Social Behavior of Early Hominins

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Interest in the evolution of human behavior has always featured large in evolutionary biology, challenging the imaginations not just of paleoanthropologists and archeologists, but also of virtually any scientific discipline that touches on human evolution. It certainly has sparked the popular imagination for more than a century, inspiring books and films; pop culture theories; and of course skepticism, doubt, and even hostility. Ever since the first hominin fossils were found, it seems to have been almost irresistible to engage in speculation about the behavior of our ancestors and close relatives, and the exercise continues to the present. For example, Dart (1957) notably emphasized a predilection to violence and power associated with carnivory in the “osteodontokeratic” culture of South African australopithecines. Campbell (1971) takes as a given that human behavior evolved from a chimpanzee-like social system. Washburn and Lancaster (1968) emphasize the role of “Man the Hunter” in the social evolution of hominins. In contrast, Tanner (1987) emphasized the role of gathering in social evolution. Lovejoy (1981) emphasized male provisioning of females in the development of pair-bonds. Wrangham *et al.* (1999) emphasize the role of cooking in the transformation from an-ape-like to human-like social system. I could go on for pages listing papers offering an enormous variety of models and hypotheses based on an equally wide variety of evidences.

Perhaps because it is so easy to tell stories about human behavior, it is easy to dismiss hypotheses about hominin behavior as unsupportable assertion, steeped in preconceptions and cultural bias, and lacking in any real scientific merit. But over the years, the fossil record of human evolution has grown substantially, including not just fossil hominins but a treasure trove of environmental and ecological data. At the same time, behavioral ecology, especially of primates, has built a tremendous body of knowledge about the evolutionary and ecological basis of behavior that has provided extraordinary insight into human behavior. The combination of progress in these disciplines is allowing more and more systematic and scientific approaches to

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constructing and testing models of the evolution of human behavior. There has never been a lack of awareness of how studies of primate behavioral ecology or the functional anatomy of fossils pertain to our understanding of hominin behavior. But the growth of knowledge and sophistication of both fields simultaneously makes it more difficult for an individual to master both, and provides unprecedented opportunity to use both to develop models and test hypotheses about the evolution of hominin social behavior. Consequently, we should encourage more cross-fertilization between behavioral ecologists and paleontologists to develop rigorous studies of what can and cannot be said about behavioral evolution in hominins. The articles presented here were gathered to foster discussion between behavioral ecologists and paleoanthropologists for just this purpose. They represent a range of approaches, providing examples of how theoretical modeling of comparative social behavior can inform us about the forces that must have shaped hominin behavioral evolution, detailed modeling of the ecological forces that determine grouping patterns, the use of life-history correlates of growth and development to develop hypotheses of the evolution of hominin social structure, careful assessment of direct anatomical correlates of life history variables that is valuable for inferring patterns of life history in early hominins, and the value of evaluating changes in the anatomical correlates of social behavior over time in the context of comparative analyses.

Malone, Fuentes, and White bring a broad perspective, in providing a reevaluation of extant hominoid social systems, with a view to identifying the essential factors that must have characterized a shift from a hominoid social system to that of modern humans. They emphasize that hominoids share a highly developed role of behavioral plasticity and niche construction in the evolution of social behavior. This, they suggest, provides the foundation to the evolution of hominin social systems, in particular the development of highly complex, flexible social patterns of coalitions and alliances and enhanced role of reciprocity, and complex intra- and intergroup social negotiations based on physical, material, and symbolic components. The contribution of Malone *et al.* 2012 underscores the fact that interpretations of the evolution of hominin social behavior rely on an understanding of the basic components of social evolution in a comparative context.

Bettridge and Dunbar (2012) provide an analysis of time budget models based on extant baboons that they use to explore aspects of the ecology of extinct baboon species. In particular, they provide an analysis of a series of factors including annual rainfall, seasonality, and temperature variance, along with data on feeding resting, grooming, diet, home range size, predator density, and body size that generates predictive equations that are then extrapolated to the fossil record of baboons. The baboon model is relevant to hominins to the degree that the two taxa shared similar ecology, a fact that has been noted often (Jolly 2001). They note that the model suggests that feeding time may have been one of the most important ecological pressures impacting australopithecine adaptations. More importantly, the Bettridge and Dunbar (2012) approach elegantly illustrates the pragmatic approach of modeling that can be taken to the fossil record.

Lee (2012) focuses on aspects of life history, specifically early infant growth and how parental care influences when infants are likely to die, as key factors associated with brain and body size evolution in primates and therefore hominins. She evaluates data on gestation length, duration of the interbirth interval, age at weaning, mass at

birth and weaning, and their association with patterns of mortality in primates. She then engages in “scenario building,” in which data on brain size, body size, size dimorphism, and food availability are considered in the light of the life-history analyses to create “suggested life history and investment” scenarios for a series of stages of hominin evolution. She concludes “that sustaining rapid, high-cost postnatal infant growth among the later hominins and modern humans required substantial allocation of energy and care from mothers, fathers, and others, leading to alternative mating tactics as well as the prolonged period of childhood in humans.” In this sense, Lee is taking the approach of using life history data from extant primates to construct likely hypotheses about behavior based on what is known about a few key morphological variables.

Kelly and Schwartz (2012) investigate the age at emergence of M1 in *Australopithecus* and *Paranthropus*, and its implications for life history in these taxa. Data on the rate and timing of development are fundamental for developing and evaluating hypotheses about hominin behavioral evolution, as emphasized by Lee. Here, Kelly and Schwartz (2012) provide a reassessment of data that suggests that either early hominin life history was faster than that of apes, that the rate of dental development was dissociated from other life history parameters, or that ages at death in early hominins have been systematically underestimated, leading to underestimates of the age of M1 emergence. Kelly and Schwartz (2012) review the specific implications of each of these possibilities for our understanding of early hominin life history. The analysis illustrates how firmly life-history information can be grounded in morphology, but also underscores the need to assess carefully the limited data on which life-history parameters are inferred in the fossil record.

Comparative analysis of the relationship between behavior and morphology is not only essential for testing hypotheses about adaptations in species, but also serves as the justification for inferring behavior from morphology in extinct species. Plavcan (2012) provides a comparative analysis of sexual size dimorphism in hominins, and suggests that even though dimorphism is widely accepted as a product of sexual selection and mate competition in primates, it provides little information about social behavior beyond an inference of the presence of male competition. He suggests that a consideration of how changes in male and female size alter dimorphism can be more informative, incorporating recent advances in understanding the factors that alter male and female size independently of each other.

Finally, the symposium from which these manuscripts arose was a collaborative effort between Charlie Lockwood and me. I knew Charlie Lockwood for a number of years, ever since his days at Stony Brook. To me he was a quiet, thoughtful, and extremely intelligent man who was a careful scientist and thorough scholar. We shared a common interest in the evolution of sexual dimorphism, especially in the fossil record. We talked a number of times about the interface between studies of dimorphism in the fossil record and the behavioral ecological models that form the fundamental basis for inferences of hominin social behavior. Charlie suggested that we have a symposium at the meetings of the International Primatological Society in Edinburgh, and so it came to pass. Unfortunately, Charlie’s life ended tragically just a few weeks before the conference. It was sad and painful for many of us to lose a beloved friend and colleague. The contributions that he made to paleoanthropology, and especially to our understanding of sexual dimorphism and variation in the

hominin fossil record, will stand for many years to come. The articles assembled here are all contributed in tribute to Charlie and the deepest respect that we had for him as a friend and colleague.

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