

McNab (1978, 1986) also raises the possibility that folivory in the context of an arboreal habitat may differentially depress metabolic rates in certain mammalian groups, including primates. Specifically, the depressed metabolic rates of arboreal folivores may be attributable to a combination of factors, including a low-quality diet, relatively sedentary habits, and the consequent decreases in skeletal muscle mass (McNab, 1978, 1986). Our results suggest that, like diet, habitat does exert a significant influence on metabolic rates, as arboreal species have lower RMRs than terrestrial species. However, among only arboreal species, strepsirrhines have significantly lower metabolic rates than haplorhines. *Lemur catta*, the strepsirrhine that spends the largest proportion of time on the ground, is also the most hypometabolic of the strepsirrhines (−69.22% from predicted), though the confounding effects of body mass and diet make it difficult to separate out habitat preference. While there is some support for a model that considers both low-dietary quality and arboreality in strepsirrhines, it cannot explain metabolic rates in some species, including some haplorhines. For example, *Alouatta palliata*, a folivorous and arboreal haplorhine, has a metabolic rate slightly above that predicted by Kleiber scaling relationship (+4.28%). Additionally, hominoids, such as *Pongo pygmaeus* and *Hylobates lar* have low-quality diets, but have RMRs (+0.68 and +8.93%, respectively) at or slightly above that predicted for body size.

The results presented in the current study indicate that there is a relationship between depressed metabolic rates and lower dietary quality in both strepsirrhines and haplorhines, but the metabolic differences between strepsirrhines and haplorhines cannot be explained by dietary differences alone. In fact, as discussed previously, the regressions that describe the relationships in each of the groups are parallel. These results echo those of Leonard and Robertson (1994), but with an enlarged sample size.

Another ecological variable that has been discussed in reference to hypometabolism is waking cycle, largely because of its importance in the context of thermoregulation. A relatively low RMR has been proposed to be a thermoregulatory adaptation in strepsirrhines (Charles-Dominique, 1974; Müller and Jaksche, 1980) and in certain haplorhine species, such as *Aotus* *trivirgatus* (Le Maho et al., 1981). It is suggested that this adaptation would be seen in well-insulated animals living in tropical environments with high-daytime temperatures and low-nighttime temperatures. In this view, nocturnal activity increases heat production during the coldest part of the 24-h cycle, while inactivity during the day reduces heat production during the hottest part of the 24-h cycle. This hypothesis is a continuation of a larger literature that suggests that strepsirrhines use behavioral adjustments, such as reduced activity levels and sunning behavior, in order to efficiently thermoregulate (e.g., Morland, 1993). It has been proposed that the cathemeral behavior of *Eulemur fulvus*, which is active at night during the cool dry season, is an adaptation to minimize cold stress and energy costs (Curtis et al., 1999). Thus, the thermoregulatory hypothesis for strepsirrhine hypometabolism predicts that depressed RMRs in well-insulated, nocturnal primates living in hot environments are the result of thermoregulatory adaptations.

Data from the study demonstrate that among strepsirrhines, nocturnal species have relatively higher RMRs than diurnal species, rather than lower as would be predicted by the thermoregulatory model. This difference, however, may be partially an artifact of body size and diet, as the diurnal species are the four largest of the strepsirrhines and additionally are some of the most folivorous. It should be noted that the two nocturnal haplorhine species, *Aotus trivirgatus* and *Tarsius syrichta*, have RMRs that fall substantially below those predicted by the Kleiber scaling relationship, but both are also relatively small bodied. Interestingly, *Aotus* and *Tarsius* are thought to be secondarily nocturnal (Martin, 1990). While current data do not support the thermoregulatory hypothesis, a recent colonization of the diurnal niche has been suggested for the diurnal (and cathemeral) strepsirrhines (Ross, 1996; van Schaik and Kappeler, 1996), which could partially explain metabolic rates of these diurnal strepsirrhines.

In summary, none of the ecological arguments entirely explain the level of hypometabolism observed in strepsirrhines. Depressed metabolic rates are exhibited by strepsirrhines of a range of body sizes, with diverse dietary strategies, and different activity patterns and waking cycles. While it is clear that adaptations to proximate ecological factors, such as diet, play a role in structuring metabolic costs, these factors cannot entirely explain hypometabolism in strepsirrhines.

Phylogenetic Influence on Primate Metabolic Variation

In addition to proximate ecological factors, phylogenetic inertia has been suggested as an explanation for hypometabolism in strepsirrhines and other mammal groups (e.g., Eisentraut, 1961; Elgar and Harvey, 1987; Martin, 1989; Ross, 1992). This hypothesis suggests that hypometabolism is a primitive mammalian trait that has been retained in extant strepsirrhines. While Kurland and Pearson (1986) discuss the possibility that strepsirrhines are hypometabolic because of phylogenetic inertia, they do not test this hypothesis. Ross (1992) lends some support to the role of phylogenetic effects on strepsirrhine hypometabolism, though problems with the methodology[6] preclude acceptance of her results.

The results of the present study provide support for the phylogenetic inertia model, but an understanding of the metabolic rates of closely related species is important to test this hypothesis. The superorder Archonta was originally proposed by Gregory (1910) to contain primates, bats (order Chiroptera), colugos or "flying lemurs" (order Dermoptera), and the tree shrews and elephant shrews (order Menotyphla). McKenna (1975) later removed the elephant shrews leaving primates, colugos, bats, and tree shrews (order Scandentia) in the superorder. The superorder Archonta has been the subject of numerous investigations, using morphological studies of living species, paleontological studies, and molecular investigations (see review in Sargis, 2002). The validity of Archonta has received its greatest support from the result of comparative studies of skeletal characters of the ankle region (e.g., Szalay, 1977). However, testing the integrity of Archonta is problematic because of the dearth of fossil evidence in all but the primates. Additionally, the use of morphological traits that are primitive or convergent (rather than shared derived characters), has led to false support for Archonta (Martin, 1990).

No consensus exists on the integrity of Archonta as a monophyletic unit, but there are data both from morphological and molecular studies that support the close relationship of primates with other mammalian orders.

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[6] Ross (1992) compared metabolic data for primates with a regression generated by Stahl (1967). The Stahl regression is not based on 349 mammalian species, as claimed by Ross, but 349 data points. The paper does not provide information on which species were used and the number of data points for each and, additionally, does not control for animals in the resting condition. The scaling coefficient is higher and, consequently, Ross' calculations of metabolic deviations are invalid.

However, a number of recent studies have not supported Archonta as a monophyletic group, but instead support close relationships between subsets of the members. In particular, Euarchonta, which includes primates, colugos, and tree shrews (but not bats) has received support from molecular studies (Adkins and Honeycutt, 1991, 1993; Madsen et al., 2001; Murphy et al., 2001a,b; Stanhope et al., 1993), as well as combined morphological and molecular evidence (Liu and Miyamoto, 1999; Liu et al., 2001). Interestingly, some studies have indicated a close evolutionary relationship between Euarchonta and Glires (rodents and lagomorphs), together forming Euarchontoglires (Madsen et al., 2001; Murphy et al., 2001a,b).

Metabolic data for members of the superorder Archonta were available for tree shrews and bats. Unfortunately, no metabolic data are available for colugos. Both tree shrews and bats have, on average, lower metabolic rates than similar-sized mammals according to the Kleiber scaling relationship. In the two studies of RMR in tree shrews that were conducted under standardized conditions, both species measured were shown to be hypometabolic. *Ptilocercus lowii*, a nocturnal and arboreal tree shrew species, has an RMR 39.1% below that predicted by the Kleiber equation. *Tupaia glis*, which is diurnal and partially terrestrial (Martin, 1990; Nowak, 1991), is also hypometabolic and has an RMR 25.5% below that predicted by Kleiber scaling relationship. Both species are omnivorous and include various amounts of insects and fruits as the main items in their diet (Martin, 1990). Tree shrews have often been used as models of early primate morphology and behavior (and were classified by some authorities [e.g., Simpson, 1945] at one time as members of the primate order), largely because of their inferred close phylogenetic relationship and certain morphological similarities shared with primates. However, there is a good deal of morphological and behavioral variation between species of tree shrew, and many of the shared morphological traits may actually be either primitive or convergent (Martin, 1990). That said, there are indications from both molecular and morphological studies that Scandentia is closely related to primates, possibly as a sister group.

Bats have metabolic rates that average 10% below those predicted by the Kleiber equation, though this average masks considerable variation found within the order. While bats have metabolic rates lower than expected, they are not hypometabolic by previously described criteria. The scaling relationship between RMR and body mass in bats is: RMR = $53.5M^{0.71}$. Microbats ($n = 34$) have metabolic rates nearly identical to megabats (family Pteropodidae; $n = 12$) and a similar range of variation in body size is seen in the two groups. Microbats on average deviate from that predicted by the Kleiber equation by −10%, whereas megabats deviate by on average −9%. Despite these low-metabolic rates, bats have the highest capacity gas exchange system found in living mammals (Szewczak, 1997).

The phylogenetic position of tarsiers among primates makes them an important group to examine in the phylogenetic argument since they possess numerous primitive mammalian traits that were subsequently lost in anthropoids (Martin, 1990). Molecular studies, using protein and DNA sequence evidence (Bonner et al., 1980; DeJong and Goodman, 1988; Dijan and Green, 1991; Koop et al., 1989a,b; Miyamoto and Goodman, 1990; Pollock and Mullin, 1987; Porter et al., 1995; Shoshani et al., 1996; Zietkiewicz et al., 1999), lend support to the classification of tarsiers as a sister clade of the anthropoids, both subsumed within the suborder Haplorhini. Additionally, many morphological studies based on derived features support the grouping of tarsiers as haplorhines (Beard et al., 1991; Martin, 1990; Ross, 1994; Szalay et al., 1987).

The only tarsier species with available metabolic measurements taken under standardized conditions is *Tarsius syrichta*, which has an RMR well below (−34.8%) that predicted by the Kleiber equation. Tarsiers are nocturnal, arboreal, and small-bodied, and the only primates that consume 100% animal material (mostly insects and some vertebrates). The depressed metabolic rates of tarsiers may be the result of the retention of a primitive mammalian trait, as is hypothesized for the strepsirrhines.

Taken as whole, metabolic rates in the closest living relatives of primates provide some evidence for hypometabolism as a primitive trait that has been retained in living strepsirrhines. However, further resolution of primate superordinal relationships, as well as further studies of metabolism in close relatives, are needed.

The phylogenetic explanation is often used as an unenlightening nonexplanation (e.g., Hayssen and Lacy, 1985), but in order to fully understand phylogenetic inertia as an explanation, the reasons for the evolution of hypometabolism must be addressed. Additional questions that must be addressed are why hypometabolism was maintained in descendant lineages and whether there was active selection to maintain it in the extant species, or whether it was retained because there was not active selection against it.

Unfortunately, it is often difficult to unravel the effects of phylogeny from current adaptations, since phylogenetically close animals also tend to have similarities in both ecology and biology (Elgar and Harvey, 1987; McNab, 1986).

Body Composition and Primate Metabolic Variation

Differences in body composition are important in influencing variation in metabolic energy requirements, given marked differences in mass-specific metabolic rates across tissues. Muscle mass, for example, varies from 24 to 61% of total body weight in mammals, with slow-moving arboreal mammals, such as sloths, occupying the low end and terrestrial carnivores, such as lions, occupying the high end (Calder, 1984; Grand, 1977; Muchlinski et al., 2003). McNab (1978) postulates that the depressed RMRs of arboreal mammals are partly the result of low levels of muscularity. Thus, variation in tissue size and concomitant variation in tissue metabolic rates contribute to the structuring of energy costs and provide a mechanism for deviations from predicted metabolic rates.

The relative size of the brain has been linked by a number of researchers to metabolic rate, since both scale to the three-quarters power of body mass (i.e., 0.75) (Armstrong, 1983, 1985; Hoffman, 1983; Martin, 1981, 1996). While some have hypothesized that brain size and its associated high tissue metabolic rates partially structure RMR (e.g., Holliday, 1986), others have taken the opposite approach and hypothesized that metabolic rates influence brain size (e.g., Armstrong, 1983, 1985). The latter relates to a proposed relationship between the size of the brain and the ability of the body to support brain metabolism. Martin's (1981) maternal energy hypothesis is an extension of this reasoning and postulates that brain size is related to maternal metabolic rate. The relatively small brains of strepsirrhines (compared to haplorhines) could be related to depressed metabolic rates in strepsirrhine females and specifically to the transfer of nutrients during pregnancy and lactation. Importantly, the corollary is that the evolution of higher metabolic rates in anthropoids (or possibly in haplorhines, depending on the position of tarsiers) may have allowed these animals to grow and support relatively larger brains. Strepsirrhines invest less in the prenatal development of their offspring than haplorhines, but when controlled for metabolic rate, this difference disappears (Richard and Dewar, 1991; Young et al., 1990). Female feeding priority is also most common in strepsirrhines, especially those with low-metabolic rates, and this has been suggested to help females cope with high maternal energy costs associated with reproduction (Richard and Dewar, 1991).

The study clearly demonstrates that strepsirrhines are less encephalized than haplorhines for any given body size. However, the available primate data also show that the relationship between brain size and RMR is comparable between the two groups. This result suggests that strepsirrhines and haplorhines spend comparable proportions of their RMR on brain metabolism; this supports the conclusions of Armstrong (1985), who used a smaller sample of species. It is possible that the lower levels of encephalization in strepsirrhines relative to haplorhines may be a consequence of metabolic stress (i.e., the low-metabolic rates of strepsirrhines are unable to support relatively large brains). However, this picture is overly simplistic since numerous species deviate from the brain size to RMR relationship. Additionally, as noted by Martin (1996), the range of variation in the relationship between brain size and body mass exceeds that between RMR and body mass. Finally, humans have extraordinarily large brains that account for roughly 20–25% of RMR but do not have elevated RMRs compared to those predicted for body mass (Leonard and Robertson, 1994). How this could have evolved has been the subject of intense debate (e.g., Aiello and Wheeler, 1995; Leonard and Robertson, 1994).

Implications for Models of Primate Origins

The nature and origins of metabolic variation in strepsirrhines and haplorhines have important implications for our understanding of the ecology and evolution of the earliest primates. For any given size, primates and other mammals consume considerably more energy than similar-sized reptiles. Mammals have total daily energy costs that average about 17 times that of comparably sized reptiles (Nagy, 1987).

The earliest true primates appeared in the Late Paleocene and Early Eocene and are defined by a suite of cranial and postcranial features not present in the plesiadapiforms or other mammals. While once considered within the primate order (as archaic primates), plesiadapiforms have recently been removed (Fleagle, 1999; Martin, 1990; Rose, 1995). Some authorities place the plesiadapiforms with colugos within the order Dermoptera (Beard, 1993), while others consider them a separate mammalian order (Fleagle, 1999). In fact, all plesiadapiforms with the exception of *Purgatorius* are too derived dentally to be ancestral to living primates (Rose, 1995). The first true primates (i.e., Euprimates) show a suite of derived cranial characters, such as orbital convergence and frontation, which are associated with increased reliance on vision. They also show derived postcranial features, such as nails instead of claws, and grasping hands and feet, which have been linked to increased manipulative abilities within an arboreal environment. The earliest fossils attributed to primates are highly fragmentary but nonetheless show characters that link them with living primates (Rose, 1995). These species include *Altiatlasius koulchii* from the Late Paleocene of Morocco and *Altanius orlovi* from the Early Eocene of Mongolia (Fleagle, 1999; Rose, 1995). *Altiatlasius* is thought to have had a body size on the order of between 50 and 100 g, while *Altanius* is thought to have had a body size of about 10 g. These fossils appear to be more primitive and generalized than adapoids or omomyoids. Early mammalian forms were similarly small bodied and all appear to have been under 500 g. Fossils of *Hadrocodium wui* from the Early Jurassic of China had an adult body weight estimated to be about 2 g (Luo et al., 2001), while other groups were slightly larger, (e.g., *Morganucodon*, at 27–89 g and *Sinoconodon*, at 13–517 g; Luo et al., 2001).

The Eocene primates are typically divided into two major groups, the adapoids (superfamily Adapoidea) and the omomyoids (superfamily Omomyoidea) (Fleagle, 1999). The former have been compared to living lemurs in certain aspects of craniodental and postcranial morphology, while the latter have been likened to living tarsiers; however, the exact phylogenetic relationship with living primates remains unclear (Martin, 1990). While both groups exhibit considerable diversity, the earliest members of each are similar in many aspects. Some of the earliest genera include *Donrussellia* and *Cantius* of the adapoids and *Teilhardina* and *Steinius* of the omomyoids (Rose, 1995). Reconstructed body size of *D. provincialis* was about 140 g (Rose, 1995), though some of the other species may have been slightly larger (210–730 g; Fleagle, 1999). *Cantius* is thought to have been considerably larger and had a body mass range on the order of 1–3 kg for nine species (Fleagle, 1999). *Teilhardina*, like most other omomyoids, was small bodied, with estimates for the genus (four species) ranging from 60 to 135 g in adult body size (Fleagle, 1999; Rose, 1995). *Steinius* was on the order of about 300–400 g (Fleagle, 1999). Adapoids later diversified and obtained body sizes up to 7–8 kg (Fleagle, 1999). Some exhibited sexual dimorphism, most appear to have been diurnal, and most were likely frugivores or folivores (Rose, 1995). Omomyoids remained primarily small bodied (<100 g) though a radiation of omomyoids took place in North America and included larger bodied species (exceeding 2 kg) after the extinction of most of the adapoids. Most adapoid and omomyoid species went extinct at the Grande Coupure extinction event, which occurred about 34 MYA at the end of the Eocene and appears to be associated with decreased temperature and humidity in the Northern Hemisphere (Fleagle, 1999; Köhler and Moyà-Solà, 1999).

A number of models have been offered to explain the evolution of primates. Early models of primate origins (e.g., Jones, 1916) explained the suite of distinctive primate characters as adaptations to life in an arboreal environment that favored emphasis on the visual system and grasping hands and feet. However, as pointed out by numerous critics (e.g., Cartmill, 1974), this explanation ignores the fact that most nonprimate arboreal animals possess claws rather than nails, do not have grasping hands and feet, have laterally directed eyes, and rely heavily on olfaction. Thus, a generalized adaptation to an arboreal environment is unlikely to account for the evolution of these derived traits in primates. Additionally, it has become evident that the closest living relatives of primates (the archontans) are all at least partly arboreal; suggesting that the adaptive shift in early primates involved something beyond simply colonization of the trees.

More recent models have sought to explain the origin of primates as result of specific adaptive shifts within the arboreal environment. Cartmill's visual predation model (1974, 1992) explains the evolution of primate characteristics as an adaptive suite of features related to visual prey detection and predation (primarily on insects) on terminal branches and in the forest undergrowth. In contrast, Sussman (1991) has argued that it was not visual predation that led to the evolution of the primate traits but instead they are related to terminal branch feeding on the products of flowering plants (e.g., fruit, nectar, etc.), as well as the insects that pollinate these flowering plants. Terminal branch feeding as the impetus for the evolution of prehensile hands and feet, irrespective of diet, has received support in comparative studies of didelphid marsupials (Lemelin, 1999).

Information on primate bioenergetics has important implications for evaluating alternative models of primate origins. In particular, since body size has important energetic consequences and is critical in shaping dietary patterns, information on the size of early primate ancestors provides an important link to energetics and metabolism.

In general, among primate species there is an inverse relationship between body size and DQ (Leonard and Robertson, 1994; Sailer et al., 1985). This relationship (the "Jarman-Bell" relationship; Bell, 1971; Gaulin, 1979; Jarman, 1974) appears to be a consequence of the Kleiber scaling relationship between mass and metabolic rate. Large primates have high total energy needs, but relatively low mass-specific requirement, and are able to meet their energy demands by feeding on resources that are widely abundant but lower in quality (e.g., leaves, other foliage). In contrast, small primates have low total energy needs, but extremely high requirements per unit mass. These species tend to subsist on food items that are limited in their abundance but rich in energy and nutrients (e.g., insects, small vertebrates, saps, and gums).

Thus, as data on extant species show, body size greatly shapes and constrains the types of foods on which a primate can subsist. For example, insectivorous diets can only be sustained in very small animals and folivorous diets can only be sustained in considerably larger animals (Kay, 1984). Insects are excellent energy and protein sources for small animals, given their high relative energy demands. Conversely, leaves can provide an ample source of energy for larger bodied animals because of relatively lower energy requirements and longer gut passage times that allow for more nutrient extraction. However, animals smaller than about 700 g have a difficult time sustaining themselves energetically on a diet largely based on leaves. Fruits typically provide an ample source of available carbohydrates but are limited in terms of available protein. Frugivorous animals must supplement their diet with other sources of protein such as insects, leaves, or vertebrates.

Fossil and comparative studies of living animals suggests that the earliest primates were small bodied, with body sizes considerably smaller than 500 g and likely under 100 g. These early primates were likely primarily arboreal, nocturnal, inhabited tropical forests, and were adapted for climbing, grasping, and leaping in a fine-branch niche (Rose, 1995; Martin, 1990). As noted by Martin (1990), this ancestor was similar in many respects to living mouse lemurs and dwarf bushbabies, and contrasts markedly with the tree shrews, which are commonly used as early-primate analogs.

Considering the metabolic data on two strepsirrhines under 100 g (*Galagoides demidoff* and *Microcebus murinus*), we find that both are hypometabolic, with deviations from predicted RMR of −23.85 and −37.51%, respectively. While no haplorhines in the sample are below 100 g, the 105 g *Cebuella pygmaea* and the 113 g *Tarsius syrichta* are both also hypometabolic, with deviations of −21.78 and −34.80%, respectively. These species all have relatively high-quality diets and all obtain considerable energy from insects. While tarsiers are the only living primates to subsist on 100% animal prey (primarily insects), the living strepsirrhines under 100 g, *G. demidoff* and members of the genus *Microcebus* (including *M. murinus* and *M. rufus*), consume high-quality diets with varying amounts of insects and vertebrates (Atsalis, 1999; Charles-Dominique, 1977; Mittermeier et al., 1994). *Galagoides demidoff* consumes roughly 70% insects and supplements these primarily with fruit and gums (Charles-Dominique, 1977). *Microcebus murinus* has an omnivorous diet that includes insects, fruits, flowers, small vertebrates, insect secretions, gums, nectars, and other plant products (Corbin and Schmid, 1995; Hladik et al., 1980; Martin, 1973). *Microcebus rufus* appears to be heavily reliant on both fruit and insects, and has been described as a frugivore–faunivore (Atsalis, 1999). Interestingly, while *M. rufus* consumes a variety of plant species, it is heavily reliant upon several varieties of *Bakerella* (a type of mistletoe) known to have a very high fat content. Both *M. murinus* and *M. rufus* show seasonal shifts in diet (Atsalis, 1999; Hladik et al., 1980).

The ancestral primate most likely relied heavily on insects, especially during certain seasons, and supplemented its diet with high-quality plant parts, such as fruits, as well as small vertebrates. As pointed out by Martin (1990) it is in the terminal branches of tropical trees and shrubs that insects and fruit resources would have been most readily available to the earliest primates. Terminal branch feeding and its associated anatomical features in primates may have evolved to exploit changing patterns of insect and fruit availability that resulted from radiation of angiosperms during the Early Cenozoic. Low maintenance and total energy costs may have enhanced survival in early primates, especially in environments with low overall productivity and/or marked seasonality.

While hypometabolism can enhance survival in certain environments, there are important reproductive consequences of hypometabolism. Mammalian species with relatively low-metabolic rates also tend to have low-intrinsic rates of population growth (McNab, 1980, 1986). However, while population growth may be slower in hypometabolic species, there are environments where this would clearly be favored. The depressed metabolic rates of some mammal and bird species from isolated oceanic islands appear to be the result of selection for resource minimization in an environment with limited resources (McNab, 1994). It has been suggested that hypometabolic insectivores are better able to deal with seasonal fluctuations in food abundance (McNab, 1980). There is also evidence from bats that indicates that low-metabolic rates are important for coping with variation in food availability (i.e., avoiding starvation during periods of low-insect availability) (Audet and Thomas, 1997). Additionally, nonseasonal torpor and hibernation can confer considerable energy savings to small-bodied mammals (Wang and Wolowyk, 1988).

Thus, the physiological ecology of extant small-bodied strepsirrhines strongly suggests that the earliest primates were hypometabolic and heavily reliant on insects. The specific explanations for why hypometabolism is so common among small-bodied primates remain unclear; however, the patchy and seasonally variable nature of key food resources for these species may have played an important role. Further, it appears that the low-metabolic rates common among all extant strepsirrhines may have a deep evolutionary history. Such an interpretation implies that increased rates of metabolic turnover (and greater encephalization) occurred with the evolution of larger-bodied primates that were reliant on a different suite of food resources.

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