Symposium on Primate Ecomorphology: introduction

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DOI:
10.1111/joa.12455

Ecomorphology

Introduction

This volume is the result of a joint conference for the Anatomical Society and Primate Society of Great Britain (PSGB) on Primate Ecomorphology, which was held at the University of Birmingham, UK in December 2014. Many of the papers in this volume provide excellent introductions to the ecomorphological framework (see for example Elton and Colleagues and Soligo and Smaers), which I shall not attempt to compete with here; suffice to say ecomorphology is broadly the study of the association between an animal's morphology and habitat, and the behavioural responses that mediate it. While ecomorphological relationships are perhaps most richly documented in studies of the diet and locomotion of fish and lizards, the papers in this volume remind us of the many early pioneers of primate ecomorphology such as Matt Cartmill, Bob Sussman, John Fleagle and Peter Rodman (for references see Elton et al. and Soligo and Smears, this volume). Their work, among others, laid the foundations for this contribution,, which aims to review current understanding of key topics in primate ecomorphology and ask how modern research can overcome the challenges to understanding the ecomorphology of extant and extinct primates.

The ecomorphological framework is grounded on the concept that morphology is an accurate and predictable reflection of an animal's current behaviours and ecology. In an age where technological advances have allowed the generation and analysis of datasets of unimaginable complexity, the apparent simplicity of this framework is appealing. Nevertheless, the recent growth of the field and particularly studies that have considered the relationship between microhabitat specialization and morphological specialization in a broad quantitative framework (e.g. Brandl et al., 2015) have revealed areas of unanticipated complexity, and shown that many ecomorphological relationships are less clear, much less linear and much more multifaceted than expected. Nowhere is this likely to be more so than in the primates. Many factors might confound the ecomorphological relationship; for example, morphology may be subject to non-functional influences on form, such as genetic drift and phylogenetic inertia and morphological traits may not keep pace with environmental change, such that observed traits reflect past rather than current environments. For primates however, the complexity increases. Primates are highly social, and their complex social organisations and hierarchies exert a strong influence on the way different individuals are able to exploit and interact with their habitat. Moreover their high intelligence and high proportion of muscle to tendon means that they are highly plastic in their behaviour and morphology. Indeed, Elton and colleagues ask in their contribution, can we ever identify a primary ecological determinant of a given primate trait because compromises between different functional pressures may result in a feature being just adequate for any particular task. These issues present considerable challenges for quantifying clear patterns in the ecomorphology of extant primates and transferring this framework to extinct taxa introduces yet another layer of complexity.

All the papers in this issue of the Journal of Anatomy were prepared by speakers at the Primate Ecomorphology symposium, together with their research colleagues. Most authors have taken such a holistic view of the opportunities and challenges of applying an ecomorphological framework to quantifying the dynamic interactions between both extant and extinct primates and their physical and social environments that the core themes of plasticity, sociality and interpreting the ecomorphology of extinct species run throughout the volume rather than separating contributions into topical groups. A further repercussion of the holistic nature of the papers is that I cannot possibly do justice to the wealth of information in each paper in this short introductory piece. The description that follows therefore details some of the many highlights I have found in each of the papers. I thank the authors wholeheartedly for their hard work, which has resulted in this amazing, far reaching and stimulating volume of Journal of Anatomy.

The volume begins with **Sarah Elton and colleagues** who, through a detailed consideration of the ecomorphological framework, pose a holistic suite of questions about the nature of the ecological signals that might be expressed in the generalised skeletons that are typical of many monkeys, how we can interpret these signals and how these factors might influence reconstructions of locomotor behaviours and habitat preferences in extinct species. This is a fascinating and detailed paper, but I was particularly struck by one of their conclusions: They point out that whilst it is heuristically useful to think in terms of ‘terrestrial’ or ‘arboreal’ in palaeobiological research, an animal faced with a predator or a tasty foodstuff is unlikely to be so prescriptive. This alludes to the important concept that we may have been overly narrow in our interpretations of the locomotor behaviour of fossil primates, which has wide ranging ramifications for our current understanding of primate evolution.

In the 2nd paper **Erin Butler and Nate Dominy** provide an excellent example of the confounding effect of primate muscular plasticity on reconstructions of the ecomorphology of extinct species. They show that the limited availability of human cadaveric material, which has forced a general assumption that minimal variation exists in human populations and/or that industrialized populations represent the human species as well as any other, has significantly hampered our understanding of early hominin locomotor efficiency. Expanding on their earlier work that demonstrated that exploitation of arboreal resources by small-bodied (pygmy) rainforest hunter-gatherers is largely facilitated by muscular adaptation, they present a more detailed interpretation of their ecomorphology. They show convincingly that despite the volume of research on humans, we still don't fully understand how human muscle-tendon architecture can be tailored to specific ecological or environmental demands. Their conclusion that the human pygmy phenotype is a promising model system for understanding hominin bipedal efficiency links to many of the other papers in the volume that argue arboreality was more important in our ancestry than has been previously thought.

In the 3rd paper **Tracy Kivell** continues the plasticity theme, with a detailed and candid review of the evidence for whether the plasticity of trabecular bone can provide a strong functional signal of how a bone or joint was used during an individual's lifetime, to supplement the more limited functional information that can be gleaned from external skeletal morphology. Kivell reveals a myriad of unexpected complexities that have become apparent in making functional inferences about locomotor behaviour from variation in trabecular architecture. Nevertheless she argues that ongoing methodological advances combined with the associated accumulation of sample sizes and increased understanding of the relationship between ecology, biomechanics, morphology and behaviour in extant species, will mean that analyses of trabecular structure will be able to tease out functional signals in fossil bones in the near future.

Anne Burrows and colleagues, in the 4th paper, accepted perhaps the greatest challenge set; to develop the case that a primate's social environment should be considered within the ecomorphogical framework. While linking broad social behaviours to specific morphologies might not always be straightforward, Burrows et al. exploit the fact that mimetic muscle morphology is directly linked to social communication since contraction of the musculature leads directly to the facial display. They present 2 case studies 1) comparing gross morphology of the mimetic muscles around the external ear in Rhesus and Sulawesi macaques that are closely related but have very different methods to maintain social cohesion and 2) comparative physiology of the orbicularis oris muscle in humans, chimpanzees and siamangs to show the contrasting demands of facial and vocal communications. They conclude that observed morphology might reflect a compromise between the demands of the physical and social environments. This is an exciting and young field, and the authors outline several future direction of research. Clearly the next step is to demonstrate that primate adaptations to social behaviour compromise adaptations to the physical environment and result in less than optimal solutions to the latter.

Christophe Soligo and **Jeroen Smaers** deliver a comprehensive review of current perspectives on the origin and early evolution of primates, coupled with a thought-provoking ecomorphological synthesis of primate origins. Among many other topics, these authors develop the plasticity theme with consideration of the role of the brain in buffering a species'anatomy against natural selection. They reason that the brain determines how an individual perceives its environment, and the behaviours it uses it interacts with it. Thus, in the absence of direct evidence of ancestral primate behaviour, they suggest that one of the most significant new sources of information on the adaptive context and behavioural flexibility of early primates could come from application of the increasingly sophisticated comparisons possible on the brain anatomy and phylogenetic mapping of neural characteristics of extant species.

In the 5th paper, **Kevin Hunt** delivers an incredible synthesis of the broad ecomorphology of apes and monkeys to ask 'why are there apes?' He brings together a detailed comparison of monkey and ape morphology, locomotion, habitat and social organisation to show (among other components) that intense competition between apes and monkeys drove apes to evolve large bodies and suspensory features and monkeys to evolve the ability to digest unripe fruits. I first referenced this paper the day after it was accepted for publication, it's a important contribution to a topic that has appeared intractable, due to limited fossil evidence.

In the 6th paper **Robin Crompton** reflects his delivery of the 2014 Osman Hill Memorial Lecture for the Primate Society of Great Britain. His paper provides a personal synthesis of early hominin ecomorphology, which has been influenced by many of his own studies during 40 years of truly holistic research on hominin palaeontology, the locomotor biomechanics of extant referential models under lab and field conditions and the development of powerful predictive-modelling computer simulations. This engaging paper details not just current understanding of early hominin ecomorphology, but also the history and societal influences on research in this field. There is a great deal of synergy in the conclusions of many of the papers in the volume, and Crompton's conclusions on selection for ecological plasticity by early hominins and the continued exploitation of arboreal resources by hominins complement and consolidate those of Vogel and Dominy, Hunt and Senut.

In the final fascinating paper **Brigitte Senut** brings her palaeontological expertise to bear on a holistic approach to interpreting early hominin behaviour from ecomorphological signals. Through case studies of the origins of human bipedalism and the springing adaptations in fossil rodents (Pedetidae), which track the processes of desertification, she demonstrates the efficacy of an integrated approach in which locomotor reconstructions can be used to understand the environment, and knowledge of past environments can help to better reconstruct the behavioural repertoires of fossil species. She shows that to flesh out the fossil record most effectively we need ecomorphological studies not just of the descendents or models of the primates we are interested in, but of the extant species that may be models of the fossil species the primates coexisted with.

A key theme in the papers in this volume is that understanding the ecomorphological relationships of extant primates is central to reconstructing the ecomorphology of extinct species. It is true that we cannot expect all fossil forms to be reflected in extant species, but the referential modelling process does not necessarily require that to be true. Of course, as Vogel and Dominy show, we need to be careful in our selection of models. But by understanding how living species *can* and *do* interact with their habitat, *despite* skeletal constraints, we can garner a better understanding of the envelope of behaviours a particular fossil species might exhibit without expression in the skeleton and the range of ways that multiple conflicting selective pressures (from the physical and/or social environment) might be resolved in the skeleton. A living referential model need not necessarily be the whole animal; it might be a single feature or system from one or multiple living species, such as the gastrocnemius muscle-tendon unit of small-bodied rainforest hunter-gatherers, or the brain or trabecular morphology of the femur of a range of extant species. Through this holistic approach, the living world still has much to tell us about the dynamic between morphology and ecology in fossil forms.

References

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