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RESEARCH ARTICLE

Muscle Mass Scaling in Primates: An Energetic and Ecological Perspective

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Body composition is known to vary dramatically among mammals, even in closely related species, yet this issue has never been systematically investigated. Here, we examine differences in muscle mass scaling among mammals, and explore how primate body composition compares to that of nonprimate mammals. We use a literature-based sample of eutherian and metatherian mammals, and combine this with new dissection-based data on muscularity in a variety of strepsirrhine primates and the haplorhine, *Tarsius syrichta*. Our results indicate an isometric scaling relationship between total muscle mass and total body mass across mammals. However, we documented substantial variation in muscularity in mammals (21–61% of total body mass), which can be seen both within and between taxonomic groups. We also found that primates are under-muscled when compared to other mammals. This difference in body composition may in part reflect the functional consequences of arboreality, as arboreal species have significantly lower levels of muscularity than terrestrial species. Am. J. Primatol. 74:395–407, 2012. © 2012 Wiley Periodicals, Inc.

Key words: muscle mass; scaling; body composition; energetics; ecology

INTRODUCTION

Food is a key limiting resource among mammals, and how energy is extracted and allocated throughout the body has consequences for survival and reproductive success [Calder, 1984; McNab, 2002]. Despite major differences in morphology and ecology, mammalian species have broadly similar metabolic requirements relative to body size [Aiello & Wheeler, 1995; Kleiber, 1961; McNab, 2002; Radinsky, 1972]. This commonality suggests that the total energy available for meeting the metabolic needs of the various somatic organs and tissues is constrained, which thus necessitates that available energy be allocated differentially depending upon the metabolic needs of each species. This is the basis of the expensive tissue hypothesis (ETH), which proposes an explanation for how humans are able to maintain large, energy-expensive brains while having resting metabolic rates that are not substantially different from other mammals [Aiello & Wheeler, 1995]. In this model, the size of certain organs such as the liver, kidneys, and heart appear to be constrained as they maintain a comparable mass relative to body size [Schmidt-Nielson, 1984], while other organs and tissues such as the brain and gastrointestinal tract vary in size depending upon functional demands [Aiello & Wheeler, 1995; Schmidt-Nielson, 1984]. According to the ETH approach, over the course of human evolution, brain size increased while the size of the gut—another metabolically expensive tissue—appears to have decreased in size in response to the consumption of an energy-dense and nutrient-rich diet [Aiello & Wheeler, 1995; Leonard & Robertson, 1994; Snodgrass et al., 2009]. This approach provides a useful theoretical framework for examining primate evolution since interspecific variation in body composition can be used to identify key adaptive shifts, and can help answer the question of how nonhuman primates are able to support their relatively large brains [Aiello & Wheeler, 1995; Kappelman, 1996; Snodgrass et al., 2009].

While the allometry and functional variability of certain aspects of body composition (e.g. brain size) have been extensively investigated, other organs and tissues have attracted considerably less attention. Skeletal muscle is another energetically expensive tissue, yet it has been neglected in studies of primate energetics and ecology. Whereas the resting

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muscle metabolism of a 65-kg human requires only 351 kcal/day [Aiello & Wheeler, 1995], metabolic requirements of this tissue can increase by 100-fold during activity [Sterck, 2002]. Thus, even small changes in muscle mass could substantially alter total daily energy requirements. If the overall skeletal muscle mass were reduced, the "saved" energy could theoretically be allocated to the brain or gastrointestinal tract. However, very little research has focused on skeletal muscle mass from a comparative metabolic perspective, even though this tissue makes up a relatively large component of body weight in humans and other primates [Isler & Van Schaik, 2006]. Furthermore, the existing data on muscle mass have not been systematically compiled or analyzed.

The limited information that is available on comparative muscularity suggests that relative muscle mass varies substantially among mammals [Calder, 1984; Elia, 1992; Grand, 1978; Holliday, 1986]. Several hypotheses have been proposed to explain this variation, yet no studies to date have tested these hypotheses or even systematically compiled data on muscle mass in mammals. McNab [1978] documented relatively low muscularity in species with relatively low resting metabolic rates, and hypothesized that metabolic differences could potentially explain the observed residual variation in muscle mass. Further, both Grand [1978, 1990, 1997] and McNab [1978] attributed low muscle mass among mammals to differences in ecology. Specifically, they linked a low-quality diet (e.g. folivory), an arboreal lifestyle, or a combination of arboreality and diet with hypomuscularity. The present study was designed as a preliminary step toward addressing this major gap in the literature on primate ecology and energetics.

The objectives of the present study are threefold. First, in order to assemble a comparative data set on muscularity, we combine new muscle mass data collected for a variety of strepsirrhine primates and the haplorhine, *Tarsius syrichta,* with values available in the published literature. Second, this comparative data set is used to assess similarities and differences between primates and nonprimate mammals in relative muscularity. Third, we use muscle mass data along with information on body mass, brain size, diet, and ecology in primates to test several hypotheses related to the adaptive dimensions of muscle mass. We evaluate the following hypotheses regarding primates.

(1) We predict that muscle mass will scale isometrically among primates. Given that muscle is a large component of total body mass [Saladin, 2012], we expect that muscle mass will be closely tied to overall body mass. Furthermore, earlier studies on body composition by Calder [1984] and then later by Raichlen et al. [2010] document a strong isometric scaling relationship between muscle mass and body mass across mammals. We anticipate a similar pattern will be found for primates.

(2) We predict that hypometabolic primate species will be relatively less muscular when compared to primates with higher resting metabolic rates. Although muscle mass at rest is relatively inexpensive, metabolic costs of muscle increase substantially when an animal is active. Thus, primates with low muscularity are expected to expend less energy overall (even during peak activity) when compared to other primate species. A relationship between metabolic rate and muscle mass is outlined by McNab [1978].

(3) We predict that primates that consume low-quality foods such as leaves will have lower muscle mass values than those that consume higher quality foods such as insects. This hypothesis was outlined first by Grand [1978, 1990, 1997] and McNab [1978]. There is some evidence that folivorous mammals tend to move more slowly and have smaller home ranges than insectivorous or frugivorous mammals and, as a result, have lower overall metabolic requirements [Milton, 1981, 1993]. Further, because low-quality foods are generally more difficult to digest then higher quality foods and require relatively large, energy-expensive guts [Lucus, 2004; Martin, 1990], folivorous primates may reduce overall energetic costs by decreasing muscle mass [McNab, 1978]. Thus, we predict that folivorous primates will have reduced muscularity compared to primates that feed on higher quality foods such as insects or fruits.

(4) We predict that arboreal species will be less muscular than terrestrial species. This hypothesis is based on earlier work by Grand [1978, 1990, 1997] and McNab [1978]. Grand [1978, 1990, 1997] found that arboreal mammals move slower and more deliberately than terrestrial species. In contrast, terrestrial species tend to be heavily muscled and emphasize hindlimb propulsion. Given these preliminary findings, we expect that arboreal taxa will have relatively less muscle than terrestrial forms. Further, we expect that primates, as a result of their arboreal heritage, will be less muscular compared to other mammals.

(5) We predict that among primates, there will be a negative correlation between brain size and muscularity, such that primates with relatively large brains will be hypomuscular. Leonard and Robertson [1994] and later Aiello and Wheeler [1995] discussed the physiological implications of brain evolution in primates. Despite having relatively larger brains than most nonprimate mammals, humans and nonhuman primates do not have significantly different overall metabolic requirements for their body size [Aiello & Wheeler, 1995; Radinsky, 1972]. Thus, given that muscle

tissue requires a substantial portion of overall daily metabolic requirements, we hypothesize that muscle mass will be lower in primates with relatively large brains. By reducing muscle mass, a species could "save" energy, which could then be allocated to other tissues, such as the brain.

METHODS

Primates used in this study died of natural causes; cadavers were obtained from the Duke University Primate Center. Thus, no animals were sacrificed for this study. The research presented here is compliant with animal care regulations and applicable national laws. This study also adhered to the American Society of Primatologists principles for the ethical treatment of primates.

We compiled published data on skeletal muscle mass (g) and body mass (g) for 72 mammalian species, including 15 primates (N = 36 individuals; Table I) and 57 nonprimate mammals (N = 224 individuals; Table II). For each species, we calculated single unweighted averages for both muscle and body masses. Currently, few published data exist on muscularity in primates, and no data are available for Malagasy strepsirrhines. To add to the published data, we collected muscle mass data on eight strepsirrhine species (N = 10 individuals) and one tarsier species (*Tarsius syrichta*). The muscle mass data for our sample and those compiled from the literature bring the primate species count for this study to 24 (N = 47 individuals). For our nonprimate mammal sample, both wild and captive mammals were used in the analysis. All values obtained from Pitts and Bullard [1968] were wild caught (N = 38). All other nonprimate mammals used in this study were captive prior to death (N = 17). For the primate sample, all animals were captive except *Callithrix jacchus*, which all lived in the wild prior to death. It is important to note that although many of the animals in our sample were captive, several lived in semi-free-ranging environments and were not housed in particularly small enclosures. In addition to potential issues associated with using a mixed wild and captive sample (e.g. different muscle/fat ratio in wild vs. captive individuals), we understand and appreciate the possible problems with using a small sample to represent each species. Small sample size does not capture the substantial variation observed in body composition due to age and sex.

Dissection Study

All animals used in this study were adults, and all were dissected according to techniques and standards described by Grand [1977]. One side of the body was dissected to measure total bone, muscle, skin, and fat masses. For the other side of the body, separate weights for bone, muscle, skin, and fat were calculated for each body segment (head, trunk, tail, hind limb, and forelimb). Segments and tissues were weighed to the nearest 0.1 g. Body masses at death were available for all individuals except for three species sampled (*Perodicticus potto*, *Hapalemur griseus*, and *Tarsius syrichta*). For these species, we calculated a body mass value by averaging documented weights recorded during these animals' last year of life. These weights were then compared to published species averages [Smith & Jungers, 1997; Terranova & Coffman, 1997]; all fell well within the range of known weight values. If more than one individual of the same species was sampled, single unweighted averages for both body mass and muscle mass were calculated.

Interspecific Comparisons

In order to compare muscle mass values across species and groups, body mass must be considered. Previous studies [Grand, 1977, 1978, 1983, 1990, 1997; Grand & Barboza, 2001; McFarland and Zihlman, 2001; Zihlman, 1984; Zihlman & McFarland, 2000] have expressed muscle mass as a percentage of total body mass (percentage of TBM = muscle mass divided by body mass multiplied by 100). An analysis of ratios, such as muscle as a percentage of TBM, is a frequently used size adjustment technique. Residual-based analyses are also commonly employed. In residual-based analyses, the dependent variable (in the present study, muscle mass) is regressed against an independent variable (body mass), and the residual values are obtained from the line fit. The derived residual values are used as the size-adjusted values for each species included in the analysis. Unlike residual-based analyses, analyses of ratios such as muscle as a percentage of TBM reflect the relationship between intrinsic properties of an organism. Residual values, unlike ratio analysis, can change with a study's sample composition [Smith, 2002]. Raichlen et al. [2010] found that muscle mass scales isometrically with body mass in mammals; if this result holds, residual and ratio-based analyses should produce identical results. However, for the sake of completeness and comparison, both ratio-based (muscle as a percentage of TBM) and residual-based size adjustment techniques are employed throughout this study.

Group Comparisons

Our first objective is to examine the relationship between muscle mass and body mass across all mammals (primates and nonprimate mammals), with the prediction that muscle mass will scale isometrically with body mass in all sample subsets. Allometric relationships were determined using ordinary least squares (LS) regressions and reduced major axis (RMA) regressions of natural log-transformed data.

TABLE I. Primate Muscle Mass Data

Species	N	Body mass (g)	Muscle mass (g)	ECV[a]	Muscle (%TBM)	S[a]	DQ[b]	BMR[c] (ml O_2 hr^{-1})	Muscle mass source
Alouatta caraya	2	6,075	1,677	52.63	27.6	A	160	2,055	Grand [1977]
Aotus trivirgatus	4	628.8	193	16.85	30.7	A	194	456	Grand [1977]
Ateles sp.	1	7,600	3,480	105.09	45.8	A	193		Grand [1977]
Callithrix jacchus	4	186	87.9	7.24	47.3	A	259	152	Pitts and Bullard [1968]
Cebus sp.	1	3,800	1,742	66.63	45.8	A	199		Grand [1977]
Otolemur crassicaudatus	3	994.1	377.9	11.78	38.0	A	208	412	This study; Grand [1977]
Galago moholi	2	134.5	45	3.71	33.4	A	278	51	This study
Galago senegalensis	2	245.5	90	1.63	36.7	A	278	137	Grand [1977]
Gorilla gorilla	4	163,800	64,810	490.41	39.6	T	180		Zihlman and McFarland [2000]; McFarland and Zihlman [2001]
Hapalemur griseus	1	800	193.6	14.09	24.2	A	105		This study
Loris tardigradus	1	144	40	5.87	27.8	A	163	128	This study
Macaca mulatta	3	6,043.3	2,498.3	88.98	41.3	T	163	2,239	Grand [1977]
Macaca nemestrina	1	14,500	7,120	105.59	49.1	T	163		Grand [1977]
Macaca nigra	1	9,400	3,460	94.90	36.8	T	198		Grand [1977]
Mandrillus leucophaeus	1	25,260	11,160	153.88	44.2	T	194		Grand [1977]
Microcebus murinus	2	61.2	17.5	1.63	28.6	A	250	49	This study
Mirza coquereli	1	310	78.9	5.80	25.5	A	275		This study
Nycticebus coucang	5	1,157.4	298.2	10.13	25.8	A	245	273	Grand [1977]
Nycticebus pygmaeus	1	317	82.5	7.23	26.0	A	235		This study
Pan paniscus	1	29,500	13,511	341.29	45.8	T	163		Zihlman [1984]
Pan troglodytes	1	31,500	11,025	368.35	35.0	T	186	5,773	Zihlman [1984]
Perodicticus potto	4	989.3	214.25	12.42	21.6	A	217	327	This study; Grand [1977]
Tarsius syrichta	1	125	27.2	3.36	21.7	A	350	149	This study

ECV = endocranial volume measured in cubic centimeters. Values were obtained from Isler et al. [2008].
S = substrate preference, where (A) indicates arboreal and (T) indicates terrestrial. DQ = dietary quality, BMR = basal metabolic rate.
[a]Rowe [1996].
[b]National Research Council [2003].
[c]Raichlen et al. [2010]; Savage et al. [2004]; White and Seymour [2003].

Statistical analyses were performed using JMP v8 and IBM SPSS v19. Significance was set at $P < 0.05$ for all statistical comparisons.

To examine how muscle mass differs across mammals, *ln muscle mass* was regressed separately against *ln body mass* for nonprimate mammals and for primates, and an analysis of covariance (ANCOVA) was used to test for differences in *ln muscle mass* (with *ln body mass* as the covariate). ANCOVAs were used only when data met model assumptions (i.e. regression slopes not significantly different). Only the results for differences in y-intercept are presented.

Two-tailed independent sample t-tests were also used to determine whether relative muscularity (muscle as a percentage of TBM and residual values derived from an all-mammal regression of *ln muscle mass* and *ln body mass*) differed between nonprimate mammals and primates.

Ecological, Dietary, Metabolic, and Anatomical Variables

Data from published sources were used to assign each primate species to a particular substrate and dietary preference category (Table I). For substrate preference, animals in our study were described as either primarily arboreal or terrestrial. There are obvious limitations inherent in simplistic habitat classifications, but these classifications are informative when a general ecological picture of the subjects under study is needed. Independent sample t-tests were used to determine whether relative muscularity (muscle as a percentage of TBM and residual values derived from an all-mammal regression of *ln muscle mass* and *ln body mass*) in primates and nonprimate mammals differed by substrate preference.

To evaluate associations between diet and muscularity, a dietary quality (DQ) value was calculated for each primate species. DQ is an index developed by Sailer et al. [1985] that considers the relative energy and nutrient density of dietary items. The DQ index (DQ = s + 2[r] + 3.5[a]) is a weighted average of the proportions of various food sources in an animal's diet, where s represents the percentage of diet derived from structural plant parts (e.g. leaves, stems, and bark), r represents the percentage of diet derived from reproductive plant parts (e.g. fruits, flowers, and nectar), and a represents the percentage of the diet derived from animal parts (including both vertebrates and invertebrates). The DQ ranges from a minimum of 100 for animals with diets consisting of

TABLE II. Nonhuman Primate Sample: Body Mass, Muscle Mass, and Substrate Preference

Species	N	Body mass (g)	Muscle mass (g)	Muscle % TBM	S[a]	H[b]	Muscle mass data source
Artibeus jamaicensis	14	40.5	18	44.5		W	Pitts and Bullard [1968]
Artibeus lituratus	5	63.7	29.1	45.6		W	Pitts and Bullard [1968]
Bradypus infuscatus	1	3,600	850	23.6	A	C	Grand [1977]
Caluromys philander	6	303	98.8	32.6	A	C	Grand [1983]
Castor canadensis	2	9,331	4,622.4	49.5	T	W	Pitts and Bullard [1968]
Choloepus hoffmanni	2	4,595	1,232	26.8	A	C	Grand [1977]
Clethrionomys gapperi	1	18.3	9.3	50.4	T	W	Pitts and Bullard [1968]
Clethrionomys rutilus	20	25.3	11.3	44.9	T	W	Pitts and Bullard [1968]
Cuniculus paca	1	1,565	737.4	47.1	T	W	Pitts and Bullard [1968]
Dasyprocta aguti	2	2,097	1,115.1	53.2	T	WC	Pitts and Bullard [1968]; Grand [1977]
Dendrolagus matschiei	2	6,110	2,077.4	34	A	C	Grand [1990]
Didelphis sp.	2	949.4	441.9	46.5	T	W	Pitts and Bullard [1968]
Didelphis marsupialis	2	1,441	682	48.3	T	W	Pitts and Bullard [1968]
Eptesicus fuscus	2	17.9	7.4	41.6		W	Pitts and Bullard [1968]
Erethizon dorsatum	2	5,339	2,197.1	41.2	T	W	Pitts and Bullard [1968]
Euphractus sexcinctus	2	2,459	864.1	35.1	T	W	Pitts and Bullard [1968]
Felis lynx	1	7,688	4,341.5	56.5	T	W	Pitts and Bullard [1968]
Felis rufus	3	6,152	3,600.3	58.5	T	W	Pitts and Bullard [1968]
Glossophaga soricina	3	7.2	3.9	53.5		W	Pitts and Bullard [1968]
Gulo luscus	1	9,362	5,271.2	56.3	T	W	Pitts and Bullard [1968]
Hippotragus niger	12	166,280	79,810	48	T	C	Grand [1997]
Lemmus trimucronatus	5	41.6	19.9	47.9	T	W	Pitts and Bullard [1968]
Lepus californicus	1	1,867	868	46.5	T	C	Grand [1977]
Macropus rufogriseus	2	9,900	4,950	50	T	C	Grand [1990]
Macropus rufus	2	23,900	11,233	47	T	C	Grand [1990]
Madoqua kirkii	6	4,400	1,980	45	T	C	Grand [1997]
Marmosa murina	2	51.5	15	29.1	A	C	Grand [1983]
Marmota caligata	2	3,558	1,671.4	47	T	W	Pitts and Bullard [1968]
Marmota monax	2	2,194	817.1	37.2	T	W	Pitts and Bullard [1968]
Metachirus nudicaudatus	1	391	179	45.8	T	C	Grand [1983]
Microtus oeconomus	9	24.8	11.1	44.8	T	W	Pitts and Bullard [1968]
Microtus pennsylvanicus	7	31.4	14.5	46.1	T	W	Pitts and Bullard [1968]
Microtus pinetorum	7	19.4	9.5	48.7	T	W	Pitts and Bullard [1968]
Molossus major	3	11.1	5.5	49.8		W	Pitts and Bullard [1968]
Monodelphis brevicaudata	1	73.1	29	39.7	T	C	Grand [1983]
Mus musculus	4	15.9	7.1	44.5	T	W	Pitts and Bullard [1968]
Mustela erminea	3	183.3	104.7	57.1	T	W	Pitts and Bullard [1968]
Mustela vison	2	1,032	581.5	56.4	T	W	Pitts and Bullard [1968]
Ochotona collaris	1	120.9	57.18	47.3	T	W	Pitts and Bullard [1968]
Ondatra zibethicus	8	1,180	679.4	57.6	T	W	Pitts and Bullard [1968]
Oryzomys palustris	1	61.6	26.9	43.7	T	W	Pitts and Bullard [1968]
Peromyscus leucopus	9	17	8	47.2	T	W	Pitts and Bullard [1968]
Phascolarctos cinereus	10	5,974.5	1,818.3	30.4	A	C	Grand and Barboza [2001]
Philander opossum	5	364.8	141.4	38.8	T	C	Grand [1983]
Phyllostomus discolor	7	34.4	16.5	48		W	Pitts and Bullard [1968]
Phyllostomus hastatus	2	92.3	47	50.1		W	Pitts and Bullard [1968]
Potorous tridactylus	2	1,026.5	451.7	44	T	C	Grand [1990]
Procyon lotor	3	6,040	2,920.7	48.4	T	W	Pitts and Bullard [1968]
Pseudocheirus peregrinus	5	939.6	300.7	32	A	C	Grand [1990]
Scalopus aquaticus	1	44.6	21.9	49	T	W	Pitts and Bullard [1968]
Sciurus carolinensis	1	499	306.5	61.4	A	W	Pitts and Bullard [1968]
Spermophilus undulatus	4	479	257.9	53.8	T	W	Pitts and Bullard [1968]
Sturnira lilium	2	15.4	6.3	41.1		W	Pitts and Bullard [1968]
Tamiasciurus hudsonicus	11	192.8	114.2	59.2	A	W	Pitts and Bullard [1968]
Tupaia glis	4	151.3	49.8	32.9	A	C	Grand [1977]
Vampyrops lineatus	3	22	10.6	48.1		W	Pitts and Bullard [1968]

[a] S = substrate preference, where (A) indicates arboreal and (T) indicates terrestrial. DQ = dietary quality, BMR = basal metabolic rate.

[b] H = Perimortum habitat, where (W) indicates wild-caught individuals and (C) indicates the animals were obtained from captivity.

100% foliage to a maximum of 350 for animals with diets composed of 100% animal material. Pearson's correlations were used to examine links between relative muscularity (muscle as a percentage of TBM and residual values derived from an all-mammal regression of *ln muscle mass* and *ln body mass*) and DQ.

Basal metabolic rates (BMRs) were more difficult to obtain for primates given the paucity of data available in the literature. When available, basal (or resting) metabolic data were compiled for the primates sampled [Raichlen et al., 2010; Savage et al., 2004; White & Seymour, 2003] and these values were compared to the predicted values determined by the Kleiber [1961] scaling relationship between BMR and adult body mass, where BMR scales to the three-quarter power of body mass. Pearson's correlations were run between relative muscularity (muscle as a percentage of TBM and residual values derived from an all-mammal regression of *ln muscle mass* and *ln body mass*) and the percentage deviation between observed and expected BMR in order to better understand the proposed relationships between metabolism and muscle mass [Savage et al., 2004; White and Seymour, 2003].

In order to consider potential links between brain size and muscularity in primates, we used a Pearson's product-moment correlation to test the relationship between relative endocranial volume (ECV; cubic centimeters) and relative muscularity. ECVs were obtained from Isler et al. [2008] for 22 primate species.

Phylogeny

Because closely related species are more likely to share anatomical similarities than more distantly related species, phylogenetic information should be considered in bioenergetic analyses. Phylogenetically independent contrasts (PIC) were calculated using the PDAP:PD-TREE module of Mesquite version 1.07 (http://mesquiteproject.org). Contrast data were calculated using a tree with equal branch lengths, a method shown to be robust by Martins and Garland [1991]. The mammalian phylogenetic supertree was constructed from a published source [Bininda-Emonds et al., 2007].

The first set of analyses used the PIC to compare differences between clades. To control for the effects of body mass, independent contrasts of the dependent variable (*ln muscle mass*) were regressed on positivized contrasts of *ln body mass*, using a LS regression forced through the origin [Garland et al., 1993]. The residual values from these analyses represent size-adjusted contrasts. To test the hypothesis that a particular order is grade-shifted from its sister group, a t-test was used to determine whether primates fall more than two standard deviations from the regression line.

The second group of analyses explored the proposed relationship between relative muscle mass (muscle as a percentage of TBM) and the ecological and physiological variables. Pearson's product-moment correlations were used to test the relationships between relative muscularity (*contrast muscle as a percentage of TBM* or *contrast residual values*, which were obtained from a LS regression between *ln muscle mass* and *ln body mass*) and *contrast substrate preference*, *contrast DQ*, *contrast BMR, and contrast ECV*.

RESULTS

Intra- and Interspecific Variation in Muscle Mass

Muscle mass as a percentage of TBM ranges from 22–61% among mammals in the sample. Among arboreal mammals, muscle mass averages 33% of TBM; for terrestrial mammals, this value is 48%. Henceforth, when relative muscularity is discussed, the term "ratio" will be applied to calculations that use muscle as a percentage of TBM and "residual" to calculations that used values obtained from a LS regression of muscle mass (g) versus body mass (g) for all mammals.

Skeletal muscle mass and body mass scale isometrically among all mammals in the sample (LS: $ln\ muscle\ mass = -0.86 + 0.99\ ln\ body\ mass$, CI = 0.93–1.05; RMA: $ln\ muscle\ mass = -0.90 + 1.00\ ln\ body\ mass$, CI = 0.98–1.02). This scaling relationship does not significantly change when primates are removed from the sample (LS: $ln\ muscle\ mass = -0.76 + 0.99\ ln\ body\ mass$, CI = 0.97–1.01; RMA: $ln\ muscle\ mass = -0.79 + 1.00\ ln\ body\ mass$, CI = 0.97–1.02). Skeletal muscle mass and body mass in primates scales with slight positive allometry (LS: $ln\ muscle\ mass = -1.57 + 1.06\ ln\ body\ mass$, CI = 1.02–1.10; RMA: $ln\ muscle\ mass = -1.62 + 1.07\ ln\ body\ mass$, CI = 01.02–1.07), and the primate regression slope is significantly different from that documented for nonprimate mammals (Fig. 1; $P < 0.05$). Because the primate regression line was significantly different than the one calculated for nonhuman primates, differences in relative muscularity could not be calculated using an ANCOVA.

Our results indicate that primates are significantly less muscular when compared to nonprimate mammals, at 35% and 46% TBM, respectively (Fig. 2; ratio: $t[1,77] = -5.18$, $P < 0.0001$; residual: $t[1,77] = -5.03$, $P < 0.0001$). These findings did not change when phylogeny was considered (Fig. 2; ratio: $t[1,77] = 4.47$, $P < 0.0001$; residual: $t[1,77] = 5.01$, $P < 0.0001$). We also tested whether differences between primates and nonprimate mammals reflect the extremely low values found among the strepsirrhines. However, when strepsirrhines were excluded from the sample, haplorhine primates remained less

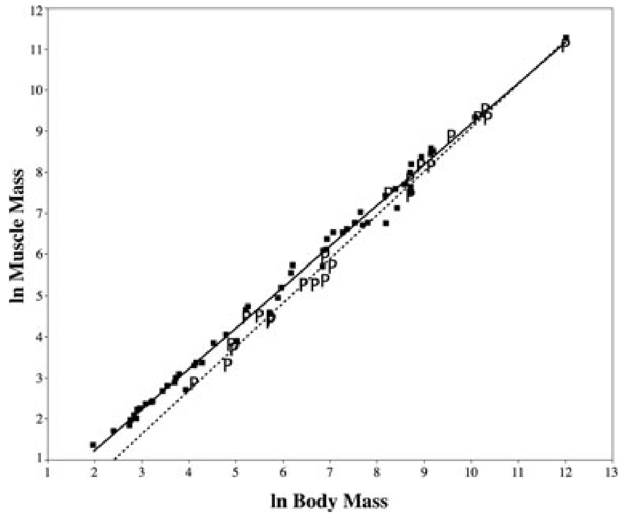

Fig. 1. A scatterplot of *lnmuscle mass* versus *lnbody mass* for all mammals sampled, including nonprimate mammals (■) and primates (**P**). LS regression lines were fit to all nonprimate mammals (——) and primates (……). Both slopes scale isometrically, but the primate slope is significantly different from that documented for nonprimate mammals ($P = 0.03$).

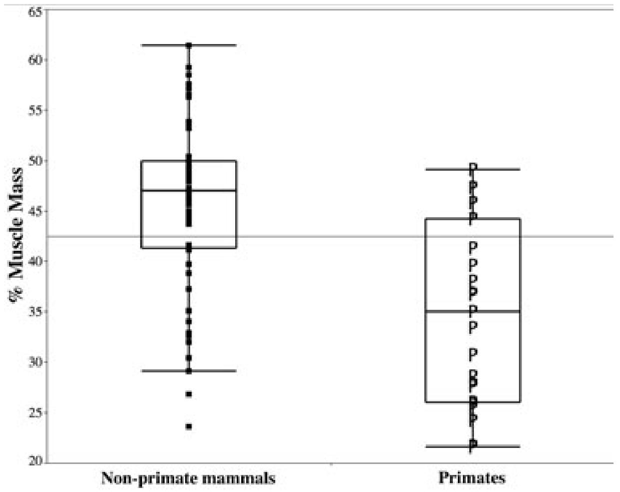

Fig. 2. A box and whisker plot illustrating the variation in *muscle as a percent of total body mass* among nonprimate mammals (■) and primates (**P**). A Student's *t*-test indicates that primates are under-muscled compared to nonprimate mammals (ratio: $t[1,77] = -5.18$, $P < 0.0001$).

muscular compared to nonprimate mammals (ratio: $t[1,67] = -2.43$, $P < 0.01$; residuals: $t[1,67] = -2.19$, $P < 0.05$).

Muscle Mass, Brain Size, Ecology, and Physiology

We tested whether differences in ecology and physiology might explain variation in relative muscle mass (ratio and residual) among primates. DQ (Fig. 3; ratio: $R^2 = 0.12$, $P = 0.09$; residual: $R^2 = 0.15$, $P = 0.07$) and BMR (Fig. 4; ratio: $R^2 = 0.48$, $P = 0.13$; residual: $R^2 = 0.47$, $P = 0.11$) are not significantly correlated with muscularity. The relationship between DQ, BMR, and relative muscle mass was not significant when phylogeny was considered (DQ ratio: $R^2 = 0.003$, $P = 0.78$; DQ residual: $R^2 = 0.006$, $P = 0.72$; BMR ratio: $R^2 = 0.007$, $P = 0.79$; BMR residual: $R^2 = 0.02$, $P = 0.62$).

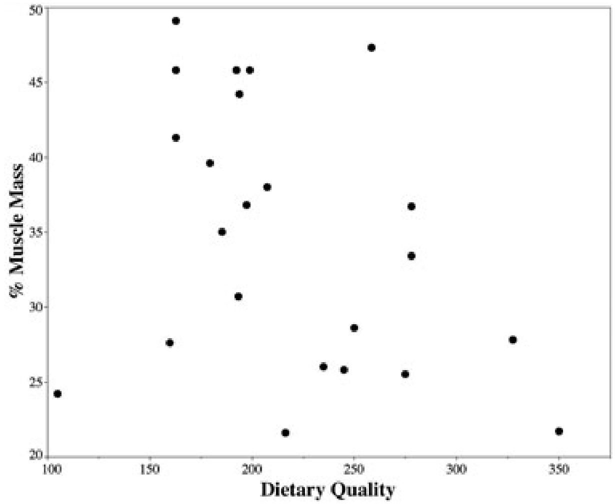

Fig. 3. A scatterplot of *muscle as a percent of total body mass* versus *DQ index* for primates. There is no relationship between DQ and muscularity (ratio: $R^2 = 0.12$, $P = 0.09$).

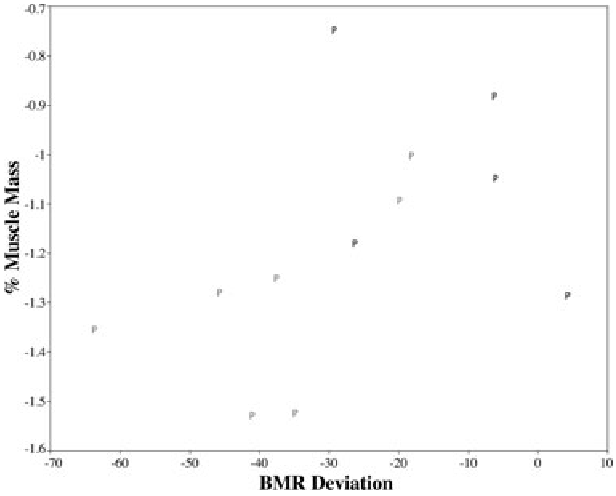

Fig. 4. A scatterplot of *muscle as a percent of total body mass* versus *BMR* (percent deviation from Kleiber's [1961] BMR predicted values) for primates. There is not a significant relationship between BMR and muscularity (ratio: $R^2 = 0.48$, $P = 0.13$).

Our results show that in this sample, arboreal primates are less muscular compared to terrestrial primates, at 32% TBM (21–47% of TBM) and 42% TBM (35–49% of TBM), respectively (Fig. 5; ratio: $t[1,21] = 2.91$, $P < 0.0001$; residuals: $t[1,21] = 3.05$, $P < 0.0001$). When substrate differences were examined among all mammals (including primates), arboreal species were significantly less muscular

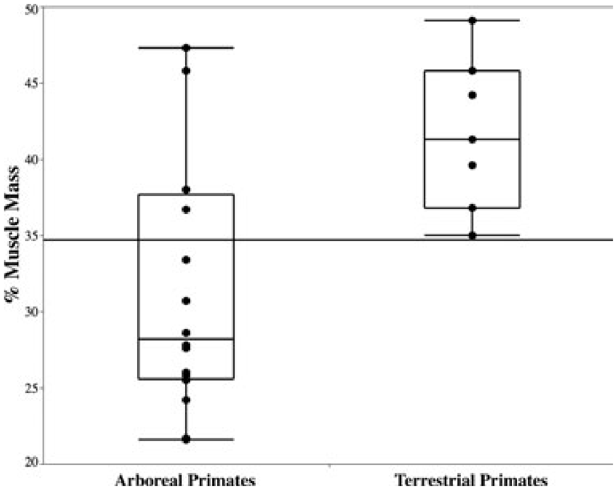

Fig. 5. A box and whisker plot illustrating the variation in *muscle as a percent of total body mass* among arboreal and terrestrial primates. A Student's *t*-test indicates that arboreal primates are under-muscled when compared to terrestrial primates ($t[1,21] = 2.91$, $P < 0.0001$).

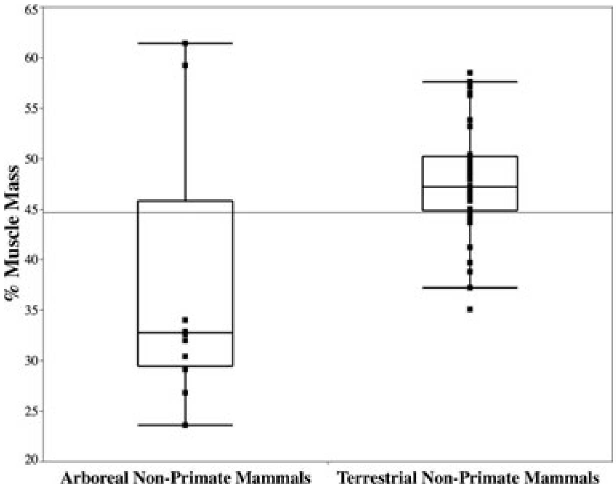

Fig. 6. A box and whisker plot illustrating the variation in *muscle as a percent of total body mass* among arboreal and terrestrial nonprimate mammals. A Student's *t*-test indicates that arboreal nonprimate mammals are under-muscled when compared to terrestrial taxa ($P < 0.0001$).

compared to terrestrial species (ratio: $t[1,68] = 6.82$, $P < 0.0001$; residuals: $t[1,68] = 7.57$, $P < 0.0001$). When all primates were removed from the mammalian sample, the observed differences between arboreal and terrestrial nonprimate mammals remained highly significant (Fig. 6; ratio: $t[1,52] = 5.06$, $P < 0.0001$; residuals: $t[1,52] = 5.04$, $P < 0.0001$). These findings did not change substantially when phylogeny was considered (primates—ratio: $t[1,21] = 2.10$, $P < 0.05$; residuals: $t[1,21] = 2.11$, $P < 0.05$; all mammals—ratio: $t[1,68] = 4.16$, $P < 0.0001$; residuals: $t[1,68] = 4.78$, $P < 0.0001$; nonprimate mammals—ratio: $t[1,52] = 4.15$, $P < 0.0001$; residuals: $t[1,52] = 4.76$, $P < 0.0001$).

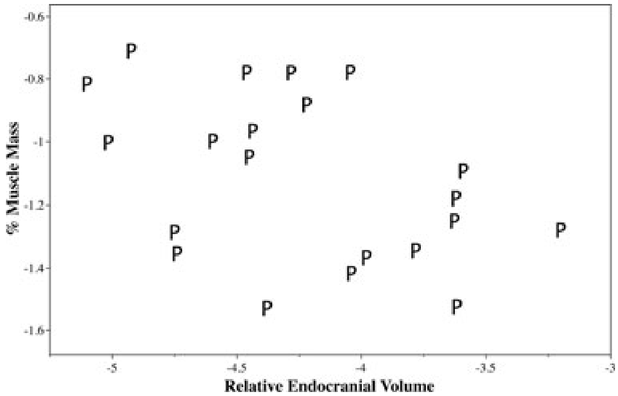

Fig. 7. A scatterplot of *muscle as a percent of total body mass* versus *relative endocranial volume* (ratio-based values) for primates. There is a significant relationship between BMR and muscularity (ratio: $R = -0.44$, $P < 0.05$).

Among the primates sampled ($N = 22$), ECV scales with negative allometry when regressed against body size (LS: $ln\ ECV = -2.60 + 0.78\ ln\ body\ mass$, CI = 0.70–0.86; RMA: $ln\ ECV = -2.73 + 0.80\ ln\ body\ mass$, CI = 0.71–0.89). Because ECV and body mass scale with negative allometry, ratio analysis is the most appropriate method to size-adjust the ECV. Relative ECV was calculated by dividing ECV by body mass, and relative muscularity was calculated by dividing muscle mass over body mass. For consistency and comparison, we have also included results from an analysis that used residual-based size-adjusted variables. Ratio size-adjusted ECV results indicate a significant negative correlation between relative ECV and relative muscle mass (Fig. 7; $R = -0.44$, $P < 0.05$). However, residual-derived relative ECV and relative muscle mass show no significant relationship ($R = -0.19$, $P = 0.38$). When phylogeny was considered, neither the ratio-based analysis nor the residual-based analysis between relative ECV and relative muscle mass yielded a significant result.

The Influence of Captivity on Muscularity

Our findings that hypomuscularity in primates compared to nonprimate mammals and hypomuscularity among arboreal species could potentially be an artifact of differences in activity patterns resulting from individual habitat differences experienced during life (i.e. captivity vs. wild). To further explore this issue, we conducted a series of post-hoc analyses. First, we compared muscle as a percentage of TBM in species that had muscle mass values for individuals obtained from both captive and wild settings. We found that captive animals had lower muscle mass values than wild animals. For example, the wild-caught *Dasyprocta aguti* had 60% muscle while the captive specimen had 52% muscle. Unfortunately, samples were not large enough to evaluate if these differences were statistically significant or simply reflected normal variation within a species.

To further explore the potential effects of captivity on body composition, we next compared relative muscularity (ratio and residual values) between captive and wild arboreal nonprimate mammals and between captive and wild terrestrial nonprimate mammals. We found no significant differences between the groups. As another strategy, we removed all wild nonprimate mammals from the sample and compared differences in relative muscularity between captive arboreal and terrestrial nonprimate mammals. We found significant differences in relative muscularity between captive arboreal and terrestrial nonprimate mammals (ratio: $t[1,17] = 8.22$, $P < 0.0001$; residuals: $t[1,17] = 8.01, P < 0.0001$).

Finally, we were interested in evaluating if our findings of hypomuscularity in primates remained if we removed all wild mammals from our sample. Results of the analysis did show that captive primates were less muscular compared to captive nonprimate mammals (ratio: $t[1,40] = 2.34$, $P < 0.05$; residuals: $t[1,40] = 2.33, P < 0.05$).

DISCUSSION

Muscle Mass Scaling and Interspecific Variation

There is considerable variation in mammals in the scaling relationship of anatomical structures. The relative size of the brain, nervous/endocrine system, and skin decrease with an increase in body mass, while the heart, lungs, and kidneys scale isometrically [Calder, 1984; Schmidt-Nielson, 1984]. Furthermore, some somatic tissues show little variation beyond that related to body weight, while others such as the brain, gastrointestinal tract, and adipose tissue show considerable variation. Human body composition deviates from the nonhuman primate pattern in several important dimensions, including the former having relatively large brains and stores of body fat [Wells, 2010], as well as a relatively undersized gut [Aiello & Wheeler, 1995]. In the present study, we examined muscle mass allometry and tested hypotheses related to proposed links between muscularity and several metabolic, anatomical, and ecological variables.

Hypothesis 1: Muscle mass scaling

We predicted that muscle mass would scale isometrically among primates. This hypothesis was based on earlier studies of mammals by Calder [1984] and Raichlen et al. [2010], which documented that muscle mass and body mass scale isometrically. The results from our study also indicate that muscle mass scales isometrically across mammals. In contrast, primates have a higher scaling coefficient than that of nonprimate mammals (1.05 vs. 0.99; based on a LS regression). Further, despite the strong relationship between muscle mass and body mass, we documented substantial variation in muscle mass both within and between orders. For instance, among all mammals, muscle mass as a percentage of TBM ranges from 22% to 61%, with primates represented at the lower range of this spectrum (22–49% of TBM).

Anatomical, Physiological, and Ecological Variables

Based on a small and taxonomically limited sample of mammals, Grand [1978] and McNab [1978] suggested that hypomuscularity was a reflection of low metabolic rates, diets made up of low-quality foods, and/or arboreality. We examined how differences in substrate preference, diet quality, and metabolism related to differences in relative muscularity.

Hypothesis 2 and 3: DQ, BMR, and muscle mass

We hypothesized that primates that consume low-quality foods such as leaves would have lower muscularity than those consuming higher quality foods such as insects. Our results show that DQ is not significantly correlated with muscle mass. We also predicted that primate species with lower metabolic rates would be relatively less muscular compared to primates with higher resting metabolic rates. Our results show that there is no significant relationship between BMR and muscle mass.

Although our results show that DQ and BMR are not significantly correlated with muscle mass among primates, we did observe an interesting pattern in the data associated with patterns of muscularity in these animals. For example, the lowest levels of muscularity in our sample are seen among hypometabolic species such as the Malagasy strepsirrhines and the haplorhines *Tarsius syrichta* and *Aotus trivirgatus*. Although our study is the first to systematically test how relative muscularity in primates varies with specific ecological and physiological parameters, the interplay between muscle mass and ecology and physiology remains unclear (e.g. *H. griseus* is both hypometabolic and feeds on low-quality foods). Without further testing on a larger and more biologically and ecologically diverse sample, it is impossible to isolate which variable or combination of variables contributes to low levels of muscularity.

Hypothesis 4: Substrate preference and muscle mass

Based on research by Grand [1978, 1990, 1997] and McNab [1978] on substrate preference and muscularity in mammals, we hypothesized that arboreal species would be less muscular compared to terrestrial species. Further, we expected that because of their arboreal heritage, primates would be less muscular compared to other mammals. The findings from the present study support both predictions.

Our findings show that there is a significant relationship between relative muscle mass and substrate preference. Arboreal primates are significantly less muscular (~32% of TBM) compared to terrestrial primates (~42% of TBM). The relationship between hypomuscularity and arboreality remains significant regardless of the group under consideration. When we considered all mammals (including primates), we found that arboreal mammals are less muscular than terrestrial species, yet we were concerned that the largely arboreal primate order unduly influenced the comparisons between arboreal and terrestrial mammals. However, when the relationship between arboreality and relative muscle mass was examined using a nonprimate mammalian sample, the pattern remained the same, which indicates that arboreal mammals are significantly less muscular than terrestrial species.

The relationship between muscularity and substrate preference has been documented in several smaller studies that focused on specific mammalian lineages. For example, muscle mass in terrestrial kangaroos averages approximately 50% of TBM, while the muscle mass of the arboreal taxon (*Dendrolagus*) averages around 35% of TBM [Grand, 1990]. Arboreality and terrestriality impose very different biomechanical challenges on an animal. Arboreal animals generally move across an oscillating substrate and, as a result, tend to move more slowly than terrestrial mammals [Raichlen, 2004]. Arboreal animals also have low stride frequencies and may maintain a crouched posture to keep their center of mass close to the substrate for better balance [Schmitt, 1999]. Conversely, terrestrial animals may have a higher percentage of muscle mass for greater power output since they move on a stable substrate [Grand, 1977]. Many terrestrial animals also have a greater muscle mass in their hind limbs (~50% of total muscle mass) than in their forelimbs (~10% of total muscle mass), which allow propulsive movements across a terrain [Grand, 1977; Raichlen, 2004]. Further, the ability to move quickly is essential for terrestrial animals because they are often more exposed to predators than arboreal mammals, which are partially protected by the trees they inhabit. While predators can be found at all heights in the forest, many (e.g. canids and snakes) are less agile in trees than primates [Sterck, 2002]. Interestingly, a reduced risk of predation has been used to explain the increased longevity documented among arboreal mammals [Shattuck & Williams, 2010].

The combination of a deeply rooted evolutionary history in arboreality [Martin, 1990] and the continued use of arboreal resources in virtually all primate species may explain the observed differences in muscularity between primates and many of the nonprimate mammals included in this study. Support for this position also comes from an examination of closely related species. Morphological and molecular data support a close evolutionary relationship between primates, scandentians (tree shrews), and dermopterans (flying lemurs) [Bininda-Emonds et al., 2007; Diogo, 2008; Murphy et al., 2001; Silcox et al., 2005], which together form Euarchonta. Primates and dermopterans are highly arboreal, while scandentians, as a group, can be considered semiarboreal [Emmons, 2000]. Most modern scandentian taxa prefer foraging in the understory of the canopy [Emmons, 2000]; however, scandentians, such as primates, appear to also have a deeply rooted history associated with arboreality. *Ptilocercus lowii*, the most morphologically primitive scandentian, is strictly arboreal [Emmons, 2000; Luckett, 1980; Szalay & Drawhorn, 1980]. Moreover, all scandentians have retained very complex and derived functional adaptations associated with arboreality [Szalay & Drawhorn, 1980] and, thus, it appears that all living scandentian species are evolved from an arboreal ancestor [Emmons, 2000]. Muscle mass data are not currently available for dermopterans, but data for the semiarboreal scandentian *Tupaia glis* indicate that it has relatively low muscularity. Therefore, although terrestrial primates have relatively more muscle mass than arboreal primates, the fact that *all* primates are less muscular than most mammals may be a functional consequence of an arboreal heritage.

Although there were significant differences in our sample between arboreal and terrestrial primates and arboreal and terrestrial nonprimate mammals, there are several species that deviate from this observed pattern. The highest percent muscularity is found in two arboreal squirrels, *Sciurus carolinensis* (61% TBM) and *Tamiasciurus hudsonicus* (59% TBM). Within primates, *C. jacchus* is hypermuscular for an arboreal primate (47% TBM). It is possible that these animals deviate from the observed pattern associated with most arboreal mammals because they are hindlimb-dominant quadrupeds [Garber, 1992; Grand 1977, 1983; Schmitt & Lemelin, 2002]. Grand [1977] found that muscle mass can vary between animals that move differently through their environment. For example, Grand [1977] demonstrated that climbers tend to be less muscular than high-speed runners, and that hoppers/leapers are generally hypermuscular (muscle mass $\geq$50% of TBM). Squirrels and *C. jacchus* both prefer larger substrates (~70–80% of all activity occurs on nonterminal branches) and even converge anatomically and kinematically [Schmitt & Lemelin, 2002]. This pattern represents a divergent adaptation from most arboreal primates and many arboreal nonprimate mammals, which forage for leaves, fruits, flowers, and insects on terminal branches. Further, kinematic studies indicate that similar to most other mammals, *C. jacchus* has higher peak vertical substrate reaction forces on its forelimbs relative to hindlimbs. Schmitt and Lemelin [2002] suggest that higher peak reaction forces in the forelimb in *C. jacchus* may be an adaptation for moderately rapid locomotion in an arboreal setting. It is possible that the combination of a small body size and claws (or claw-like nails in the case of *C. jacchus*) may facilitate higher muscle mass values and terrestrial-like locomotion within an arboreal setting.

The Influence of Captivity

One limitation of the present research is that all primates with the exception of *C. jacchus* lived in captivity prior to death. One critical issue is that obesity is a relatively common occurrence in captive primates [Goodchild & Schwitzer, 2008; National Research Council, 2003]. High adiposity in primates in general (see Discussion section titled "The Importance of Body Fat") and particularly among those living in captivity may help explain why the primates in our sample were hypomuscular and also why the free-ranging *C. jacchus* has higher muscularity than other nonhuman primates. For example, the captive male pigtail macaque (*Macaca nemestrina*) in our sample weighed 14,500 g, of which 7,120 g is muscle [Grand, 1983]; thus, 49.1% of TBM is muscle. However, if we consider muscularity relative to fat-free mass (rather than total body mass), overall muscularity would increase to around 54% of body weight.

The observed differences in muscularity in primates compared to nonprimate mammals, as well as the finding that arboreal mammals are hypomuscular when compared with terrestrial mammals, may be related to the distribution of captive versus wild animals in our sample. However, this explanation seems unlikely given that we performed a series of analyses that considered this potentially confounding factor. Our results suggest that although captive environments likely influenced body composition among some individuals in our study sample, habitat differences during life cannot explain our findings of low levels of muscularity among primates and among arboreal mammals.

The Importance of Body Fat

The differences documented in the present study between primates and nonprimate mammals in muscularity may, in part, be shaped by the extent of fat stores in each species. Some primates, particularly humans, have relatively large fat stores and this appears to be shaped by ecological factors such as seasonality [Forbes, 1987; Wells, 2010]. Fat increases overall body mass, which potentially decreases relative muscularity in primates. The relatively large fat stores in humans (and possibly several other species of primate) appear to be closely related to encephalization and the high and obligate metabolic costs that brain expansion brings [Leonard et al., 2003; Wells, 2010]. A related issue, discussed by Leonard and colleagues [2007] but not systematically tested by Leonard and his colleagues, is the question of whether hypomuscularity in humans and other primates is shaped by the relatively large brain sizes seen in humans and other primates.

Hypothesis 5: ECV and muscle mass

In order to consider potential links between brain size and muscularity in primates, we explored the relationship between ECV and muscle mass. We predicted a negative correlation between relative muscle mass and relative ECV among the primates in our sample. This hypothesis stems from Leonard and colleagues' [2007] work that questions whether body composition (specifically fat and muscle) in humans and other primates is shaped by the relatively large brain sizes seen in humans and other primates. Results from this study were inconclusive. Ratio-based analysis yielded a significant negative correlation between relative ECV and relative muscle mass. However, similar results were not obtained using residual-based size-adjusting methods. ECV scales negatively with body mass. Given that ECV and body mass do not scale isometrically ratio-based analysis is the most appropriate means of size standardizing ECV [see Jungers et al., 1995]. Thus, given that ratio size-adjusted ECV correlates negatively with body mass, our findings, although preliminary, partially support the idea that decreased muscularity among primates (likely in conjunction with increased adiposity) is a metabolic adaptation for offsetting the high energetic costs associated with a large brain. However, there are two important items that need to be noted. First, when phylogeny was considered, primates ECV and muscle mass did not significantly negatively correlate. Second, although we did find that primates with relatively large brains are generally less muscular, our limited primate sample and our mixed findings, means that our results should be interpreted with extreme caution.

CONCLUSIONS

This study presents new data on muscularity in primates, which indicate that arboreal mammals, including primates, are hypomuscular. Primates are unique because, regardless of a given species' substrate preference, they have relatively low levels of muscularity compared to nonprimate mammals. These differences between primates and nonprimate mammals may be strictly a result of arboreal ancestry, or possibly a combination of factors such as arboreality, increased adiposity, and an increase in brain size.

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