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Scaling of primate forearm muscle architecture as it relates to locomotion and posture

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ABSTRACT

It has been previously proposed that distal humerus morphology may reflect the locomotor pattern and substrate preferred by different primates. However, relationships between these behaviors and the morphological capabilities of muscles originating on these osteological structures have not been fully explored. Here, we present data about forearm muscle architecture in a sample of 44 primate species (n = 55 specimens): 9 strepsirrhines, 15 platyrrhines, and 20 catarrhines. The sample includes all major locomotor and substrate use groups. We isolated each antebrachial muscle and categorized them into functional groups: wrist and digital extensors and flexors, antebrachial mm. that do not cross the wrist, and functional combinations thereof. Muscle mass, physiological cross-sectional area (PCSA), reduced PCSA (RPCSA), and fiber length (FL) are examined in the context of higher taxonomic group, as well as locomotor/postural and substrate preferences. Results show that muscle masses, PCSA, and RPCSA scale with positive allometry while FL scales with isometry indicating that larger primates have relatively stronger, but neither faster nor more flexible, forearms across the sample. When accounting for variation in body size, we found no statistically significant difference in architecture among higher taxonomic groups or locomotor/postural groups. However, we found that arboreal primates have significantly greater FL than terrestrial ones, suggesting that these species are adapted for greater speed and/or flexibility in the trees. These data may affect our interpretation of the mechanisms for variation in humeral morphology and provide information for refining biomechanical models of joint stress and movement in extant

and fossil primates.

Key words: primate, forearm, locomotion, arboreal, terrestrial, muscle architecture

INTRODUCTION

Multiple studies have suggested that osteological differences in the distal humerus among primates may reflect variation in the force production capabilities of the forearm musculature, likely necessitated by differences in substrate interaction between primates practicing different locomotor patterns (Jenkins, 1973; Ziemer, 1977; Szalay and Dagosto, 1980; Feldesman, 1982; Fleagle and Simons, 1982; Fleagle and Meldrum, 1988; Harrison, 1989; Frost and Delson, 2002). However, in addition to osteological features associated with mechanical advantage, muscle strength may be affected by a number of variables, including muscle mass and muscle fiber architecture.

Jenkins (1973) describes a condition by which torsional stresses at the elbow joint are produced by the force of the extrinsic digital and wrist flexors during pronated hand postures. According to his model (Jenkins, 1973), this force can be counterbalanced in three ways: 1) reducing the flexor muscle mass, 2) increasing the extensor muscle mass, or 3) shifting the flexor muscles posteriorly to run behind the elbow joint. This elegant explanation has been highly cited in the literature and appears to correspond well with the observed skeletal morphology of cercopithecoid primates (Napier and Davis, 1959; Birchette, 1982; Fleagle and Simons, 1982; Harrison, 1989; McCrossin et al., 1998; Frost and Delson, 2002). Although analyses of extrinsic forearm muscle weights have been performed for hominoids and some catarrhine monkeys (Tuttle, 1969; Tuttle, 1972), there is little information available for platyrrhine and strepsirrhine primates.

While the argument that large medial epicondyles support large flexor muscles is clearly logical, muscle force is not reliably predicted by muscle mass or volume (Gans and Bock, 1965). Rather, muscle action is affected by muscle architecture, including fiber length and degree of pennation. The use of physiological cross-sectional area (PCSA) and reduced physiological cross-sectional area (RPCSA) takes these variables into account and provides a better estimate of maximum muscle force than weight measurements alone (Payne et al., 2006; Taylor and Vinyard, 2008). Theoretically, a given muscle compartment of an animal could produce more force with less total volume by altering muscle architecture. Subtle differences in muscle architecture introduce the possibility that the bony area of muscular insertion does not reflect the muscle mass, but instead reflects the force produced by that muscle. Tuttle (1972) was aware of this fact and avoided the use of absolute muscle mass and/or volume in his study of anthropoid hands and feet.

The model proposed by Jenkins (1973) implies that the frequency of use of a particular muscle group in locomotion is reflected in variable volume of the musculature and its osteological origin (i.e., greater employment in locomotion = bigger muscle volume = larger bony insertion). Following this model, we would expect animals involved in locomotor categories employing frequent gripping (i.e., arboreal quadrupedalism, climbing, and suspension) to require greater force of the digital flexors compared to animals that are predominantly terrestrial. Terrestrial animals would be expected to require generation of large forces by their deep digital flexors (in toe-off) and their pronators (in quadrupedalism), but less force in their wrist and superficial digital flexors. The model predicts that greater force will be generated by either increased muscle volume of the appropriate groups, or an appropriate change in muscular architecture. Further, any increase in muscle volume is expected to generate a larger bony origin site (greater epicondylar projection).

Muscle fiber architecture and its relationship to posture, substrate use and locomotor patterns

In our previous studies (Perry and Hartstone-Rose, 2010; Hartstone-Rose and Perry, 2011; Hartstone-Rose et al., 2012b; Hartstone-Rose et al., 2015) the muscle architecture of the masticatory system in felids and lemurs co-vary with the mechanical requirements of differing diets—specifically with gape and bite force. In both clades, the length of the masticatory muscle fibers seems to be adapted for the size of food items, while force variables scale isometrically with body size. In other words, the mass and physiological cross-sectional area of the masticatory muscles scale tightly with body mass, but provide no real dietary behavioral signals. Muscle fiber length, on the other hand, does reveal information about dietary behavior. Because of this common pattern in the masticatory muscles, we suspect that muscle fiber architecture plays an important role in other anatomical regions, for instance as an indicator of adaptation in the muscles of locomotion. An examination of muscle fiber architecture in the limb muscles may indicate whether limb muscles are adapted for strength or speed—the latter, for instance, may be of optimum advantage in aid of vertical leaping. We might also find correlations between muscle fiber structure and substrate use (e.g., terrestrial vs. arboreal) as arboreal primates rely more heavily on quick movement through the trees than terrestrial primates do on land, or higher taxonomic group (between catarrhines, platyrrhines, and strepsirrhines) since selection or drift could drive morphological changes in muscle fiber architecture as well. Fiber type analysis would add even greater depth to this type of analysis, but is beyond the scope of the current study.

Muscle fiber architecture

Skeletal muscle fiber structure should vary across skeletal regions and across taxa in patterns that are related to the selective pressures of that anatomical region – for instance those imposed on the muscles of mastication by specific diets and those imposed on the forelimb muscles by specific locomotor behaviors. Skeletal muscles can be seen as a collection of fibers arranged in parallel. While these fibers have a relatively consistent diameter in muscles of varying sizes, the spatial arrangement of fibers can vary significantly. It is the arrangement of these fibers that is responsible for muscle contraction and force production (Brinckmann, 2002). Muscle fibers may be oriented longitudinally to the force generating axis of the muscle, or they may be pennate (oriented at an angle). In muscles of equivalent gross dimensions, muscles with longitudinally-oriented fibers are longer, and thus the muscle has greater potential to stretch (since stretch is proportional to the resting length of the muscle) and also to move more quickly (since each muscle fiber theoretically contracts at the same rate and longer fibers cover more distance in that same amount of time). Pennation serves to increase the number of muscle fibers with in a given muscle volume. Fibers have a relatively consistent cross section, and cross-sectional area is directly proportional to force production. Pennation increases muscle strength as a consequence of this increase in fiber number. However, pennate muscles have shorter fiber lengths for the same muscle volume. Thus, a fundamental tradeoff exists in muscle fiber architecture: for a given muscle volume, muscles can be adapted for stretch and speed (fewer longer fibers), or adapted for strength (greater number of shorter fibers). If a muscle needs to be both strong and fast and/or flexible, then the muscle must be of greater volume than one that is adapted for only one of these states, or for a compromise thereof (Anapol and Barry, 1996).

As a consequence of differences in muscle fiber orientation, the *anatomical* cross-sectional area of a muscle is not always proportional to its force generating capacity. The *physiological* cross-sectional area (PCSA) of a muscle – the cross-sectional area measured perpendicular to the longitudinal axis of fiber orientation – is a more accurate measure of muscle force production because it represents the sum of the individual muscle fiber cross-sectional areas (Maughan et al., 1983; Brinckmann, 2002). *Reduced* physiological cross-sectional area (RPCSA) – another measure of muscle force – takes into account the amount of force lost due to the angle of muscle fibers in a pennate muscle that runs orthogonal to the muscle's line of action – essentially by removing the vector of force imparted by pennation that is perpendicular to the total muscle's line of action (Anapol and Barry, 1996; Perry et al., 2011).

Locomotor Pattern

The primate order is characterized by a great diversity of locomotor behaviors (Hunt et al., 1996; Fleagle, 1999). Field research has established that greater variation in locomotion exists among primates than was originally thought, both between and within species. Since the early attempts to classify primate locomotion into categories (Prost, 1965a, 1965b) it has been clear that such a task is quite difficult, though anatomists and especially students who use biomechanical approaches have long recognized that a complete understanding of primate musculoskeletal system must rely especially on quantitative primate positional behavior data (Hunt et al., 1996). The aim here is to provide only broad locomotor distinctions, recognizing that some variability in locomotor/postural behavior exists within the taxonomic groups shown in Table 1. As described in the methods section below, we have assigned each species represented in our sample to locomotion/posture and substrate use categories based on the available behavioral literature.

HYPOTHESES AND PREDICTIONS

The primary goal of this study is to evaluate the potential correlation between extrinsic hand/wrist muscle architecture and locomotor patterns/posture, substrate use, and higher taxonomic group across the Order Primates. We explore the scaling patterns of individual architectural variables with body size, in an attempt to elucidate whether there are differences in allometric scaling patterns associated with contrasts in higher taxonomic group, locomotion/posture, and substrate categories. We also test predictions related to the distribution of relative muscle volume and muscle among these groups—i.e. do statistically significant differences occur among primates of differing higher taxonomic group, locomotion/posture, and substrate preferences, when variation related to body size is taken into account?

Our hypotheses regarding forearm muscle architecture and the behaviors in question are as follows:

1) Because of their reliance on speed to move through their habitat, arboreal primates will have relatively greater forearm flexor fiber length (FL) compared to terrestrial primates. Alternatively, because of their reliance on grip strength to hang onto trees, arboreal primates will have relatively high PCSA and RPCSA compared to terrestrial primates.

2) Vertical clingers and leapers will, because of their reliance on quick movement through the trees, have relatively greater forearm FL compared to quadrupedal and suspensory primates. Alternatively, because of their more obtuse wrist position, vertical clinging and leaping primates will have relatively shorter forearm FL compared to

quadrupedal and suspensory primates.

How these variables interact with higher taxonomic group (to examine the influence of founder/drift effects) and across body size (to examine allometric effects) will also be assessed.

MATERIALS AND METHODS

The specimens in this study include ten species of strepsirrhines, fifteen species of platyrrhines, and twenty species of catarrhines (Table 1). More than one individual of eleven species was dissected (*Eulemur fulvus*, *Aotus azarae*, *Callithrix jacchus*, *Callithrix geoffroyi*, *Cebuella pygmaea*, *Saimiri sciureus*, *Sapajus apella*, *Chlorocebus aethiops*, *Miopithecus talapoin*, *Cercocebus atys*, *Gorilla gorilla gorilla*); in these cases the masses of the individuals dissected were averaged, as well as all functional values. If the individual's weight was unavailable, the average for its sex was taken from Fleagle (1999)—if the sex was unknown, a species average was taken from the same reference. All were adult animals and (except the aye-aye, *Daubentonia madagascariensis*) were from captive facilities in the United States and Spain, with the majority of specimens being from Spanish zoos and dissected at the Universidad de Valladolid. The aye-aye was a wild born specimen that died at Parc Tsimbazaza, Antananarivo Madagascar. The same specimen was used for a previous study on the masticatory muscle structure

(Perry et al., 2013). All specimens were fresh frozen with minimal degradation of the muscle tissue.

All antebrachial muscles were dissected from one forearm of each specimen. Each muscle was isolated, removed from its insertion points on the bone, and measured for volume and muscle architecture variables. Data for each muscle was considered both individually and as a part of a broader functional group—i.e. categorized into the broad group of “flexors” (flexor carpi radialis, palmaris longus, flexor carpi ulnaris, flexor digitorum superficialis, flexor digitorum profundus, flexor pollicis longus), “extensors” (extensor carpi radialis longus, extensor carpi radialis brevis, extensor digitorum, extensor carpi ulnaris, abductor pollicis longus, extensor digiti minimi, extensor indicis, extensor pollicis longus, extensor pollicis brevis) and “others” – muscles that do not flex or extend the wrist (brachioradialis, pronator teres, pronator quadratus, supinator). Subgroupings of these (e.g., wrist and digital flexors and extensors) were also analyzed. Some of these specific muscles, particularly those involving fine motor control, were not distinctly identifiable in some specimens. In contrast, some species had notable elaborations and subdivisions of these muscles; for instance, the aye-aye (*Daubentonia*) had a distinct muscle that extended its third digit. It is not surprising that this unique “tap forager” has a unique muscle configuration. Since we analyzed muscles in broader groups (e.g., *all* digital extensors combined) and not in terms of individual identifiable muscles, these variations did not preclude analyses across the whole sample; all species-specific muscle variants were easily combined into their functional groupings.

For those muscles crossing the radiocarpal joint, the tendons were uniformly cut at the level of the flexor and extensor retinacula, rather than excised from their insertion point within the hand. The external tendon was cut from the muscle at the level in which no muscle fibers continued to inset upon it (Stern, 1971). The muscle belly length, width, and thickness were then recorded with respect to their anatomical placement within the forearm, each measured to the nearest 0.01mm using digital calipers. The muscle bellies were then weighed to 0.0001g using a digital scale.

Muscle fiber length was measured using a protocol modified from Rayne and Crawford (1972). Each muscle was immersed in 10% sulfuric acid (for all but the aye-aye) and cooked in an oven at 60°C. Cooking time varied between 45 minutes and 6 hours depending on muscle size and the amount of connective tissue present. The aye-aye (*Daubentonia*) was opportunistically dissected on site in Madagascar, where sulfuric acid was not readily available; instead, its muscles were cooked over longer periods (~1.5 times longer) in white vinegar (~acetic acid). This substitution was validated prior to using it on this specimen, and found to yield equivalent results. The acid cooking process dissolves the collagenous connective tissue and allows individual fascicles to be carefully manipulated with forceps without breakage. The fascicle lengths are then measured using digital calipers. An average of 40 representative fascicle bundles were measured per muscle, ensuring that all regions of the muscle were represented. The mean of these measurements was taken as the fascicle/fiber length (FL) for that muscle.

Muscle mass (MM) and FL are used to calculate PCSA for each muscle from the following equation using a formula modified from Schumacher (1961):

$q = m/lp$

Here, q is PCSA, m is muscle mass, l is mean fiber length, and ρ is a constant: the specific density of muscle. The ρ value used was 1.0564 g/cm^3 (Murphy and Beardsley, 1974). PCSA is in cm^2, muscle mass is in grams (g), and fiber length is in centimeters (cm). Calculations were made after converting FL from millimeters to centimeters.

Muscle thickness, measured perpendicular to the direction of pull of the muscle (bony origin to bony insertion) in the coronal plane, is used for calculating the pennation angle (θ) to then calculate RPCSA. The following formula is used for determining θ (Anapol and Barry, 1996), in which a is muscle thickness and l is mean fiber length:

$\sin\theta = a/l$

Reduced physiological cross-sectional area (RPCSA) provides information about the portion of muscle cross section that applies force parallel to the muscle's overall line of action. The equation for calculating RPCSA includes pennation angle (θ) and, as its name implies, RPCSA is always smaller than PCSA unless all of the muscle fibers run parallel to the long axis of the muscle – that is, the muscle has no pennation at all. We again follow the method of Anapol and Berry (1996) in using the following equation:

$q_r = m(\cos\Theta)/lp$

Muscle data were separated into functional groups: all flexors, all extensors, wrist and digital flexors, wrist and digital extensors, others (pronators, supinator, and brachioradialis), and all muscles combined. MM, PCSA, and RPCSA were calculated as the sum of those values for all muscles in a particular group for an individual specimen. A weighted average FL for each muscle group was calculated by adding the products of each muscle's FL by its MM and then dividing that by the total MM for the group. Prior to regression of logged variables, the cube root of the cubic variables (masses) and the square root of squared variables (PCSA and RPCSA) was taken so that all predicted regression slopes for logged data would be equal to 1.

Predominant locomotion, posture and substrate use were derived from the literature (Table 1). We grouped the species included in this study into three broad locomotor categories: "quadrupedal," which includes primates (both arboreal and terrestrial) that move mainly using a quadrupedal gait; "vertical clinging/leaping," which includes primates that exhibit leaping behavior as a substantial portion of their locomotion; and "suspensory," which includes primates that rely mainly on their forelimbs for locomotion in the trees. We grouped both strepsirrhines (like *Hapalemur griseus* and *Galago senegalensis*) and leaping anthropoids (callitrichines) in the vertical clinging and leaping (VCL) category following Kinzey et al. (1975) and Garber (1992).

Many primates, though primarily arboreal, spend some time on the ground foraging and moving from one foraging site to the next, while others are mainly terrestrial and climb up trees only to escape predators or to sleep (Fleagle, 1999). However, the generally adopted subdivision between arboreal and terrestrial primates does not fully take into account the complexity of substrate use patterns. The degree of terrestriality of different primates can change considerably, even among species that are closely related (Gebo, 1987; McGraw, 1998, 2000). We recognize that many species of guenons, for example, spend different amounts of time on the ground (Gebo and Sargis, 1994); however, for the purpose of this study we classified each species as either arboreal or terrestrial, with terrestrial species spending the majority of their feeding time on the ground (Marchi et al., this issue). In the future, the inclusion of more species in studies of this nature could allow for more specific categorizations concerning substrate use.

In order to test the prediction that there are differences in forearm muscle architecture across primates based on higher taxonomic group, locomotor/posture pattern, and substrate use, scaling patterns were evaluated using Reduced Major Axis (RMA) regressions of each functional variable (MM, FL, PCSA, RPCSA, organized into their functional groups) on the independent variable of body mass. RMA regression was applied across the entire primate sample, and within-group scaling patterns were assessed via RMA of subsets of data parsed by taxonomic group, locomotor category, and substrate use.

Residuals were calculated as the perpendicular distance from the RMA regression line in log space. Multiple pairwise comparisons were applied to evaluate statistical differences in these "size-adjusted" muscle masses among taxonomic, locomotor/postural, and substrate-use groups. All analyses were done in JMP13 (SAS), using a significance criterion of alpha < 0.05.

RESULTS

Allometry across the whole sample

All muscle masses correlate strongly with body mass ($r^2 \geq 0.96$). Across the entire sample, muscle mass scales with body mass via significant, albeit often weak, positive allometry (confidence intervals for slope > 1.0) for the following muscle groups: total flexors + extensors, flexors, total forearm muscles, other muscles, wrist flexors (Table 2). Based on the allometry of the slopes, we can infer that larger primates have relatively larger muscle mass overall than smaller primates. Interestingly, the extensor muscle groups by themselves scale with body mass at a slope statistically indistinguishable from isometry (95% CI overlaps 1.0).

PCSA scales with positive allometry (slopes range from 1.13 to 1.47, see Table 2) with body mass for all muscle groups, with the exception of wrist extensors (WE), which trend weakly towards positive allometry (slope = 1.13, 95%CI = 0.98 to 1.29). Judging from this, it is clear that larger primates have relatively stronger forearm muscles overall, and in particular, relatively stronger forearm flexors than smaller primates. A similar scaling relationship occurs between RPCSA and body mass; however, in this case WE scales with weak positive allometry (slope = 1.13, 95% CI = 1.00 to 1.27) on body mass. Thus, even when "correcting" for pennation, larger primates' forearms are still relatively stronger than those of smaller primates. FL scales isometrically with body mass across every muscle group, indicating that larger primates would not be expected to have relatively greater fiber lengths in their forearm muscles than smaller primates. Although there is a scaling relationship with the strength variables (larger animals are relatively stronger) there is not one with the speed/flexibility variable (FL).

The same trends hold true when looking at the scaling of specific divisions of the muscles across the primate sample. That is, PCSA and RPCSA scale with positive allometry (slopes range from 1.13 to 1.31), while FL scales with isometry tending toward weak, but insignificant (95% CI for slope encompasses 1.00) negative allometry for the flexors and extensors when analyzed both as groups, and when separated into digital and wrist subdivisions. While MM for the combined flexors and extensors was significantly positively allometric, isometric scaling cannot be statistically excluded for the extensor group or the digital or wrist extensor subgroup muscle masses. As with the combined flexor and extensor statistics, larger primates have relatively larger PCSA and RPCSA (signifying greater strength) across all separate forearm functional groups. Likewise, they also have isometric FL trending toward negative allometry for each functional group. However, while the combined flexor and extensor muscles tend to be relatively larger (greater MM) in larger primates, this is driven only by relatively larger flexor MM – the MM of the extensors, although trending toward positive allometry, are statistically isometric.

Analyses of the residuals of architectural variables by higher taxonomic and functional group

No significant differences were found among higher taxonomic groups (strepsirrhines, platyrrhines and catarrhines) in size-adjusted variables (residuals from RMA regression on log body mass). Thus, in our sample, none of these taxonomic groups is any more or less strong, fast, or flexible in any of their forearm muscle groups.

Contrary to our hypotheses, there were also no statistical differences in the forearm architectural variables between the locomotion/posture groups. That is, there are no statistical differences in the strength, flexibility or speed abilities of quadrupedal vs. suspensory vs. vertical clinging and leaping (VCL) taxa or the quadrupeds vs. the combined group of suspensory and VCL species. Also, surprisingly, the aye-aye fell within the range of similarly sized quadrupedal primates across all of the architectural variables despite its highly specialized manual abilities.

Unlike the postural/locomotor comparisons, analyses show that arboreal and terrestrial species are significantly different in PCSA and RPCSA (Table 3): Although there are not significant differences in any of the MM variables between arboreal and terrestrial taxa (i.e., both have equally massive forearm muscles), there is some evidence that terrestrial species have relatively higher PCSA and RPCSA. Although only a few of these strength variables are significant or approach significance, it does appear that terrestrial primates are, in some ways, stronger than arboreal species. The more compelling trend is clearly in the FL data (Fig. 1): arboreal primates have relatively longer forearm muscle fibers than terrestrial primates in their combined flexors and extensors, and also in the sum of all forearm muscles. Most of the other subgroups of muscles either reach or approach significance as well, but the unambiguously significant difference in the most combined categories of muscles suggests that there really is an overarching difference in the FL between terrestrial and arboreal primates – the latter clearly have either more flexible or faster forearm abilities.

DISCUSSION

This study sought to determine whether there are significant relationships between locomotor/postural or substrate groups and forearm muscle architectural variables in primates. We examined a large number of variables grouped by wrist and digital flexors and extensors, "other" muscles (a grouping of the antebrachial muscles that do not affect the wrist or digits) and various combinations thereof. We also sought to use these architectural variables to identify whether specific lineages or functional groups of primates appear to be adapted for strength or speed/flexibility. As we have found in our previous studies of the masticatory apparatus (Hartstone-Rose and Perry 2011; Hartstone-Rose et al. 2012; Perry and Hartstone-Rose 2010) and our similar analysis of leg muscles (Marchi et al., this issue), muscle fiber architecture clearly demonstrates the functional trade-off between strength and stretch with notable behavioral correlates.

As we expected based on previous studies (and basic principles of allometry), our regressions indicate that larger primates have relatively larger and stronger forearm muscles than do smaller primates; when the forearm muscles were analyzed in their functional compartments, PCSA and RPCSA scaled with positive allometry (or with isometry trending toward positive allometry) with body mass in nearly every muscle category. Fiber length, however, scales with isometry with body mass (though this is not always the case with other animals; e.g. Herrel et al. (2002)). From this, we would expect that larger primates would have relatively larger and stronger forearm muscles; they would not, however, have relatively faster or more flexible muscles. This suggests that larger primates benefit more from stronger forearm muscles than they do from faster-moving forearm muscles. With that said, in much of our previous work (e.g. Hartstone-Rose et al. (2012a)), we have found positive allometry in muscle masses and cross-sections, but isometry in fiber lengths – not necessarily because stretch/speed simply scales directly with body size, but because FL tends to be where we see the strongest functional signals. Thus, there is variation in FL between species because of behavioral needs (e.g., frugivory vs. folivory adaptations in masticatory muscles), and this variation reduces the coefficient of correlation sufficiently to reduce any positive or negative allometry signal.

When considering the residuals data, there were no statistically significant patterns independent of body mass supporting the existence of any taxonomic effects within forearm muscle architecture.

Surprisingly, we also did not find architectural signals related to locomotor/postural categorizations; forearm muscle fiber architecture does not reveal statistical differences between quadrupedal primates and those that grip trees vertically or leap propulsively. (Admittedly, that propulsion is achieved almost entirely by the hind-limb musculature; see Marchi et al., this issue).

We did find a strong signal separating primates by substrate use: by some metrics, terrestrial primates are significantly stronger than arboreal primates, and by more substantial signals, arboreal primates have significantly greater FL than terrestrial primates suggesting adaptations for speed and flexibility in the trees. These results demonstrate how the functional tradeoff between strength vs. speed, a tradeoff that we have explored more extensively as we have related masticatory muscle fiber architecture to dietary specializations, applies to the forearm muscles. Although we could find no indication supporting our hypothesis that vertical clingers and leapers have relatively stronger muscles than those in other locomotor groups, it does seem clear that arboreality requires a different architecture than terrestriality.

In the context of Jenkins' model (1973), it would be expected for groups such as arboreal, suspensory, and terrestrial primates to have larger digital flexor volumes and larger bony insertions because of their employment in locomotion. However, only our results for terrestrial primates fit this model, which suggests that the use of bony origins on the distal humerus may not always be an accurate method to predict the force production capabilities of the forearm musculature in primates.

As an extension of this project, our lab is currently examining the covariation of muscle force production with the osteology of their origins – the epicondyles of the distal humerus. Future work will benefit from data on antebrachial muscle strength, allowing for reconstructions of the biomechanical loads resulting from muscle action around the joint, which may speak directly to the models proposed by Jenkins (1973). Although previous work has demonstrated that the length and retroflexion of the medial epicondyle may be a significant predictor of substrate use (arboreality v. terrestriality) in the fossil record, our findings imply a lack of support for hypotheses relating posture (i.e. quadrupedal/orthograde) and locomotion (quadrupedal/suspensory/vertical clinging and leaping) to the distal humerus, as we could not find the soft-tissue relationships that those hypotheses were based on.

However, we are now collecting data on the humeri of the same individuals from this study to test these hypotheses that have related that morphology to specific behaviors requiring differences in strength.

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Table 1. Species used in this study with their body mass, locomotor/postural category and substrate designations; species with two individuals included in the sample are indicated by ⁺.

Species	Common Name	Superfamily[1]	Body Size (g)[2]	Locomotion		Substrate
				Category[3]	Subtype[4]	
Eulemur fulvus⁺	Brown Lemur	Lemuroidea	2215*	Quadrupedalism	Branch walking and running; Leaping; Vertical climbing; Suspension	Arboreal
Eulemur macaco	Black Lemur	Lemuroidea	1880	Quadrupedalism	Branch walking and running; Leaping, Vertical climbing; Suspension	Arboreal
Hapalemur griseus	Gray Bamboo Lemur	Lemuroidea	709*	Vertical Clinging/Leaping	Leaping; Branch walking and running; Vertical climbing; Suspension	Arboreal
Varecia rubra	Red Ruffed Lemur	Lemuroidea	3300[5]	Quadrupedalism	Branch walking and running; Leaping; Vertical climbing; Feet suspension	Arboreal
Microcebus murinus	Gray Mouse Lemur	Lemuroidea	59	Quadrupedalism	Branch walking and running; Leaping	Arboreal
Daubentonia madagascariensis	Aye-Aye	Lemuroidea	2555.00	Tapper	Branch walking and running; Vertical climbing; Leaping	Arboreal
Galago senegalensis	Senegal	Lorisoidea	213*	Vertical	Leaping; Branch walking and running;	Arboreal

	Bushbaby			Clinging/Leaping		
Nycticebus coucang	Slow Loris	Lorisoidea	652.50*	Quadrupedalism	Quadrupedal walking; Vertical climbing	Arboreal
Aotus nancymaae	Nancy Ma's Night Monkey	Ceboidea	787	Quadrupedalism	Quadrupedal walking; Leaping	Arboreal
Aotus azarae+	Azara's Night Monkey	Ceboidea	1230	Quadrupedalism	Quadrupedal walking; Leaping	Arboreal
Ateles fusciceps	Black-Headed Spider Monkey	Ceboidea	8890.00	Suspensory[7]	Brachiation; Leaping; Bipedal walking	Arboreal
Callithrix jacchus+	Common Marmoset	Ceboidea	320.5	Vertical Clinging/Leaping	Branch walking and running; Leaping	Arboreal
Callithrix geoffroyi+	White-Headed Marmoset	Ceboidea	359	Vertical Clinging/Leaping	Branch walking and running; Leaping	Arboreal
Cebuella pygmea+	Pygmy Marmoset	Ceboidea	116	Vertical Clinging/Leaping	Branch walking and running; Leaping; Vertical climbing	Arboreal

Leontopithecus chrysomelas	Golden-Headed Lion Tamarin	Ceboidea	577.50*	Vertical Clinging/Leaping	Branch walking and running; Leaping	Arboreal
Leontopithecus rosalia	Golden Lion Tamarin	Ceboidea	609*	Vertical Clinging/Leaping	Branch walking and running; Leaping	Arboreal
Saguinus bicolor	Pied Tamarin	Ceboidea	429*	Quadrupedalism	Branch walking and running; Leaping	Arboreal
Saguinus labiatus	White-Lipped Tamarin	Ceboidea	539	Vertical Clinging/Leaping	Branch walking and running; Leaping	Arboreal
Saguinus oedipus	Cotton-Top Tamarin	Ceboidea	404	Vertical Clinging/Leaping	Branch walking and running; Leaping	Arboreal
Saguinus imperator	Emperor Tamarin	Ceboidea	475	Vertical Clinging/Leaping	Branch walking and running; Leaping	Arboreal
Saguinus midas	Golden-Handed Tamarin	Ceboidea	515	Vertical Clinging/Leaping	Branch walking and running; Leaping	Arboreal
Saimiri sciureus[+]	Squirrel Monkey	Ceboidea	723.50*	Quadrupedalism	Branch walking and running; Leaping	Arboreal

Sapajus apella+	Tufted Capuchin	Ceboidea	3085*	Suspensory[7]	Quadrupedal walking and running; Leaping	Arboreal
Cercopithecus hamlyni	Hamlyn's Monkey	Cercopithecoidea	3360	Quadrupedalism	Quadrupedal walking and running; Leaping	Arboreal
Cercopithecus cephus	Moustached Guenon	Cercopithecoidea	4290	Quadrupedalism	Quadrupedal walking and running; Leaping	Arboreal
Cercopithecus neglectus	De Brazza's Monkey	Cercopithecoidea	10635	Quadrupedalism	Quadrupedal walking and running; Leaping	Arboreal
Cercopithecus petaurista	Lesser Spot-Nosed Monkey	Cercopithecoidea	2900	Quadrupedalism	Quadrupedal walking and running; Leaping	Arboreal
Cercopithecus cambelli	Campbell's Mona Monkey	Cercopithecoidea	1505	Quadrupedalism	Quadrupedal walking and running; Leaping	Arboreal
Cercopithecus mona	Mona Monkey	Cercopithecoidea	5100	Quadrupedalism	Quadrupedal walking and running; Leaping	Arboreal
Chlorocebus aethiops+	Grivet	Cercopithecoidea	3620*	Quadrupedalism	Quadrupedal walking and running; Leaping	Terrestrial
Erythrocebus patas	Patas Monkey	Cercopithecoidea	8185*	Quadrupedalism	Ground walking and running (hand digitigrady)	Terrestrial

Miopithecus talapoin[+]	Angolan Talapoin	Cercopithecoidea	1380	Quadrupedalism	Quadrupedal walking and running; Leaping	Arboreal
Cercocebus atys[+]	Sooty Mangabey	Cercopithecoidea	10350	Quadrupedalism	Ground walking and running (hand digitigrady)	Arboreal
Cercocebus torquatus	Collared Mangabey	Cercopithecoidea	6230	Quadrupedalism	Ground walking and running (hand digitigrady)	Arboreal
Macaca sylvanus	Barbary Maque	Cercopithecoidea	16000	Quadrupedalism	Quadrupedal walking and running	Arboreal
Mandrillus sphinx	Mandrill	Cercopithecoidea	6900	Quadrupedalism	Ground walking and running (hand digitigrady); Vertical climbing	Terrestrial
Mandrillus leucophaeus	Drill	Cercopithecoidea	20000	Quadrupedalism	Ground walking and running (hand digitigrady); Vertical climbing	Terrestrial
Papio sp.	Baboon	Cercopithecoidea	78200[6]	Quadrupedalism	Ground walking and running (hand digitigrady)	Terrestrial
Colobus guereza	Mantled Guereza	Cercopithecoidea	9200	Quadrupedalism	Quadrupedal walking and running; Bounding; Leaping	Arboreal
Hylobates lar	Lar Gibbon	Hominoidea	5340*	Suspensory[7]	True Brachiation, Leaping, Bipedal walking	Arboreal
Gorilla gorilla gorilla[+]	Gorilla	Hominoidea	120950*	Suspensory[7]	Ground walking and running (knuckle-walking); Vertical climbing; Modified Brachiation	Terrestrial
Pan troglodytes	Chimpanze	Hominoidea	45466*	Suspensory[7]	Ground walking and running (knuckle-walking);	Terrestrial

	e				Vertical climbing; Modified Brachiation	

[1]Ankel-Simons (2007).

[2]Fleagle (1999) except as noted; average mass for sex if sex known; average for species if sex unknown (annotated by “*”)

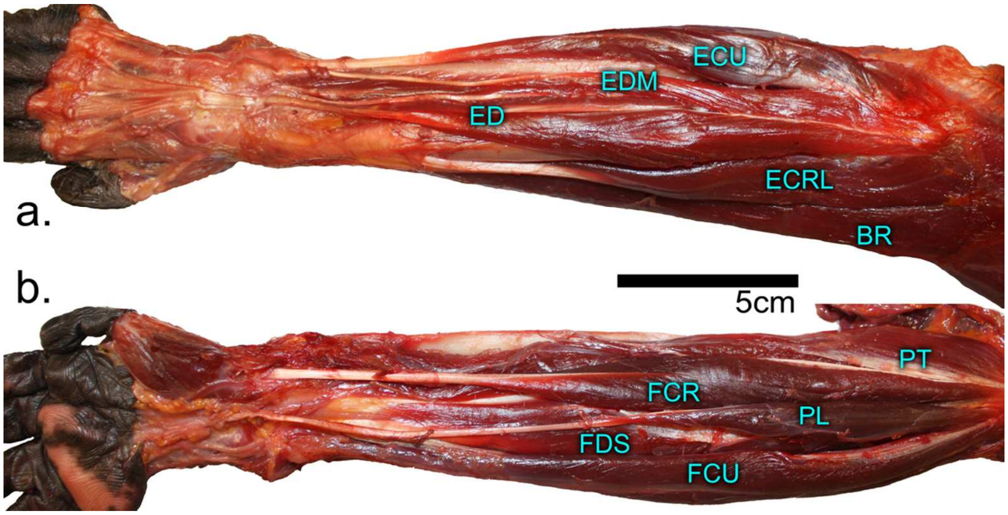
[3]Napier and Napier (1967) except as noted

[4]Hunt et al. (1996)

[5]Body size for *Varecia variegata*

[6]*Papio* sp. body mass calculated as average mass for genus based on Fleagle (1999)

[7]Cant et al. (2003)



Posterior (a) and anterior (b) views of a representative primate forearm, with the muscles of interest labeled.

55x28mm (600 x 600 DPI)

Table 2. Descriptive statistics for RMA regressions of architectural variables against body mass across the whole sample. As described in the methods, because the cube-root and square-root was taken of the volumetric and area variables respectively, all expected slopes = 1.

Y-variable	Slope (β)^b	Y-intercept	r	Lower β CL	Upper β CL
		Log Muscle Mass (g) ^ 1/3			
Total Flexors and Extensors	1.08	-0.79	0.98	1.02	1.16
Flexors	1.09	-0.85	0.98	1.02	1.17
Extensors	1.05	-0.91	0.97	0.97	1.13
Total Muscles	1.11	-0.78	0.98	1.04	1.18
Other Muscles	1.20	-1.14	0.96	1.09	1.32
Digital Flexors	1.07	-0.89	0.98	1.00	1.15
Wrist Flexors	1.18	-1.13	0.97	1.08	1.28
Digital Extensors	1.08	-1.08	0.96	0.98	1.19
Wrist Extensors	1.01	-0.96	0.96	0.92	1.12
		Log FL (mm)			
Total Flexors and Extensors	0.93	0.22	0.96	0.84	1.02
Flexors	0.93	0.22	0.94	0.83	1.05
Extensors	0.98	0.16	0.90	0.83	1.15
Total Muscles	1.00	0.17	0.94	0.88	1.13

Other Muscles	1.30	-0.12	0.77	0.98	1.71
Digital Flexors	0.96	0.22	0.93	0.84	1.09
Wrist Flexors	0.86	0.21	0.88	0.72	1.03
Digital Extensors	0.90	0.19	0.90	0.77	1.06
Wrist Extensors	1.01	0.17	0.92	0.88	1.17
		Log PCSA ^1/2			
Total Flexors and Extensors	1.20	-0.83	0.97	1.10	1.31
Flexors	1.26	-0.99	0.95	1.14	1.40
Extensors	1.17	-1.04	0.95	1.05	1.30
Total Muscles	1.24	-0.82	0.97	1.14	1.35
Other Muscles	1.33	-1.27	0.94	1.17	1.50
Digital Flexors	1.18	-1.01	0.95	1.06	1.32
Wrist Flexors	1.47	-1.46	0.94	1.29	1.66
Digital Extensors	1.33	-1.40	0.92	1.15	1.54
Wrist Extensors	1.13	-1.16	0.92	0.98	1.29
		Log RPCSA ^1/2			
Total Flexors and Extensors	1.24	-0.89	0.97	1.14	1.35
Flexors	1.30	-1.05	0.97	1.19	1.43
Extensors	1.15	-1.03	0.96	1.04	1.27
Total Muscles	1.25	-0.87	0.97	1.15	1.36
Other Muscles	1.31	-1.38	0.94	1.15	1.50
Digital Flexors	1.28	-1.16	0.93	1.12	1.47
Wrist Flexors	1.46	-1.43	0.96	1.31	1.62

Digital Extensors	1.20	-1.27	0.93	1.05	1.39
Wrist Extensors	1.13	-1.14	0.95	1.00	1.27

Figure 2. shows the Flexor FL plotted against Log BM for arboreal and terrestrial primates. The black line indicates the orthogonal fit across the whole sample; the blue line indicates fit for arboreal species and the red line indicates fit for terrestrial species. Strepsirrhines are denoted as green shapes, Platyrrhines as blue shapes, and Catarrhines as red shapes. Open shapes indicate terrestrial species; filled shapes indicate arboreal species. Quadrupedal primates are denoted by squares, VCL primates are denoted by triangles, and suspensory primates are denoted by circles. *Daubentonia madagascarensis* alone is indicated by an asterisk, as it is classified as a tapper.

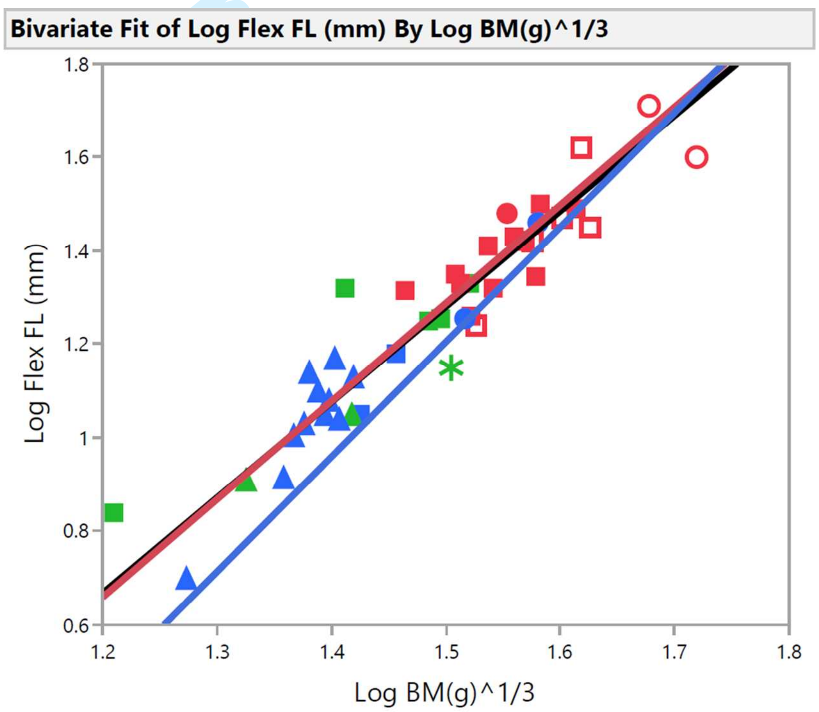


Table 3. Descriptive statistics for one-way analyses of residuals of architectural variables grouped by substrate use. P-values annotated by "*" are significant at an alpha of 0.05, "**" alpha >0.01 and those annotated "~" approach significance.

Substrate Use

	Means		p-value
	Arboreal	Terrestrial	
	Log Muscle Mass(g)^1/3		
Total Flexors and Extensors	0.00	0.01	0.40
Flexors	0.00	0.01	0.40
Extensors	0.00	0.00	0.84
Total Muscles	0.00	0.01	0.48
Other Muscles	0.00	-0.01	0.63
Digital Flexors	0.00	0.01	0.40
Wrist Flexors	0.00	0.01	0.51
Digital Extensors	0.00	0.00	0.96
Wrist Extensors	0.00	0.00	0.98
		Log FL(mm)	
Total Flexors and Extensors	0.00	-0.03	0.01*
Flexors	0.00	-0.02	0.11
Extensors	0.00	-0.02	0.25
Total Muscles	0.01	-0.04	0.01*
Other Muscles	0.02	-0.10	0.009**
Digital Flexors	0.01	-0.04	0.04*

Wrist Flexors	0.00	-0.03	0.14
Digital Extensors	0.01	-0.03	0.12
Wrist Extensors	0.01	-0.03	0.13
		Log PCSA^1/2	
Total Flexors and Extensors	0.00	0.02	0.10~
Flexors	0.00	0.02	0.34
Extensors	0.00	0.00	0.85
Total Muscles	0.00	0.02	0.09~
Other Muscles	0.00	0.00	0.88
Digital Flexors	0.00	0.02	0.20
Wrist Flexors	0.00	0.01	0.75
Digital Extensors	0.00	-0.01	0.72
Wrist Extensors	0.00	0.00	0.98
		Log RPCSA^1/2	
Total Flexors and Extensors	0.00	0.03	0.03*
Flexors	0.00	0.04	0.05*
Extensors	0.00	0.02	0.20
Total Muscles	0.00	0.03	0.09
Other Muscles	0.00	0.02	0.48
Digital Flexors	0.00	0.03	0.26
Wrist Flexors	0.00	0.01	0.59
Digital Extensors	0.00	-0.02	0.43
Wrist Extensors	0.00	0.04	0.08~