Complexity in Biological Anthropology in 2011: Species, Reproduction, and Sociality

ABSTRACT In 2011, the research of biological anthropologists contributed to the emergence of increasingly complex explanations of biological phenomena from previous, simpler interpretations. Major subjects of bioanthropological research in 2011 include new developments in understanding ancient hominin species and archaic Homo population histories; the physiological, neurological, and social effects of mating and reproducing in both humans and nonhuman primates; and the evolution of primate sociality and human cooperation. This review considers these topics of research from a perspective of complexity using conference proceedings, published articles, and social media. In closing, this article demonstrates the natural extension of our scholarly research to modern social networks and illustrates how they may act as a platform by which to increase intradisciplinary engagement and to highlight the complex, wide-reaching, and innovative research that our field contributes to society.

I t is a testament to the strength of our discipline that our research questions are so many and wide ranging. This year, bioanthropologists made discoveries about extant and extinct species, added to the growing literature on human sociality, proposed a model for the evolution of primate sociality, tested the hormonal and neurological effects of mating and parenthood on primates, and produced insights on the myriad facets of infant development—and this list barely skims the surface of what biologically inclined anthropologists were up to. Although these research topics cover a wide swath of bioanthropology, they share a unifying theme: complexity. These trending topics both focused on inherently complex systems (e.g., social systems, the interaction between physiology and behavior) and also advanced our understanding of complexity within each.

The year’s research encompasses many levels of biological organization and complexity. At the population and species level, our understanding of hominin species diversity, phylogeny, and population histories continues to grow through contributions from new genetic data on modern humans, Denisovans, and Neanderthals. At the level of the individual, recent work on the physiological and neurological effects of mating, reproduction, and raising offspring has resulted in an evolving view of primate parental ecology. And, our understanding of the evolution of primate (incl. human) social systems has been advanced by ancestral state reconstructions and modeling techniques. I conclude this review with a forward-looking summary of the “state of the field” and argue for the importance of online social networks as both a natural extension of and a locus for our scholarly work and as a venue for public engagement.

SPECIES AND POPULATION HISTORIES

The recovery of the remarkably complete skeletons of Australopithecus sediba from Malapa Cave in South Africa constitutes one of the most fascinating fossil finds in the past 50 years (Berger et al., 2010). Together, the skeletons (MH1, a juvenile male, and MH2, an adult female) preserve cranial anatomy, an endocast, arm and leg anatomy, pelvic and shoulder girdles, hand and foot bones, and ribs and vertebrae. This year, a special series of articles published in Science detailed the morphology of the brain (Carlson et al., 2011), pelvis (Kibii et al., 2011), hand and wrist (Kivell et al., 2011), and foot and ankle (Zipfel et al., 2011) of the new species. Based on the available fossil and geological data, A. sediba is a 1.98 Ma small-brained hominin that shares some derived features of the hand and pelvis with Homo but also exhibits many primitive morphologies (e.g., long arms, small brain, apelike foot) that it shares with australopiths (Carlson et al., 2011; Kibii et al., 2011; Kivell et al., 2011; Pickering et al., 2011; Zipfel et al., 2011). These fossils reveal an increasingly complex (and unexpected) picture of...
Plio-Pleistocene hominin evolution in which a small-brained species with primitive body proportions was contemporaneous (but not necessarily sympatric) with early Homo.

The mosaic of primitive and derived features that characterizes *A. sediba* makes the interpretation of its phylogenetic relationship to other hominins, especially *Homo*, unclear. Berger et al. (2010) contend that the primitive features of *A. sediba* suggest it is an australopith and that its derived features indicate that it is ancestral to *Homo*. However, not all researchers agree, and the interpretation that the Malapa hominins are directly ancestral to *Homo* (Pickering et al., 2011) dismisses the earliest evidence of fossil *Homo* at 2.3 Ma (a maxilla from Hadar, Kimbel et al., 1997). Furthermore, this scenario requires a tremendous amount of morphological change (e.g., substantial increase in brain size, shift to modern body proportions) to have occurred in the short time between *A. sediba* at 1.98 Ma and the emergence of several *Homo* species around 2 Ma (Spoor, 2011). Another interpretation is that the Malapa fossils represent a “relic population” at the tail-end of the time range during which *A. sediba* lived but that the earlier members of the species were ancestral to *Homo* (Berger et al., 2010). Counter to both of these ideas is that *A. sediba* should actually be subsumed within genus *Homo* because it shares synapomorphies with *Homo* and postdates the earliest fossil attributed to genus *Homo*.

A further complication for interpreting both the phylogenetic position and functional significance of *A. sediba*’s morphological traits is that many of the features used to describe the species are based on the juvenile MH1 skeleton. This is because it is more complete than the adult MH2. However, it is unclear how different the adult and juvenile morphologies of this species were. What is clear is that these fossils represent a previously unknown species and significantly contribute to the increasingly complex picture of a diverse group of contemporaneous hominin species living in the Pleistocene (2.6 Ma to 11 ka).

In addition to debate on species histories, the expansion of our ancestors out of Africa, the dispersal of *Homo sapiens* to all corners of the earth, and what we did along the way is always a major topic of discussion. This year, that discussion revolved around questions concerning the importance of a little-known population of archaic hominins—the Denisovans—to the Neanderthal–human interbreeding debate and to understanding the number and timing of dispersals of *H. sapiens*.

Between 30 and 48 ka, a finger bone and a molar settled in Denisova Cave in the Altai Mountains of Siberia (Derevianko et al., 2008; Reich et al., 2010). These specimens came from two individuals known as “Denisovans” and were located in a stratigraphic layer that holds artifacts from both the Middle and Upper Paleolithic tool industries (Derevianko et al., 2008). A comparison of nuclear genetic data of humans, Neanderthals, and Denisovans suggests that (1) Neanderthals and Denisovans are sister taxa who shared a common ancestor that diverged from the modern human lineage around 800 ka, and (2) Neanderthals and Denisovans diverged from each other around 640 ka (Reich et al., 2010). At the moment, it appears that Denisovans may be descendants of *H. erectus* or *H. heidelbergensis* (Reich et al., 2010), but this will remain equivocal until more genetic and morphological analyses are completed.

Although relatively little is known about this population, genetic data can inform our understanding of the route and number of waves of *Homo sapiens* dispersals out of Africa by tracing the genetic “signature” of Denisovans in modern human populations. This year, David Reich and colleagues (2011) published an article in the *American Journal of Human Genetics* that analyzed SNPs from 33 populations from India, Southeast Asia, Oceania, and Australia and noted the presence or absence of Denisovan DNA (previously extracted from the fossils, Reich et al., 2010) in these populations. The results suggest that Southeast Asia was settled in at least two waves. The first wave included the ancestors of modern New Guineans and Australians, the second those of East Asians and Indonesians. Because all non-Africans share the same amount of Neanderthal DNA, these results are consistent with one major dispersal of *H. sapiens* out of Africa followed by several dispersals along the southern coastal route from Africa to Asia. In addition, the data suggest that interbreeding between *H. sapiens* and Denisovans occurred around the time of the first wave of dispersal to Southeast Asia (Rasmussen et al., 2011; Reich et al., 2011). Reich et al. (2011) posit that this admixture occurred in Southeast Asia because the descendants of the first wave shared 4–6 percent of Denisovan DNA, while the descendants of the second wave do not carry Denisovan DNA. This pattern of Denisovan DNA in modern populations is taken by Reich et al. (2011) to indicate that Denisovans occupied a large range between Siberia and Southeast Asia. Others, however, are more reticent to describe the numbers and mode of dispersal of archaic humans (Martinón-Torres et al., 2011) and suggest that Denisovans may have originated in Asia and later migrated to Siberia (Martinón-Torres et al., 2011; Skoglund and Jakobsson 2011).

What is perhaps most interesting about the Denisovan hominins is what we don’t know. We currently have genetic material from one tooth and one phalanx, and the population structure and history that those data suggest are already complicated. Imagine how intricately detailed the explanations of human population movements and admixture might become when we have a large sample of Denisovan fossils. As Rasmussen et al. (2011) note: “the true history of human diversification is likely to be more complex than the simple demographic models considered here” (2011:97).

As with most new discoveries, the year’s research on human paleontology illustrates a more complicated scenario of human evolution than was previously understood. A hominin species with primitive body proportions and a small brain, but an apparently derived, *Homo*-like pelvis that lived at nearly the same time as *Homo erectus*, with its more modern body type, was unexpected. Likewise, the genetic data
on Denisovans complicates our previous understanding of human Old World migrations by demonstrating that there were multiple dispersals of *H. sapiens* into East Asia. These findings allow us to embrace complex narratives of human origins that will become more and more intricately detailed as future findings unfold.

**MATING, REPRODUCTION, AND OFFSPRING REARING**

Although our understanding of species and population histories has become more nuanced, so too has our study of biological variation at the level of the individual. Topics of papers and conference presentations this year covered the intersection among the physiological, hormonal, and social aspects of reproduction and offspring rearing. Although some researchers focused on maternal–fetal ecology, others presented research on the neurobiological and hormonal effects of reproduction and parental interaction with offspring. Clancy and Rutherford organized a symposium at the American Association of Physical Anthropologists conference in Minneapolis titled: “Eating for Two: Maternal Ecology and Nutrition in Human and non-Human Primates,” that turned out to be standing-room only. The contributors to this symposium discussed the effects of maternal nutrition, social experience, and lactation on infant development and biology. Hinde and colleagues (2011) presented a review of recent research on “Mother’s milk and commensal gut bacteria” and noted the presence of 106 strains of 19 species of gut bacteria in mother’s milk. They suggested a transmission model in which maternal gut bacteria translocate to the mammary gland and are then passed to and populate the infant’s gut through nursing. In a similar vein, Yildirim and colleagues (2011) discussed maternal vaginal microbes and Miller (2011) presented data on the immune functions of mother’s milk. Clancy and colleagues (2011) discussed the maternal reproductive effects of consuming foods that incite or fight inflammation (refined carbohydrates and prebiotics, respectively), such as miscarriage and infertility, and presented preliminary data linking systemic inflammation (as represented by C-reactive protein) to the presence of gluten antibodies.

Another theme of the Eating for Two symposium was the cost of reproduction, discussed by Dunsworth and colleagues (2011) and by Piperata and Guatelli-Steinberg (2011). Dunsworth et al. (2011) presented data that refute the “obstetrical dilemma” hypothesis and introduced a new hypothesis that explains human infant altriciality based on maternal physiology and energetics. The obstetrical dilemma—the tradeoff between selection for large-brained infants and selection on narrow pelvic girdles to reduce the biomechanical costs of bipedality in early hominins (Washburn, 1960)—has been largely unchallenged. Recent work on maternal energetics (Dunsworth et al., 2011) and the effects of pelvic width on bipedal cost of locomotion suggests that this particular trade-off model does not fit the data: first, human relative gestation length is comparable to that of other mammals (Dunsworth et al., 2011); second, there is no statistical relationship between pelvic width and the cost of bipedal walking in modern humans (Warren et al., 2011; Lewton et al., 2012). Therefore, contrary to the prediction of the obstetrical hypothesis, altricial birth in humans is likely not a result of biomechanical considerations but instead may be related to a tradeoff between minimizing the maternal cost of gestation and maximizing fetal growth.

Although the effects of mating and reproduction on maternal ecology have always been and continue to be a focus of bioanthropology, recent work has also explored the impacts of mating and reproduction on paternal physiology. Research presented by Hinde and colleagues at the Society for Neuroscience conference (2011) suggests that father and nonfather titi monkeys (*Callicebus cupreus*) experience differential responses to separation from and reunion with their pair mates. Functional brain MRIs of these males after separation and reunion with their pair mates reveal that, compared to nonfathers, fathers exhibit increased glucose uptake in regions of the brain that are responsible for social recognition and emotional memory. These results add to a growing body of literature that examines the physiological effects of parenthood on males and complements the historical emphasis on maternal ecology.

Another study on the hormonal effects of parenting (this time in human males) was presented by Gettler and colleagues in the *Proceedings of the National Academy of Sciences* (2011). This study used longitudinal data from the Cebu Longitudinal Health and Nutrition Survey to investigate the effect of partnering and fathering on male testosterone levels. Previous work by Gray and colleagues has demonstrated that partnered human males have lower levels of testosterone than single males (Gray et al., 2002) and that fathers have lower levels of testosterone than nonfathers (Gray et al., 2006). Gettler et al. (2011) build on this work, demonstrating that males with high levels of testosterone are more likely to become fathers, but that after becoming a partner and father, the same males’ interactions with their children causes their testosterone levels to decline. Gettler et al.’s (2011) results suggest that testosterone mediates the tradeoff between investing in mating and investing in parenting. Ultimately, Gettler et al. suggest that “human males have an evolved neuroendocrine architecture that is responsive to committed parenting, supporting a role of men as direct caregivers during hominin evolution” (2011:16196).

This body of research on reproduction and parenting challenges the traditional narrative of primate parental care, in which females are considered caretakers of offspring and males are considered resource providers. There are some primate taxa for which male parental care has already been demonstrated (owl monkeys, callitrichids, and gibbons), but this phenomenon has generally been considered uncommon. The emerging view of primate parental ecology is now upending the previous paradigm and generating many questions for future research.
SOCIAL NETWORKS

Today, in the Digital Age, the phrase “social network” has an entirely different meaning than it used to. But social networks characterize the primate clade and have always been important areas of research for all of anthropology, including archaeology, sociocultural anthropology, and primatology. Recently, anthropologists have been asking how and when the many forms of primate social structures evolved and how primate sociality was primed to facilitate the evolution of complex sociality that is marked by cooperative behavior in humans. Shultz et al. (2011) tested several models of the evolution of primate social systems using ancestral node reconstructions and found that the best-supported model was one in which solitary foraging evolved into multimale—multifemale groups with the transition from nocturnality to diurnality, suggesting that large social groups may have been an antipredator strategy. Pair bonding and one-male—multifemale groups likely evolved later from multimale—multifemale groups. Shultz and colleagues (2011) suggest that this second transition to kin-based groups, which are rare in mammals, was a key, preadaptive feature of anthropoid primates that ultimately facilitated the evolution of cooperation in humans.

Although social group living has advantages that are exploited by most primates, it also has individual costs. The effects of social relationships on physiological states are complex, and there are conflicting reports of the physiological costs of social rank in primates (see Gesquiere et al., 2011). In some primate studies (which tend to be on cercopithecoid monkeys that inhabit multimale—multifemale groups), low-ranking individuals demonstrate increased levels of physiological indicators of stress (e.g., fecal glucocorticoids, fGC), perhaps in response to decreased access to resources and increased levels of experienced aggression from others. In other studies, an interaction effect has been found between dominance hierarchies and their stability such that in stable social groups, dominant individuals exhibit lower levels of stress hormones than high-ranking individuals, but in unstable groups, dominant individuals experience high levels of testosterone and stress hormones (Sapolsky, 1992). In a report in Science, Gesquiere and colleagues (2011) further nuance previous understanding of social causes of physiological stress. Gesquiere et al. (2011) compared stress hormone levels (fGC) among male baboons and found that, in general, high-ranking males had lower fGC levels than low-ranking males but that the alpha male exhibited higher fGC levels than lower ranking males. These results held regardless of the stability of dominance hierarchies. At least in these baboons, it is more stressful (and likely energetically costly) to be the alpha male, and thus, being the second-ranking beta male may have more health benefits.

Although previous research on primate social systems has generally focused on nonhuman primates, there has been a shift in recent years to a focus on understanding human social systems from a behavioral ecology perspective. The complex system of cooperation and punishment that characterizes human societies is an especially important topic because it is unique among primates and is part of what makes us human. There were several papers this year on human sociality, including a Sackler Colloquium in the Proceedings of the National Academy of Sciences: “In the light of evolution V: Cooperation and conflict” (Strassmann et al., 2011). For example, Strassmann (2011) found that patterns of care and mortality of children in the agriculturalist Dogon of Mali supported predictions derived from kin selection theory but not those from a hypothesis of cooperative breeding. Although other work has supported the categorization of humans as cooperative breeders (for a review, see Kramer, 2010), Strassmann suggests that humans exhibit a diversity of social systems and that one societal descriptor does not accurately fit all (Strassmann, 2011). Cheney (2011) and Silk and House (2011) discussed cooperation in other animals (e.g., felids, canids, birds, bats, and nonhuman primates), and Silk and House (2011) made a compelling case for the need for more comparative experimental research on altruism, cooperation, and punishment in nonhuman primates to understand the evolution of these behaviors in our own species. Boyd et al. (2011) concluded the colloquium with the hypothesis that social learning is a hallmark of human sociality that facilitated the evolutionary success of our species.

Further work on human social groups emphasizes the importance not just of social learning but also of cooperation with non-kin and suggests that, together, large social networks, cooperation with non-kin, and social learning enabled our species to flourish. Mathew and Boyd’s (2011) study of warfare in the nomadic pastoralist Turkana society suggests that large-scale, non-kin groups facilitated the evolution of cooperation in humans. They describe large-scale cooperative warfare efforts that are maintained via direct punishment of defecting warriors through third-party groups, which benefit the entire Turkana ethnolinguistic group, as opposed to smaller kin-based groups within the Turkana as a whole (Mathew and Boyd, 2011). In addition, Hill and colleagues (2011) recently proposed that the success of H. sapiens resulted from a social structure that is unique among primates. In a broad demographic analysis of modern hunter-gatherer populations, Hill and colleagues (2011) found that both sexes may emigrate or remain philopatric (as opposed to male dispersal or female dispersal only, which characterizes many other primates), such that residence groups were not necessarily kin-based and that the majority of individuals within a group were unrelated. Based on these observations, Hill and colleagues (2011) suggested that the emergence of non-kin based human social structure resulted in the growth of social networks that provided a context for large-scale cultural evolution and the emergence of “cumulative culture.” However, while this system of sexual dispersal and philopatry is indeed rare, it is not unique among primates; male and female howler monkeys also leave the natal group. Regardless of whether or not other primates share this uncommon system of sex dispersal, humans are, indeed, unique in their willingness to cooperate.
with non-kin, which is ultimately required for the evolution of large-scale cooperation. Thus, human social structure, which may be unique among primates, is marked by cooperation and coordinated punishment of unrelated individuals and is facilitated by cultural evolution and social learning.

SCHOLARLY AND CIVIL ENGAGEMENT

As evidenced above, the study of sociality and social networks is a defining research interest for biological anthropologists and has a rich history of scholarly study. However, bioanthropologists’ engagement in online social networks as participants instead of only as researchers is both a relatively new and necessary phenomenon. Social media has begun to enhance research and to facilitate public outreach. For example, an online network of scientists can be a helpful research tool and participating in this social network acts to enlarge one’s academic network. From accessing scholarly materials via other scientists (e.g., journal articles to which ones own academic institution does not subscribe) to engaging in a timely “backchannel” discussion of recently published articles or conference proceedings, many scientists have found social media to be an accessible means of engagement with scientists from other institutions with whom they are not personally acquainted. Additionally, social media has the power to facilitate rapid dissemination of research to the public. In a field that is guided by the desire to understand from whence we, as a species, came, our research is bound to garner a considerable amount of interest from the public, who share this curiosity. Although public lectures are one way to engage with members of our societies, online social networks offer another, more broadly based way to share, dialogue, and engage with the local and global public, and to demonstrate the relevance of our research to their lives.

A recent session at the American Anthropological Association meeting in Montreal on Digital Anthropology is a good example of the use of online technologies to engage both with other anthropologists and the public. Lende wrote an extensive piece about these Digital Anthropology talks on his blog, Neuroanthropology (http://blogs.plos.org/neuroanthropology), in which he highlights the growing use of open source technologies and open access practices in producing scholarly research and in interacting with both colleagues and students (Lende, 2011a).

In a time of economic instability and uncertainty, it is now more important than ever to demonstrate our contributions to society. If we do not, we may continue to experience censures like the one from Florida Governor Rick Scott earlier this year, who encouraged undergraduates to major in STEM fields and not anthropology, saying that his state “[doesn’t] need a lot more anthropologists” because jobs are not available for graduates of undergraduate anthropology programs (Bender, 2011). Scott set up a false dichotomy: in fact, a large portion of anthropologists are in STEM fields (e.g., the Physical Anthropology Program of the Division of Behavioral and Cognitive Sciences of the National Science Foundation changed its name this year to the Biological Anthropology Program to more accurately reflect the theoretical and evolutionary underpinnings of our field). Governor Scott’s comment gained quite a bit of publicity and immediate public response was facilitated by a vast online social network that connects anthropologists from the entire discipline via Twitter, Google+, Facebook, and blogs: individual anthropologists addressed Governor Scott from their blogs (e.g., Killgrove, 2011; Lende, 2011b), the American Anthropological Association responded via its blog (2011), and students of the University of South Florida put together an informative and compelling online visual presentation titled “This is Anthropology” (Noble, 2011) that was quickly disseminated across online social networks. As we continue our studies of human nature, we must be cognizant of the mutual benefit of communicating our insights to our local and global communities.

CONCLUSION

As anthropologists, we aim to understand human nature and the ancestors from which we evolved. The narratives that we construct to inform understanding of our species have been and are constantly changing. Our current understanding of nonhuman primate and human evolution is (perhaps necessarily) more complex than it was previously; from newly discovered fossils emerged a more elaborate picture of what early hominins were like, and genetic data shed light on the migration patterns of ancient Homo sapiens, which were more complicated than we expected. In addition, we are beginning to understand how mating and offspring rearing affects both maternal and paternal physiology; this approach has challenged the prevailing narrative of mothers as caregivers and has made room for a more holistic study of parental care. As these interpretations become more varied and foster debate, it is important that we relay our current understanding of human nature to the public. Social media facilitates communication both with an interested public and across our disciplinary scholarly boundaries in support of anthropological inclusivity.

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NOTE

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