From the Ground Up: Integrative Research in Primate Locomotion

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ABSTRACT Primate locomotor adaptation and evolution is a principal and thriving area of research by biological anthropologists. Research in this field generally targets hypotheses regarding locomotor kinetics and kinematics, form–function associations in both the soft and hard tissue components of the musculoskeletal system, and reconstructing locomotor behavior in fossil primates. A wide array of methodological approaches is used to address adaptive hypotheses in all of these realms. Recent advances in three-dimensional shape capture, musculoskeletal physiological measurements, and analytical processing technologies (e.g., laser and CT-scans, 3D motion analysis systems, finite element analysis) have facilitated the collection and analysis of larger and more complex locomotor datasets than previously possible. With these advances in technology, new methods of form–function analyses can be developed to produce a more thorough understanding of how form reflects an organism's mechanical requirements, how shape is influenced by external environmental factors, and how these investigations of living taxa can inform questions of primate paleobiology. The papers in this special section of the *American Journal of Physical Anthropology* present research that builds on that foundation, by combining new data on living primates and new methodologies and approaches to answer a range of questions on extant and extinct primates. Am J Phys Anthropol 156:495–497, 2015.

Locomotion and positional behavior (hereafter "locomotion") are important components of an organism's biology, facilitating travel, foraging, social interactions, and mating, among other things. Studies of the locomotor roles of primate postcrania have been a cornerstone of biological anthropology since its modern inception as a field. This subfield has expanded in the last several decades, with rich and diverse research being undertaken in what we consider to be three broad categories: experimental studies of gait kinematics and kinetics, and the evaluation of musculoskeletal loading environments (e.g., Larson et al., 2000; Schmitt and Hanna, 2004; Shapiro and Raichlen, 2005; Demes, 2007; D'août and Vereecke, 2011), musculoskeletal functional morphology (e.g., Walker, 1974; Fleagle and Meldrum, 1988; Gebo and Sargis, 1994), and reconstructing locomotor behavior in the fossil record (Szalay and Dagosto, 1988; Begun et al., 1997; Richmond et al., 2001; Ward, 2002). We observed that primate locomotion researchers generally specialize in one or two of these three subfields, but projects that integrate across these three areas are rare. This is reasonable given that an individual researcher is not likely to be a specialist in all realms of locomotion research. Although collaboration amongst locomotor research groups provides for holistic approaches to research questions (exemplified by the cranial biomechanics research by Strait et al., 2009), it is still not widespread. One reason for this may be that project start-up can be difficult when individual labs have disparate research foci. Another barrier to cross-specialty collaboration is the difficulty of data-sharing, which is limited by a lack of shared databases in which to host what are often very large datasets, including time-series data (electromyographic, strain, and force data) and three-dimensional anatomical models.

To highlight integrative research and to promote collaboration across the primate locomotion subfields, we convened the primate locomotion symposium "From the Ground Up: Integrative Research in Primate Locomotion" on April 11, 2014 at the 83rd Annual Meeting of the American Association of Physical Anthropologists in Calgary, Alberta. This symposium provided a forum to integrate the many branches of primate locomotor research by posing a single, broad question that was addressed via symposium contributors: "How can integrative research in primate postcrania aid identification of locomotor adaptations?" There were 12 presentations by a total of 41 researchers (including presenters and coauthors) on a range of work focusing on the many ways we can investigate the relationship between form and function, and how positional behavior influences the postcrania of living and extinct primates, humans, and model animals. Six of these papers are included here as a special section of this issue of the *American Journal of Physical Anthropology*. These papers span the primate order, from living Malagasy lemurs, to New and Old World Monkeys, extant hominoids (including humans), and fossil hominins. These studies integrate new techniques and data from living primates to provide novel

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insights into primate locomotor adaptation and evolution.

Some of the research published here is based on classic investigations of form–function relationships of bony morphology, focusing on the relationships between size and shape using three-dimensional geometric morphometric methods (Green et al., in press) and phylogenetic comparative methods (Lewton, in press). Green et al. (in press) demonstrate that geometric morphometric methods are better equipped to tease apart scapular shape similarities and differences in apes and humans. These authors address what appears to be a morphological convergence between humans and orangutans in the shape of the supraspinous fossa that is at odds with the known differences in locomotor behavior between these species. Using a series of morphometric methods, Green et al. (in press) show that the morphological "convergence" between humans and *Pongo* is superficial, an observation that standard univariate measures fail to capture. Lewton (in press) uses analyses of scaling to inform understanding of pelvic adaptation to locomotion in a broad sample of primates. Scaling patterns of the height and robusticity of the lower ilium demonstrate that as primates increase in size—or as locomotor forces increase—the lower ilium becomes shorter and more robust to increase bending strength. This study highlights differences in scaling patterns across locomotor groups, suggesting that functional or mechanical requirements of locomotion affect aspects of pelvic shape that are related to resisting locomotor forces.

Other papers prioritize the use of direct measures of behavior (Nalley and Grider-Potter, in press) and the various technologies now widely available for their capture, such as magnetic resonance imaging (MRI) (DeSilva et al., in press), and electromyography (EMG) (Patel et al., in press). Nalley and Grider-Potter (in press) demonstrate that cervical vertebrae morphology is functionally related to head and neck posture across a broad range of primates. Whereas previous cervical vertebral studies have used behavioral categories with often limited success, these authors used direct measures of head and neck posture to test whether cervical bony variation correlates with differences in posture. Results show that taxa with more pronograde heads and necks exhibit an increased mechanical advantage for deep nuchal musculature and a greater resistance to translation and ventral displacement. Furthermore, results provide support for biomechanical models of the neck that incorporate a more sigmoidal or S-shaped cervical column in pronograde taxa, which may be more accurate than cantilevered beam models.

The remaining papers in this section demonstrate the power of truly integrative work by combining quantitative behavioral, morphometric, and experimental data from living primates and applying those results to interpretations of the fossil record. Patel et al. (in press) use EMG captured during locomotion to test hypotheses regarding the role of crural and pedal muscles in hallucal grasping. This work addresses the hypothesis that the large peroneal process in strepsirrhines and tarsiers—to which the peroneus longus muscle attaches, a primary evertor of the foot—is related to the role of this muscle in adducting the hallux during strong pedal grasping (Walker, 1974; Szalay and Dagosto, 1988). Patel et al. (in press) tested this hypothesis in *Sapajus apella*, and found that it is actually the adductor hallucis muscle that is the primary adductor of the hallux (not peroneus longus), and that there is no functional link between peroneal process size and the activity of the peroneus longus muscle during hallucal grasping.

DeSilva et al. (in press) integrate kinetic, MRI, and osteological data to address hypotheses regarding variability of the midtarsal break (or "midfoot flexibility") in humans and apes. These authors provide a convincing argument for why it is important to include Western, shod populations in gait studies, and they also clearly show that ranges of variation in midfoot flexibility overlap in humans and apes. This observation suggests to the authors that intraspecific variation is critically important and must be addressed when reconstructing locomotion in the fossil record. DeSilva et al. (in press) further demonstrate that foot function of the MH1 individual from the fossil species *Australopithecus sediba* can be interpreted differently based on three competing hypothetical scenarios for the evolution of the human foot, and these interpretations range from ape-like to human-like. As a result, these authors caution against making generalizations regarding foot function when fossil species are represented by single (or very few) specimens.

Chadwell and Young (in press) introduce a new framework for interpreting experimental data on primate gait parameters to evaluate hypotheses regarding locomotion in early primates. Combining kinematic and kinetic data on marmosets during arboreal locomotion on small supports, Chadwell and Young demonstrate that marmosets limit changes in angular momentum by producing torques via muscular contraction and using asymmetrical gaits. The combination of these two factors effectively transforms the limbs into "functional grasping appendages." These authors suggest that the features that are generally thought to characterize primate locomotion (compliant, diagonal sequence gaits, and grasping extremities) may actually be size-related; there may have been a size threshold in primate evolution in which as primates increased in body size, they required compliant, diagonal sequence gaits, and grasping extremities to limit fluctuations in angular momentum to maintain stability on arboreal supports.

These integrative studies demonstrate the current state of primate postcranial research as multidisciplinary and collaborative, which is essential to understanding the evolution of primate locomotion, the specific associations between morphology and behavior, and the behavior of extinct primates. Future research establishing how postcranial morphology is regulated by genetic and developmental mechanisms (e.g., Capellini et al., 2011), and how these mechanisms affect the ability of these structures to respond to the selective pressures surrounding the evolution of locomotor behaviors will be necessary as this area of locomotor research progresses. It will also be crucial to understand phenotypic plasticity of the musculoskeletal system and how morphology responds to epigenetic influences (i.e., how morphology can adapt within an individual's lifetime to changes in the mechanical loading environment in particular). In addition to increasing understanding of evolutionary development, we also need to investigate the relationship between skeletal and behavioral ontogeny within individuals to determine how differences in juvenile and adult behaviors affect form. As DeSilva et al. (in press) have shown, intraspecific variation in morphology can complicate our reconstructions of fossil species behavior given small fossil sample sizes, and a greater understanding of the effects of intraspecific variation in behavior and morphology in extant species will be crucial to reconstructions of past behavior.

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