

Zoon Politikon

The Evolutionary Origins of Human Political Systems

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We provide the most up-to-date evidence available in various behavioral fields in support of the hypothesis that the emergence of bipedalism and cooperative breeding in the hominin line—together with environmental developments that made a diet of meat from large animals adaptive as well as cultural innovation in the form of fire and cooking—created a niche for hominins in which there was a high return for coordinated, cooperative scavenging and hunting of large mammals. This was accompanied by an increasing use of wooden spears and lithic points as lethal hunting weapons that transformed human sociopolitical life. The combination of social interdependence and the availability of such weapons in early hominin society undermined the standard social dominance hierarchy of multimale/multifemale primate groups. The successful sociopolitical structure that ultimately replaced the ancestral social dominance hierarchy was an egalitarian political system in which lethal weapons made possible group control of leaders, and group success depended on the ability of leaders to persuade and of followers to contribute to a consensual decision process. The heightened social value of nonauthoritarian leadership entailed enhanced biological fitness for such leadership traits as linguistic facility, ability to form and influence coalitions, and, indeed, hypercognition in general.

Overview

This paper deploys the most up-to-date evidence available in various behavioral fields in support of the hypothesis that the emergence of bipedalism and cooperative breeding in the hominin line—together with environmental developments that made a diet of meat from large animals adaptive as well as cultural innovations in the form of fire, cooking, and lethal weapons—created a niche for hominins in which there was a significant advantage to individuals with the ability to communicate and persuade. These forces added a unique political dimension to human social life that, through gene-culture coevolution, became a human mental capacity intentionally to construct and reconstruct the social order. *Homo sapiens* became, in the words Aristotle's *Nicomachean Ethics* (2002 [350 BC]), a *zoon politikon*.

Strong social interdependence plus the availability of lethal weapons in early hominin society undermined the standard social dominance hierarchy, based on pure physical prowess,

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of multimale/multifemale primate groups. The successful political structure that ultimately replaced the ancestral social dominance hierarchy was an egalitarian political system in which the group controlled its leaders. Group success depended on the ability of leaders to persuade and motivate and of followers to submit to a consensual decision process. The heightened social value of nonauthoritarian leadership entailed enhanced biological fitness for such traits as linguistic facility, political ability, and, indeed, human hypercognition itself. This egalitarian political system persisted until cultural changes in the Holocene fostered the accumulation of material wealth, through which it became possible again to sustain a social dominance hierarchy with strong authoritarian leaders.

Self-Interest and Cultural Hegemony Models of Political Power

The behavioral sciences during the second half of the twentieth century were dominated by two highly contrasting models of human political behavior. In biology, political science, and economics, a *Homo economicus* self-interest model held sway (Alexander 1987; Downs 1957; Mas-Colell et al. 1995). In this model, individuals are rational self-regarding maximizers. In sociology, social psychology, and anthropology, by contrast, a cultural hegemony model was generally accepted. In this model, individuals are the passive internalizers of the culture in which they operate. A dominant culture supplies the norms and values associated with role performance, and

individual behavior meets the requirements of the various roles individuals are called upon to play in daily life (Durkheim 1902; Mead 1963; Parsons 1967), of which political participation is an important facet. Contemporary research has been kind to neither model.

Gene-Culture Coevolution: An Alternative to Cultural Hegemony

Contra cultural hegemony theory, daily life provides countless examples of the fragility of dominant cultures. African-Americans in the era of the civil rights movement, for instance, rejected a powerful ideology justifying segregation; American women in the 1960s rejected a deep-rooted patriarchal culture; and gay Americans rejected traditional Judeo-Christian treatments of homosexuality. In succeeding years, each of these minority countercultures was adopted by the American public at large. In the Soviet Union, communist leaders attempted to forge a dominant culture of socialist morality by subjecting two generations of citizens to intensive indoctrination. This effort was unsuccessful and was rejected whole cloth immediately following the fall of the Soviet regime. Similar examples can be given from political experience in many other societies.

There has always been an undercurrent of objection to the cultural hegemony model, which Dennis Wrong (1961) aptly called the “oversocialized conception of man.” Konrad Lorenz (1963), Robert Ardrey (1997 [1966]), and Desmond Morris (1999 [1967]) offered behavioral ecology alternatives, a line of thought culminating in Edward O. Wilson’s *Sociobiology: The New Synthesis* (1975), the resurrection of human nature by Donald Brown (1991), and Leda Cosmides and John Tooby’s withering attack in *The Adapted Mind* on the so-called standard social science model of cultural hegemony (Barkow et al. 1992). Meanwhile, the analytical foundations of an alternative model, that of gene-culture coevolution (see below), were laid by Geertz (1962), Dobzhansky (1963), Wallace (1970), Lumsden and Wilson (1981), Cavalli-Sforza and Feldman (1973, 1981), and Boyd and Richerson (1985). This gene-culture coevolution model informs our analysis of the evolution of human sociopolitical systems.

Homo Moralis

Undermining the self-interest model began in economics with the ultimatum game experiments of Güth et al. (1982) and Roth et al. (1991). In the ultimatum game, one subject, called the proposer, is presented with a sum of money, say \$10, and is instructed to offer any portion of this—from nothing to the full \$10—to a second subject, called the responder. The two subjects never learn each other’s identity, and the game is played only once. The responder, who knows that the total amount to be shared is \$10, can either accept the offer or reject it. If the responder accepts the offer, the money is shared accordingly. If the responder rejects the offer, both players

receive nothing. If the players care only about their own payoffs and have no concern for fairness (i.e., they are self-interested), a rational responder will always accept any positive amount of money. Knowing this, a rational proposer will offer \$1, and this will be accepted.

When the ultimatum game is actually played, however, this self-interested outcome is almost never observed and rarely even approximated. In many replications of this experiment in more than 30 countries, under varying conditions and in some cases with substantial amounts of money at stake, proposers routinely offer responders very generous shares, 50% of the total generally being the modal offer. Responders frequently reject offers below 25% (Camerer 2003; Camerer and Thaler 1995; Oosterbeek et al. 2004; Roth et al. 1991).

In postgame debriefings, responders who have rejected low offers often express anger at the proposer’s greed and a desire to penalize unfair behavior. The fact that positive offers are commonly rejected shows that responders have fairness concerns, and the fact that most proposers offer between 40% and 50% of the pie shows that proposers too have fairness concerns themselves or at least understand that responders’ fairness concerns would motivate them to reject low offers. Of special interest are those who reject positive offers. The explanation most consistent with the data is that they are motivated by a desire to punish the proposer for being unfair, even though it means giving up some money to do so. While initially considered odd, these and other experimental results violating the self-interest axiom are now commonplace.

These and related findings have led in recent years to a revision of the received wisdom in biology and economics toward the appreciation of the central importance of other-regarding preferences and character virtues in biological and economic theory (Gintis et al. 2005; Henrich et al. 2005; Oka-sha and Binmore 2012). It might reasonably be thought, however, that these behaviors are the product of the culture of advanced complex societies. To assess this possibility, a team of anthropologists ran ultimatum game experiments in which the subject pool consisted of members of 15 small-scale societies with little contact with markets, governments, or modern institutions (Henrich et al. 2004). The 15 societies included hunter-gatherers, herders, and low-technology farmers.

This study found that many small-scale societies mirror the results of the advanced economies, but others did not. Among the Au and Gnau people in Papua New Guinea, ultimatum game offers of more than half the pie were common. Moreover, while even splits were commonly accepted, both higher and lower offers were rejected with about equal frequency. This behavior is not surprising in light of the widespread practice of competitive gift giving as a means of establishing status and subordinancy in these and many other New Guinea societies. By contrast, among the Machiguenga in Amazonian Peru, almost three-quarters of the offers were a quarter of the pie or less, and yet of 70 offers, there was just a single rejection, a pattern strikingly different from the standard ex-

periments in advanced economies. However, even among the Machiguenga, the mean offer was 27.5%, far more than would have maximized the proposer's payoffs, given the scant likelihood of a rejection.

Analysis of the experiments led to the following conclusions: (1) behaviors are highly variable across groups; (2) not a single group conformed to or even approximated the model of self-interested agents; and (3) despite the anonymous and asocial setting of the experiments, between-group differences in behavior reflected differences in the kinds of social interaction experienced in everyday life; that is, people generally conform to cultural rules of their societies, even when there is no chance a deviation will be punished.

The evidence for this latter conclusion is compelling. For example, the Aché in Paraguay share equally among all group members some kinds of food (meat and honey) acquired through hunting and gathering. In our experiment, most Aché proposers contributed half the pie or more. Similarly, among the Lamalera whale hunters of Indonesia, who hunt in large crews and divide their catch according to strict sharing rules, the proposer's average allocation to the responder was 58% of the pie. Moreover, the Indonesian whale hunters played the game very differently from the Indonesian university students who were the subjects in another set of experiments (Cameron 1999). Indeed, where voluntary public goods provision was customary in real life (e.g., the *Harambee* system among the Orma herders in Kenya, whereby individuals contribute resources to build a school or repair a road), contributions in the experimental public goods game were patterned after actual contributions in the actual *Harambee* system. Those with more cattle contributed more. By contrast, in the ultimatum game, for which there apparently was no everyday life analog, the wealthy and nonwealthy Orma behaved similarly.

The Moral Underpinnings of Modern Political Systems

The untenability of the self-interest model of human action is also clear from everyday experience. Political activity in modern democratic societies provides unambiguous evidence. In large elections, the rational self-regarding agent will not vote because the costs of voting are positive and significant, but the probability that one vote will alter the outcome of the election is vanishingly small, and adding a single vote to the total of a winning candidate enhances the winner's political efficacy at best an infinitesimal amount (Riker and Ordeshook 1968). Thus, the personal gain from voting is too small to motivate behavior. For similar reasons, if one chooses to vote, there is no plausible reason to vote on the basis of the impact of the outcome of the election on one's personal material gains. It follows also that the voter—if rational, self-regarding, and incapable of personally influencing the opinions of more than a few others—will not bother to form opinions on political issues, because these opinions cannot affect the out-

come of elections. Yet people do vote, and many do expend time and energy in forming political opinions. Although voters do appear to behave strategically (Feddersen and Sandroni 2006), their behavior does not conform to the self-interest model (Edlin et al. 2007).

It also follows from the logic of self-regarding political behavior that rational self-regarding individuals will not participate in the sort of collective actions that are responsible for the growth in the world of representative and democratic governance, the respect for civil liberties, the rights of minorities and gender equality in public life, and the like. In the self-interest model, only small groups aspiring for social dominance will act politically. Yet modern egalitarian political institutions are the result of such collective actions (Bowles and Gintis 1986; Giugni et al. 1998). This behavior cannot be explained by the self-interest model.

Except for professional politicians and socially influential individuals, electoral politics is a vast morality play to which models of the rational self-regarding actor are not only a poor fit but also conceptually bizarre. It took Mancur Olson's *The Logic of Collective Action* (1965) to make this clear to many behavioral scientists, because virtually all students of social life had assumed without reflection the faulty logic that rational self-regarding individuals will vote and will "vote their interests" (Downs 1957).

Defenders of the *Homo economicus* model may respond that voters believe their votes make a difference, however untenable this belief might be under logical scrutiny. Indeed, when asked why they vote, voters' common response is that they are trying to help get one or another party elected to office. When apprised of the illogical character of that response, the common reply is that there are in fact close elections, where the balance is tipped in one direction or another by only a few hundred votes. When confronted with the fact that one vote will not affect even such close elections, the common reply is, "Well, if everyone thought like that, we couldn't run a democracy."

Politically active and informed citizens appear to operate on the principle that voting is both a duty and prerogative of citizenship, an altruistic act that is justified by the categorical imperative: act in conformance with the morally correct behavior for individuals in one's position, without regard to personal costs and benefits. Such mental reasoning, which is built on our urge to conform and our shared intentionality, is implicated in many uniquely human cognitive characteristics, including cumulative culture and language (Bacharach 2006; Sugden 2003). Shared intentionality rests on a fundamentally prosocial disposition (Bratman 1993; Gilbert 1987; Hrdy 2009; Tomasello and Carpenter 2007).

The Political and Economic Structure of Primate Societies

Humans are one of more than 200 extant species belonging to the Primate order. All primates have sociopolitical systems

for regulating social life within their communities. Understanding human sociopolitical organization involves specifying how and why humans are similar to and differ from other social species in general and other primate species in particular. Concerning the latter, there are two major sources of information. First, some traits are distributed widely and linked to other well-known traits and thus were almost certainly already present before humans evolved. For instance, many primate species, including humans and our closest living relatives, seek to dominate others and are adept at forming coalitions. It is thus likely that their most recent common ancestor also possessed these traits. Dominance seeking and coalition formation in humans, then, are not purely cultural. Rather, humans are endowed with the genetic prerequisites for this behavior, as are numerous other primate species (Wrangham and Peterson 1996).

A second source is similarity with our close relatives, the great apes and especially the genus *Pan* (chimpanzees and bonobos). Most nonhuman primate species have great trouble in acting collectively in conflict with neighboring groups (Willems et al. 2013). Chimpanzees are a major exception: they engage in war-like raids where larger parties cooperate closely to target and destroy much smaller ones (Goodall 1986; Wilson 2012). War among human hunter-gatherers likewise largely consists of such a raiding strategy (Keeley 1996), suggesting a shared predisposition to engage in this type of warfare (Wrangham and Glowacki 2012). Obviously, the dramatic changes in human social organization accompanying the origin of defensible wealth (discussed below) produced major changes in the nature of warfare, linked to additional genetic predispositions, such as insider favoritism (Bowles 2006, 2007, 2009; Bowles and Gintis 2011; LeVine and Campbell 1972; Otterbein 2004). Using this logic, we can examine the social structure of multimale/multifemale primate societies (de Waal 1997; Maestripietri 2007) to identify the elements of human sociopolitical organization that were already likely present among the first hominins.

Primates live in groups to reduce the risk of predation (Alexander 1974; van Schaik 1983), exchange information about food location (Clutton-Brock 1974; Eisenberg et al. 1972), and defend food sources and mates against competing groups (Wrangham 1980). These groups, however, rarely engage in organized collective action. As a result, the primate form of group living has only limited need for leaders, that is, individuals instrumental in initiating and coordinating group-level action with the approval and support of other group members. Instead, individuals vary in dominance based on motivation and pure physical prowess, and dominant males gain fitness at the expense of subordinate members of the group. This is especially true for our closest relatives, the genus *Pan*. As King et al. (2009) stress, other species do often have foraging leaders, but their power is based on hierarchical dominance rather than consensus. Despite the fact that such leaders of the hunt appropriate most of the spoils, fol-

lowers must stick with the group to avoid predation while grabbing what little of the catch they can (King et al. 2008; Krauss et al. 2009).

In most primate species, both sexes form dominance hierarchies, in which more dominant individuals gain privileged access to food and mates and, as a result, tend to have higher fitness (Maestripietri 2007; Majolo et al. 2012; Vigilant et al. 2001). In many primate species, dominant females depend on alliances to maintain their position, whereas the same is true for males in far fewer primate species (van Schaik 1996), most notably chimpanzees. Thus, dominants rarely perform any group-level beneficial acts. One exception is male displays toward predators, a behavior seen in a variety of primate species and generally linked to the protection of likely offspring. Another is triadic power interventions (e.g., Boehm 1994; de Waal 1996) that end conflicts in apes and certain monkeys.

The Origins of Primate Sociopolitical Structure

Given the variety of contemporary primate sociopolitical structures, what can we say about the social structure of the most recent common ancestor of contemporary primates, the species from which the hominin species leading ultimately to *Homo sapiens* branched off? Our answer is based on the fact that traits shared by several closely related species were very likely shared by their most recent common ancestor. The challenge is that primates exhibit a wide variety of sociopolitical structures. However, if we limit our sample to species living in woodlands and open savannah that engage in collective defense and confrontational scavenging from large carnivores, which was the probable condition faced by the primates' most recent common ancestor, all extant species live in large, multimale/multifemale groups.¹ Thus, at least from *Homo habilis* on, hominins likely lived in large multimale/multifemale groups (Dunbar 2005; Foley 1996).

Recently, sophisticated phylogenetic approaches have added precision to these inferences by reconstructing the origin of various kinds of social organization in deep time (Silk 2011). Shultz et al. (2011) completed a study based on the genetic distances and phenotypic social-structural similarities of 217 extant primate species, the most recent common ancestor of which is far more ancient than the ancestral *Pan*. Shultz et al. (2011) show that social organization tends to be similar among closely related species, which implies that social structure is determined largely by genes rather than environment in nonhuman primates. This finding runs counter to the alternative assumption that primate social structure is a re-

1. The grass and savannah-living Patas monkey (Hall 1965) is the single exception to the rule that savannah-living primates exhibit a multimale/multifemale social structure. They avoid predators by staying in trees as much as possible, cryptic behavior, wide group spread, and rapid flight.

sponse to the distribution of food resources or risks and is not affected by phylogenetic affiliation.

Shultz et al. (2011) conclude that the earliest primates lived some 72 Mya as solitary foraging individuals who came together only for mating. Multimale/multifemale aggregations appeared some 52 Mya. We can infer from the social structure of contemporary nonhuman primate species living in multimale/multifemale groups that mating was promiscuous and males formed a hierarchical power structure with a single alpha male at the apex. Indeed, most nonhuman primates that live in multimale groups today exhibit this living pattern (Chapais 2008). While this social structure is highly stable and has persisted into the present, when suitably stressed it broke down into two social forms in which a social group included only one male. The first, which may have appeared about 16 Mya, was the single-male harem, while the second, appearing about the same time, was single pair-living.

The implication is that the earliest hominids lived in multimale/multifemale promiscuous social bands, so *Pan* are archetypical species when it comes to reconstructing the origins of the human political system. Dominant male chimpanzees provide little leadership, and they provide virtually no parenting. In many primate species, dominant males have sufficiently high paternity certainty to induce them to provide protection to infants (Paul et al. 2000), but in chimpanzees, paternity is much less concentrated in top-ranked males (Vigilant et al. 2001; Boesch et al. 2006), most likely because chimpanzee females prefer multiple matings and cannot be controlled by dominant males. Thus, males tend to ignore rearing the young. The only clear service dominant males provide to the group is keeping the peace by intervening in disputes and leading predator mobbing (de Waal 1997; Rudolf von Rohr et al. 2012). In short, the political structure of chimpanzee society, like that of primates generally, is largely a system for funneling fitness-enhancing resources to the apex of a social dominance hierarchy based on physical prowess and coalition-building talent. This holds basically for the bonobo as well, where monopolization of matings by particular males is even lower.

Primate Coalitional Politics

Chimpanzee males rely significantly on coalitions and alliances. There are two major types of coalition: rank changing and leveling (Pandit and van Schaik 2003; van Schaik et al. 2006). Rank changing occurs when a male relies on supporters to acquire and maintain hegemony (de Waal 1998; Goodall 1964; Nishida and Hosaka 1996) and hence may not have the highest individual fighting ability (Boesch et al. 1998; de Waal 1998). Leveling occurs when multiple lower-ranking males form coalitions to prevent the top male or males from appropriating too large a share of the resources. These coalitions do not change the dominance ranks of the participants. Females similarly form such leveling coalitions

to counter the arbitrary power of dominant males, especially in captivity (Goodall 1986). This pattern of political power based on the hierarchical dominance of the physically powerful along with a system of sophisticated political alliances to preserve or to limit the power of the alpha male (Boehm and Flack 2010) is carried over, yet fundamentally transformed, in human society (Boehm 2000; Knauff 1991).

The best predictor for male-male coalitions among primates is simply the fact that multiple males find themselves together and no single male can fully monopolize all matings (Bissonnette et al. 2014). Thus, there are broad similarities in social dominance and coalition formation across all multimale/multifemale primate species. This fact runs counter to traditional political theory. Aristotle's *zoon politikon* notwithstanding, political theorists have widely assumed that political structure involves purely cultural evolution, whereas the primate data show roots to political behavior going back millions of years. The primate evidence is important because it lays the basis for an evolutionary analysis of human political systems (de Waal 1998). Such an analysis may elucidate the role of basic human political predispositions in reinforcing and undermining distinct sorts of human sociopolitical structures.

The Evolutionary History of Primate Societies

It would be useful to be able to read past social structure from the historical record. But we cannot. The fossil record provides the most concrete answers to our evolutionary history but is highly incomplete. There are, for instance, skeletal records of only about 500 individuals from our hominin past. Moreover, behavior does not fossilize, and social structure leaves no direct marks in the earth. This is why we must resort to the relationship between phylogenetic proximity and social organization in living primate species (Shultz et al. 2011).

The hominin lineage branched off from the primate mainstream some 6.5 million years ago or earlier (Langergraber 2012; Wood 2010). The watershed event in the hominin line was the emergence of bipedalism. Bipedalism is well developed in *Australopithecus afarensis*, which appeared 3 million years after the origin of the hominin lineage. *Homo ergaster* (2.0–1.3 Mya) or *Homo erectus* (1.9–0.143 Mya) was the first currently documented specialized biped, having a relatively short arm/leg ratio that rendered brachiation infeasible.

Bipedalism in hominins was critically dependent on the prior adaptation of the primate upper torso to life in the trees. The Miocene hominoid apes were not true quadrupeds but rather had specialized shoulder and arm muscles for swinging and climbing, as well as a specialized hand structure for grasping branches and manipulating leaves, insects, and fruit. When the hominin line was freed from the exigencies of arboreal life, the locomotory function of the upper limbs was reduced, so they could be reorganized for manipulative and projectile control purposes. Both a more efficient form of bi-

pedalism and the further transformation of the arm, hand, and upper torso became possible.

Nonhominin primate species are capable of walking on hind legs but only with difficulty and for short periods of time. Chimpanzees, for instance, cannot straighten their legs and require constant muscular exertion to support the body. Moreover, the center of gravity of the chimpanzee body must shift with each step, leading to a pronounced lumbering motion with significant side-to-side momentum shifts (O'Neil 2012). The hominin pelvis was shortened from top to bottom and, by the time *H. ergaster* emerged, had been rendered bowl shaped to facilitate terrestrial locomotion without side-ward movement, the hominin leg bones became sturdy, the leg muscles were strengthened to permit running, and the development of arches in the feet facilitated a low-impact transfer of weight from leg to leg (Bramble and Lieberman 2004). The specialized form of bipedality that arose around 2 Mya thus facilitates running efficiently for great distances, although not approaching the speed of many large four-footed mammals.

Today we celebrate specialized bipedality as the basis for human upper-body physical and psychomotor capacities for crafting tools and handicrafts. But another major contribution of these capacities, as we explain below, was for fashioning and using lethal weapons.

The Control of Fire Fosters Social Sharing Norms

The hominin control of fire cannot be accurately dated. We have firm evidence from about 400,000 years ago in Europe (Roebroeks and Villa 2011) and about 800,000 years ago in Israel (Alperson-Afil 2008), but it is likely that this key event had originated in Africa much earlier (Gowlett and Wrangham 2013). The control of fire had strong effects on hominin cultural and phylogenetic evolution. First, the transition to specialized bipedality is much easier to understand if the hominins that experienced this transition had control of fire (Wrangham and Carmody 2010). Before the control of fire, humans almost certainly took to the trees at night, like most other primates, as a defense against predators. Because predators have an instinctive fear of fire, the control of fire permitted hominins, who were already bipedal, to abandon climbing almost completely.

Second, the practice of cooking food was a related cultural innovation with broad gene-culture coevolutionary implications. Cooking favors a central location to which the catch is transported and hence requires abandoning the competitive, socially uncoordinated “tolerated theft” distribution of calories typical of food sharing in nonhuman primate species in favor of a distribution based on widely agreed-upon fairness norms (Blurton-Jones 1987; Isaac 1977). This major socio-psychological transition was probably made possible by the adoption of some form of cooperative breeding and hunting among hominins that had begun by the time *Homo erectus*

emerged (Burkart and van Schaik 2010). In sum, while the early advent of cooking is not yet firmly established, it is likely that the control of fire and the practice of cooking were an important precondition of the emergence of a human moral order.

Hominins with access to cooked food did not require the large colon characteristic of other primates, which allowed them to reduce the amount of time spent chewing food from the 4–7 hours a day characteristic of the great apes to about 1 hour per day. With a smaller gut, less need for chewing, and more rapid digestion, hominins were liberated to develop their aerobic capacity and perfect their running ability (Wrangham and Carmody 2010).

From Gatherer to Scavenger

Beginning around 2.5 million years ago, there was a major forking in the evolutionary path of our possible ancestors. The Australopithecines branched in at least two—perhaps more, but the fossil record in this area is quite incomplete—very different evolutionary directions. One led to the robust Australopithecines and a genetic dead end by about 1.4 million years ago, and the other very likely led to the first humans.

These diverging evolutionary paths appear to have been the response to novel environmental challenges. Coinciding with this hominin divergence was a shift in the global climate to frequently fluctuating conditions. Early hominins succeeded by learning to exploit the increased climatic instability (O'Connell et al. 2002; Potts 1996, 1998; Richerson et al. 2001).² The resulting adaptations enhanced hominin cognitive and sociostructural versatility. “Early bipedality, stone transport, . . . encephalization, and enhanced cognitive and social functioning,” Potts (1998) argues, “all may reflect adaptations to environmental novelty and highly varying selective contexts.”

A diet based significantly on the flesh and bone marrow of large animals provided a niche for emerging hominins quite distinct from that of other primates and thus selected for the traits that most distinguish humans from apes. This much was clear to Darwin in *The Descent of Man* (1871). However, until recently, most paleoanthropologists assumed that prey was acquired through hunting from the australopithecine outset (Dart 1925; Lee and DeVore 1968; but see Binford 1985). In fact, it now appears that early hominins, in the

2. DeMenocal (2011) notes that Darwin (1859) long ago speculated on the role of climate change in human evolution, as did Dart (1925), and that modern findings support the importance of climate-based selection pressures (Potts 1998; Vrba 1995) and, specifically, climate variability. Potts (1998) examined the environmental records of several hominin localities, finding that habitat-specific hypotheses are disconfirmed by the evidence. By contrast, the variability selection hypothesis, which states that large disparities in environmental conditions were responsible for important episodes of adaptive evolution, was widely supported.

transition from the Pliocene to the Pleistocene, were more likely scavenger-gatherers than hunter-gatherers, of which there is firm evidence dating from 3.4 Mya (McPherron et al. 2010).

The first proponents of early hominins as scavengers believed that the scavenging was passive, in that small groups of hominins took possession of carcasses only after other predators, upon being sated, abandoned their prey (Binford 1985; Blumenshine et al. 1994), but more recent evidence suggests the prevalence of competitive or power scavenging, in which organized groups of humans sporting primitive weapons chased the killers and appropriated carcasses in relatively intact shape (Dominguez-Rodrigo and Barba 2006). The implicit argument is that the combination of coordinated collective action and the lethal weapons of the period were sufficient to drive off other predators and hence presumably to kill certain live prey as well. While a large prey can be driven off a cliff or trapped in a box canyon, it requires powerful weapons to cripple or kill a large predator. Before the advent of poisoned stone-tipped spears and arrows, the active pursuit of large prey was likely impossible (Sahle et al. 2013). The earliest known use of wooden javelins (Keeley and Toth 1981; Thieme 1997) suggests medium-sized prey.

Flaked stone tool making, butchering large animals, and expanded cranial capacity all appear around 3.4 Mya (McPherron et al. 2010), but there is no evidence that *Australopithecus* and *Homo habilis* were in fact quite small, with adult males weighing less than 100 pounds and females about 75 pounds. Their tools were primitive, consisting of stone scrapers and rough hammerstones. They therefore lacked the sophisticated weapons for hunting large and swift-moving prey and hence are unlikely to have hunted effectively, but they could well have scavenged. Modern chimpanzees and baboons are known to scavenge the kills of cheetahs and leopards (Medina 2007), so this behavior was likely in the repertoire of the earliest hominins. With highly cooperative and carefully coordinated maneuvers by use of weapons, they could have chased away even the most ferocious predators.

Hunting and scavenging small animals is not cost effective for large nonhuman primates, while scavenging large animals requires group participation and efficiently coordinated cooperation in both organizing an attack on predators feeding on a large prey and protecting against predators while processing and consuming the carcass (Isaac 1978). Moreover, use of stones as weapons that might be used to scare off other predators and scavengers (Isaac 1987) has been questioned (Whittaker and McCall 2001), but most likely there was an array of tools made of softer materials—very probably including wooden spears—suitable for making bluffing attacks.

Unlike wooden weapons, stones could have been carefully amassed at strategic sites within a large scavenging area, so that when a scouting party located an appropriate food object to scavenge, it could call others to haul the stones to the

site of the carcass, as a strategic operation preceding its appropriation (Isaac 1977). These could have been the first lethal weapons, but carrying wooden spears or clubs would have served equally well to intimidate competing predators and also would have been useful in killing small game.

Stones as Lethal Weapons

Stones are used today in certain contexts by hunter-gatherers as found objects and possibly as fashioned projectiles. Barbara Isaac (1987) studied stones used by recent foragers, also found in concentrations at Olduvai sites by Mary Leakey (1971), some of which were carefully finished spheroids. She observes that the size and shapes of the Olduvai stones render them appropriate for throwing. Recent foragers do use found object stones quite effectively as fighting weapons. Isaac (1987) has documented devastating attacks by hunter-gatherers against early encroaching Europeans, when intensive stoning actually proved more effective than musketry in rapidly inflicting serious casualties. This took place at contact in various parts of the world, so the traditions were likely preexisting.

In Africa, behaviorally modern humans could have used long-range projectile weaponry (atlatl darts and arrows) in conflict for at least 50,000 years (Ambrose 2008; Roach et al. 2013; Shea 2006; Wadley et al. 2009; Wilkins et al. 2012; Wynn 2009). The recent hunting evidence includes a Levalloisian spear point embedded in a prey skeleton (Boëda et al. 1999). Group conflict likely accounts for the limited sampling we do have for humans of Pleistocene death-by-projectiles (Keeley 1996; Thorpe 2003), which includes at Grimaldi a child with a point embedded in its spine (27,000–36,000 BP), in the former Czechoslovakia weapons traumas and cranial fractures on adult males (24,000–35,000 BP), in Egypt an adult male with a point embedded in his arm (20,000 BP), and a Nubian cemetery where 40% of the interred exhibited weapon traumas (12,000–14,000 BP). Tacon and Chippendale (1994) have documented Australian rock art dating back to 10,000 BP that depicts armed combat, with increasing numbers of combatants by 4000 BP. In the Holocene, armed combat is well documented and widespread, as in the work of Lambert (1997) on the remains of California Indians, which exhibit plentiful head injuries and parrying fractures.

If behaviorally modern human beings have used long-range projectile weapons against prey for at least 50,000 years, doubtless they sometimes turned such weapons against other humans over the same period. A special instance of weapon use is documented in art from Spain's Remigia cave. Human stick figures are shown standing with bows held about their heads while a male lies on the ground with the same number of arrows pincushioning him. There are 10 men in the largest of the groups. This may express a group execution theme or possibly a raid carrying out an act of revenge (see Otterbein 2004). This art appears to date to the early Neolithic.

Technological developments such as atlatls, bows and arrows, shields, and body armor are all relatively recent. It has been widely suggested that the advent of the spear-thrower (atlatl) arrived rather late, about 30,000 BP, and the bow and arrow later still (e.g. Klein 1999). But there are recent reports (Lombard and Phillipson 2010) suggesting that bows and arrows may have been in use as early as about 60,000 BP. Some contemporary groups use poisoned projectiles, and their use in prehistory is now susceptible to study (d'Errico et al. 2012), but further research is needed.

This picture of Pleistocene weapon use is supported by that fact that the fossils of large animals that have markings on bones indicating hominin flaying and scraping with flaked stone tools are often found with stones that originated several kilometers away. Contemporary chimpanzees carry stones to nut-bearing trees that they use to crack the nuts (Boesch and Boesch-Achermann 2000), so this behavior was likely available to Australopithecines. Chimpanzees, however, carry stones only several hundred meters at most, whereas *Homo habilis* scavengers carried stones as far as 10 km, probably because they had invented portable containers (McGrew 1992).

Neither the Oldowan tools of the early period nor the later and more sophisticated Acheulean tools—which are found from the early Pleistocene up to about 200,000 years ago—show any sign of being useful as hunting weapons. However, besides stones, human power scavengers of 500,000 years ago probably had sharpened and fire-hardened spears to ward off competitive scavengers and threatening predators, at least after the domestication of fire (Thieme 1997). These weapons could also have been used against conspecifics. By contrast, nonhuman primates use tools, but they do not use weapons in conflictual encounters (Huffman and Kalunde 1993; McGrew 2004). In these species, there is simply no record of a fashioned or found object weapon being used to injure or kill a conspecific.

The cognitive potential to invent and use lethal weapons is likely present in the two *Pan* species. However, in nature, bonobos and chimpanzees fashion tools for extraction of insect or plant foods, while in both species, intimidation displays merely involve found objects being brandished or dragged. Chimpanzees use sticks fashioned from tree branches to ferret bushbabies from their tree hollow hiding places (Gibbons 2007; Pruetz and Bertolani 2007), so the use of sharpened sticks was thus likely within the cognitive capacity of *H. habilis*. However, there is a considerable distance between using sharp sticks as impaling devices and as well-aimed projectiles (Nishida 1973).

The first dedicated and unambiguously lethal weapons to appear with excellent preservation in the archeological record are the multiple all-wooden spears documented by Thieme (1997) at Schöningen, with more than a dozen butchered wild horses and some bison located nearby. These javelins are both streamlined aerodynamically and well balanced for effective throwing, so they were projectile weapons capable

of bringing down medium-sized game at a distance. They also provide a defense against dangerous prey, and they offer hunters a means of threatening other predators away from their kills. These considerations suggest that a paleorecord of lithic weaponry alone is seriously incomplete. What the lithic record does suggest, in its Acheulian continuity, is that this tradition of making wooden spears might also have had great longevity (see Kelly 2005). The emergence of lethal weapons was likely important in the evolution of hominin social organization (Roach et al. 2013). In hunter-gatherer conflicts, hunting weapons quickly become lethal, and even an outnumbered victim can inflict casualties (Lee 1979; see also Churchill and Rhodes 2009). Bingham (1999), Gintis (2000), Bingham and Souza (2009), and Boyd et al. (2010) stress the importance of the superior physical and psychomotor capacities of humans in clubbing and throwing projectiles as compared with other primates, citing Goodall (1964) and Plooij (1978) on the relative advantage of humans. Darlington (1975), Fifer (1987), and Isaac (1987) document the importance of these traits in human evolution. Boehm (1997), Bingham (1999), and Okada and Bingham (2008) document that humans have developed the ability to carry out collective punishment against norm violators, thus radically lowering the cost of punishing transgressors. Calvin (1983) argues that humans are unique in possessing the neural machinery for rapid manual-brachial movements that both allows for precision stone-throwing and lays the basis for the development of language, which—like accurate throwing—depends on the brain's capacity to orchestrate a series of rapidly changing muscle movements. Indeed, Roach et al. (2013) showed that *Homo erectus* had evolved this capacity for accurate overhead throwing, and recent work suggests that the origins of human language are also much older than commonly assumed (Dediu and Levinson 2013), originating in all likelihood more than 700,000 years ago.³

Lethal Combat Between Groups

Fighting between groups ranges from single revenge killings to careful raids in which safety of the raiders is as important as inflicting damage on the enemy, to intensive warfare with genocidal attacks and face-to-face large-scale battle (Keeley 1996; Kelly 2000; Otterbein 2004). Such fighting involves assessments of the relative fighting power of adversaries and of risk (Wrangham and Glowacki 2012), and the array of weapons available to each side obviously enters into these

3. The fossil evidence indicates that hominins developed speech on the order of 1 Mya. The hyoid bone is a key element of speech production in humans. Martinez et al. (2008) show that hominin hyoid bones from 540,000 years ago are similar and hence were inherited from their last common ancestor, *Homo rhodesiensis*, which was from 700,000 to 1,000,000 years ago. Martinez et al. (2004) use evidence from the acoustical properties of Middle Pleistocene fossil remains of the hominin inner ear to argue that hominins of this period had auditory capacities similar to those of living humans.

assessments. The result is an ethnocentric species (LeVine and Campbell 1972) whose members are predisposed to assume the risks associated with aggression, especially against outsiders, but also strive to minimize those risks.

All contemporary foragers arm themselves with lethal hunting weapons, and at times these weapons are deployed by individuals against within-group adversaries and by the group in executing serious deviants (Boehm 1997; Knauff 1991). Both types of homicide, while rare, are well documented, despite a universally strong ethos that strongly disapproves of killing a group member (Brown 1991). To keep their systems of social cooperation viable, foragers strive to peaceably adjudicate the conflicts in their midst (Boehm 2000).

These moral inhibitions are relaxed when ethnocentrism comes into play. The use of weapons between groups can entail massive casualties when desired cooperative relations among groups fail and conflict gains the upper hand (Wiessner 1977). However, even given a pattern of recurrent ethnocentric fighting between groups, hunter-gatherers may succeed in managing these conflicts (Boehm 2013). While the active management of hostilities is universal within bands, such between-group efforts remain both sporadic and unpredictable. Weapons can make forager bands very dangerous to one another to the point of genocide, and some groups live with such hostilities without trying to curtail them.

Social Hierarchy: Dominance and Reverse Dominance

James Woodburn (1982) classified hunter-gatherer societies into immediate-return and delayed-return systems. In the former, group members obtain direct return from their labor in hunting and gathering, with food lasting at most a few days. The tools and weapons they use are highly portable. In delayed-return foraging societies, individuals hold rights over valuable assets, such as means of production (boats, nets, beehives, and the like) and processed and stored food and materials. These societies exhibit forms of social stratification akin to those in modern societies: social dominance hierarchies in the form of lineages and clans. However, the fossil record suggests that delayed-return human society is a quite recent innovation, appearing some 10,000 years ago, although in ecologically suitable locations, it may have existed earlier (most such locations are now below sea level). *Homo sapiens* thus evolved predominantly in the context of immediate-return systems.

The important factor in delayed return is not the cognitive capacity for delayed gratification or long-range planning, which certainly existed in immediate-return societies, but rather the availability of cumulable material wealth. Material wealth allows those who seek social dominance to control allies and resources and thereby thwart the capacity of subordinates to disable and kill them. As long as the material gains from a position of social dominance exceed the cost of coalition building and paying guard labor, social dominance

of the sort common in other primate societies can be re-established in human society. In fact, the appearance of farming and private property in land led to high levels of political inequality in only a few societies, and states with a monopoly in coercive power emerged only after a millennium of settled agriculture. Nor were early farming societies more economically stratified than hunter-gatherer societies (Borgerhoff Mulder et al. 2009). The accumulation of material wealth is thus merely a precondition for the reestablishment of social dominance hierarchies. To avoid confusion, we will call societies that lack forms of material wealth accumulation simple rather than immediate-return societies.

Simple societies, Woodburn (1982) suggests, are “profoundly egalitarian . . . systematically eliminat[ing] distinctions . . . of wealth, of power and of status.” Fried (1967), Service (1975), Knauff (1991), and others likewise comment on the egalitarian character of simple hunter-gatherer societies. The simple versus delayed return dichotomy is in fact somewhat overdrawn, since there is in fact a continuous range of variation between the two archetypes. Many Pleistocene humans used some storage, even if they were nomadic, and they remained strongly egalitarian. The majority of the 58 Late Pleistocene appropriate foraging societies coded by Boehm (2012; see discussion below), including the !Kung considered by Knauff (1991), are of an intermediate type. What factors are responsible for such unusual egalitarianism? Here, we will argue it is due to the combination of interdependence and ability to punish transgressors.

Cut marks on bones suggest that a major investment in large game hunting increased decisively only 250,000 years ago (Stiner 2002), and delegating sharing to a single butcher began 200,000 years ago (Stiner et al. 2009). In establishing timing of this transition to heavy reliance on medium-sized game in humans, Stiner (2002) uses multiple indices—including the age structure of prey and cut marks—to suggest that at this time ungulate hunting became prominent in human subsistence. However, cut marks on bones may not be a reliable indicator of how meat is shared (Lupo and O’Connell 2002). Indeed, if Wrangham and Carmody (2010) are correct in dating the control of fire by hominins and the cooking of meat, the problem of the fair distribution of meat among families—especially important in hard times when only medium- and small-sized prey were available—may well have been solved much earlier. This was likely an early source of egalitarian sentiment that also provided the material substrate for the development of a social morality. Contemporary hunter-gatherer societies are often violent and competitive (Potts 1996), but they almost always distribute large game peacefully, if sometimes contentiously, on the basis of a commonly accepted set of fairness principles (Boehm 2004; Kaplan and Hill 1985*b*; Kelly 1995).

The human ecological niche requires food sharing not only daily but also on a longer-term basis because of the occasional injuries or illnesses to which even the best hunter or gatherer may be subjected (Hill et al. 2011; Sugiyama and

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Chacon 2000). Thus, each individual forager, especially in the immediate-return form of foraging, is utterly dependent on the others in their camp, band, or even wider sharing unit. This strong interdependence dampens the tendency to free ride on others' efforts and favors strong individual tendencies toward egalitarianism as well as sophisticated fairness norms concerning the division of the spoils (Kaplan and Hill 1985a; Whallon 1989).

Collective hunting in other species does not require a fairness ethic because participants in the kill simply eat what they can secure from the carcass and because dominants are evolved to tolerate subordinates to a point that all the hunters are adequately nourished. However, the practice of bringing the kill to a central site for cooking, which became characteristic of hominin societies, is not compatible with uncoordinated sharing and eating. In the words of Winterhalder and Smith,

Only with the evolution of reciprocity or exchange-based food transfers did it become economical for individual hunters to target large game. The effective value of a large mammal to a lone forager . . . probably was not great enough to justify the cost of attempting to pursue and capture it. . . . However, once effective systems of reciprocity or exchange augment the effective value of very large packages to the hunter, such prey items would be more likely to enter the optimal diet. (Winterhalder and Smith 1992:60)

Fire and cooking thus coevolved with the emergence of a normative order and social organization based on ethical behavior.

The second element is that egalitarianism is imposed by the community, creating what Boehm (1999) calls a reverse dominance hierarchy. Hunter-gatherers share with other primates the striving for hierarchical power, but among mobile foragers, social dominance aspirations are successfully countered because individuals do not accept being controlled by an alpha male and are extremely sensitive to attempts of group members to accumulate power through coercion. When an individual appears to be stepping out of line by threatening or killing group members, he will be warned and punished. If this behavior continues and ostracism does not work, the group will delegate one member, usually a close relative of the offender, to kill him. Boehm's message in *Hierarchy in the Forest* (1999) is that "egalitarianism . . . involves a very special type of hierarchy, a curious type that is based on antihierarchical feelings."

We can regard this phenomenon as an extension of the leveling coalitions seen among primate males (Pandit and van Schaik 2003). Female chimpanzees in captivity act collectively to neutralize alpha male bullies (de Waal 1996), and wild chimpanzees form large coalitions to banish, badly wound, or even kill high-ranking males. Bonobos in the wild have been observed to behave similarly. By comparison with humans, however, leveling coalitions among primates are limited to the genus *Pan* and generally quite small.

Because of the extremely long period during which humans evolved without the capacity to accumulate wealth, we have become constitutionally predisposed to exhibit these antihierarchical feelings. Of course, in modern democratic societies, there is still enough willingness to bend to authority in humans to ensure that a marked or tyrannical social dominance hierarchy remains a constant threat and often a reality.

Capable leadership in the absence of a strong social dominance hierarchy in band-level societies is doubtless of critical importance to their success, and leaders are granted by their superior position and with the support of their followers, with fitness and material benefits. Leadership, however, is based not on physical prowess but rather on the capacity to motivate, persuade, and help the band to reach a consensus. This account of the growth of intelligence is an elaboration upon the Machiavellian intelligence hypothesis (Byrne and Whiten 1988; Humphrey 1976; Jolly 1972) that stresses the effect of encephalization on enhancing the mean fitness of group members, not simply advancing the interests of the leader.

Reverse dominance hierarchy is documented by Boehm (2012). Boehm located 339 detailed ethnographic studies of hunter-gatherers, 150 of which are simple hunter-gatherer societies. He coded 50 of these societies from around the world. He calls these simple hunter-gather societies Late Pleistocene appropriate (LPA). Despite the fact that these societies have faced highly variable ecological conditions, Boehm finds that their social organization follows the pattern suggested by Woodburn (1982) and elaborated by Boehm (1997). The LPAs exhibit reverse dominance hierarchy and subscribe to a common human social morality. This morality operates through internalized norms, so that individuals act prosocially because they value moral behavior for its own sake and would feel socially uncomfortable behaving otherwise.⁴

How do we explain this unique pattern of sociopolitical organization? Woodburn attributes this to humans' access to lethal weapons that neutralize a social dominance hierarchy based on coercion. "Hunting weapons are lethal," he writes, "not just for game animals but also for people. Effective protection against ambush is impossible . . . with such lethal weapons" (1982:436). Woodburn adds, "In normal circumstances the possession by all men, however physically weak, cowardly, unskilled or socially inept, of the means to kill se-

4. The notions of norms and norm internalization (Durkheim 1902; Parsons 1937) are common in the social sciences. According to the sociopsychological theory of norms, appropriate behavior in a social role is given by a social norm that specifies the duties, privileges, and expected behavior associated with the role. Adequate performance in a social role normally requires that the actor have a personal commitment to the role that cannot be captured by the self-regarding public payoffs associated with the role (Gintis 2003a; Gintis and Helbing, forthcoming).

cretly anyone perceived as a threat to their own well-being . . . acts directly as a powerful leveling mechanism. Inequalities of wealth, power and prestige . . . can be dangerous for holders where means of effective protection are lacking” (1982:436).

Boehm (2012) argues that his LPAs inherited from our ancient hunter-gatherer forbears the capacity to control free riders through collective policing but using gossip and informal meetings as the method of collecting information concerning the behavior of group members. Moreover, according to our best evidence, the hunter-gatherer societies that defined human existence until some 10,000 years ago also were involved in widespread communal and cooperative child rearing (Hrdy 1999, 2000, 2009) and hunting (Boehm 1999, 2012; Bowles and Gintis 2011; Boyd and Silk 2002), thus tightening the bonds of sociality in the human group and increasing the social costs of free-riding behavior.

Nonhuman primates never developed weapons capable of definitively controlling a dominant male. Even when sound asleep, a male chimpanzee reacts to being accosted by waking and engaging in a physical battle, basically unharmed by surprise attack. In *Demonic Males* (1996), Wrangham and Peterson recount several instances where even three or four male chimpanzees viciously and relentlessly attack a male for 20 minutes without succeeding in killing him (but see Watts et al. 2006). The limited effectiveness of chimpanzees in this regard can mainly be ascribed to their inability to wield effectively potentially dangerous natural objects, for instance, stones and rocks. A chimpanzee may throw a large rock as part of a display, but only rarely will it achieve its target.

The human lifestyle, unlike that of chimpanzees, requires many collective decisions, such as when and where to move camp and which alliances to sustain or cut. This lifestyle thus requires a complex sociopolitical decision-making structure and a sophisticated normative order. Many researchers incorrectly equate dominance—as found among chimpanzees—with leadership. In some species, such as gorillas, dominants can indeed initiate or influence group movements, because others rely on the dominant male as the main protector and value his proximity. In most human foragers, there are no such dominants.

Capable leadership in the absence of a social dominance hierarchy in egalitarian human societies is of critical importance to their success. However, despite their exceptionally generous treatment of band members, human leaders are granted by their superior position—and with the support of their followers—with certain material benefits and fitness (Price and Van Vugt 2014), such as multiple wives. Leadership, as we have seen, is based not on physical prowess and coercion but rather on the capacity to motivate and persuade. Eibl-Eibesfeldt (1989) and Wiessner (2006), among many others, have stressed the importance in hominin societies of leadership based on persuasion and coalition building. In discussing mobile foragers, Wiessner remarks, “Unlike nonhuman primates, for whom hierarchy is primarily es-

tablished through physical dominance, humans achieve inequalities through such prosocial currencies as the ability to mediate or organize defense, ritual, and exchange” (2009: 197–198). Interestingly, our closest living relative, the chimpanzee, shows a tendency in the same direction, which is unusual among primates: successful top-ranked males are good social strategists (Goodall 1986; Nishida and Hosaka 1996).

It is important not to confuse reverse dominance hierarchy—which is based on a predisposition to reject being dominated—with a specific predisposition for egalitarian outcomes. Rather, persuasion and influence become a new basis for social dominance (Clutton-Brock 2009), which tends to be no less powerful for its subtlety. Wiessner observes that successful small-scale societies “encourage the capable to excel and achieve higher status on the condition that they continue to provide benefits to the group. In no egalitarian institutions can the capable infringe on the autonomy of others, appropriate their labor, or tell them what to do” (2006:198).

Are There Egalitarian Nonhuman Primates?

If there were a multimale/multifemale primate society lacking a social dominance hierarchy and lacking lethal weapons yet exhibiting reverse dominance hierarchy, the propositions offered in this paper would be compromised. Does such a society exist? Here, an important distinction can be drawn between egalitarianism flowing from weak social interaction and a low level of social contestation, on the one hand, and egalitarianism stemming from a high level of interdependence and some form of subordinate leverage over dominants (Sterck et al. 1997).

While there are clear behavioral patterns in nonhuman primates that serve as the basis for human reverse dominance hierarchy, all multimale/multifemale nonhuman primate societies are in fact based on strongly expressed social dominance hierarchies. There may be variation in the degree to which female or male dominance relations are decided, and thus their dominance hierarchies are more or less steep, depending on the strength of contest competition for resources (Sterck et al. 1997). It is often argued that bonobos (*Pan paniscus*) are more egalitarian than chimpanzees and more like humans (de Waal 1997; Hare et al. 2007). However, except for a female dominance hierarchy in feeding access for infants, the pattern of dominance in bonobos strongly resembles that of chimpanzees (Furuichi 1987, 1989, 1997), although estimates of the steepness of dominance hierarchies among males and females are not consistent across studies (Jaeggi et al. 2010; Stevens et al. 2007).

Similarly, reports indicate rather thoroughgoing egalitarianism among woolly spider monkeys, or muriquis (Strier 1992), which also live in sizeable multimale/multifemale groups, much like those of bonobos and chimpanzees. They are highly promiscuous, and males hardly compete for matings (Milton 1984; Strier 1987). In all the primate examples

of egalitarianism in sizeable groups, there is a clear reduction in the intensity of male contest competition as a result of female reproductive physiology that leads to unpredictable ovulation and thus low potential monopolization of matings—and thus paternity concentration—by top-ranking males (van Schaik et al. 2004). Thus, these egalitarian social relations are the result of scramble-like competition.

In none of these societies do we find the interdependence that we observe in human societies. The closest analog is the societies of cooperative breeders, as in callitrichids, but these are rarely multimale and multifemale. Among nonprimates, wild dogs and wolves, which are both cooperative breeders and hunters (Macdonald and Sillero-Zubiri 2004), came closest, but even there we mostly—though not always—have a single breeding pair rather than multiple cooperating pairs. We conclude that on the basis of available evidence, there are no multimale/multifemale egalitarian primate societies except for *Homo sapiens*.

Phylogenetic and Cultural Implications of Governance by Consent

We hypothesize that, following the development of lethal weapons and the suppression of dominance hierarchies based on physical prowess, successful hominin and human social bands came to value individuals who could command prestige by virtue of their persuasive capacities. While it was by no means necessary that this behavior emerge from the collapse of a social dominance hierarchy based on force, it did in fact emerge in the human line, and no other solution to the problem of leadership has been observed in the primate order.

The human egalitarian solution emerged in the context of bands insisting that their leaders behave with modesty, generosity, and fairness (Boehm 1993). A sagacious and effective leader will attempt to parley his important social position into material and fitness benefits but not so much as to induce followers to replace him with a less demanding leader. Persuasion was the name of the game, and excessive exercise of power would reverse the leader's fortunes. Persuasion depends on clear logic, analytical abilities, a high degree of social cognition (knowing how to form coalitions and motivate others), and linguistic facility (Plourde 2010). Leaders with these traits could be effective, but one intemperate move could lead to a leader's fall from power. Thus, in concert with the evolution of an ever more complex feeding niche (Kaplan et al. 2000), the social structure of hunter-gatherer life, in typical gene-culture coevolutionary fashion, contributed to the progressive encephalization and the evolution of the physical and mental prerequisites of effective linguistic and facial communication. In short, 2 million years of evolution of hyper-cooperative multifamily groups that deployed lethal weapons to hold down hierarchy gave rise to the particular cognitive and sociopolitical qualities of *Homo sapiens*.

The increased encephalization in humans was an extension of a long primate evolutionary history of increased brain

size, usually associated with increased cognitive demands required by larger group size (Byrne and Whiten 1988; Dunbar et al. 2010; Humphrey 1976; Jolly 1972).⁵ The argument presented here—which invokes coordinated collective action in cooperative foraging, made possible by a combination of interdependence and lethal weapons—extends this analysis to explain human exceptionalism in the area of cognitive and linguistic development.

This development in promoting egalitarian multimale/multifemale bands explains the huge cognitive and linguistic advantage of humans over other species. The early students of human evolution interpreted human hypercognition as a process of runaway sexual selection, in which intelligent males were more successful in attracting mates but did not otherwise contribute to the fitness of band members. This was the favored theory of Charles Darwin (1871), Ronald Fisher (1930), and, more recently, Geoffrey Miller (2001) and many others. Our reading of the evidence suggests that human hypercognition, despite the extreme energy costs of maintaining a large brain, was fitness enhancing because of increased cognitive and linguistic ability, which entailed heightened egalitarian leadership qualities. These leadership qualities increased the fitness of band members, who responded by ceding enhanced fitness benefits to leaders (Price and Van Vugt 2014).

The mating success of high-cognition males was thus grounded in their contribution to the mean fitness of band members and, hence in the long run, to the evolutionary success of ancestral humans. In a sense, hominins evolved to fill a cognitive niche that was relatively unexploited in the early Pleistocene (Tooby and DeVore 1987). In the words of Steven Pinker,

We suggest that the puzzle [of human hyper-cognition] can be resolved with two hypotheses. The first is that humans evolved to fill the “cognitive niche,” a mode of survival characterized by manipulating the environment through causal reasoning and social cooperation. The second is that the psychological faculties that evolved to prosper in the cognitive niche can be coopted to abstract domains by processes of metaphorical abstraction and productive combination, both vividly manifested in human language. (Steven Pinker 2010:8993)

Cooperative Mothering and the Evolution of Prosociality

In cooperative breeding, the care and provisioning of offspring is shared among group members. The standard estimate is that some 3% of mammals have some form of allo-maternal care, but in the order Primates, this frequency rises

5. Group size is certainly not the whole story. Multimale/multifemale monkey groups are often as large or larger than ape groups, although the latter have much larger brains and are considerably more intelligent. The full story concerning cephalization in mammals in general—and primates in particular—remains to be told (Eisler et al. 2011).

to 20% or more (Hrdy 2009, 2010). In many nonhuman primates and mammals in general, cooperative breeding is accompanied by generally heightened prosociality, as compared with related species with purely maternal care. The most plausible explanation is that cooperative breeding leads to a social structure that rewards prosocial behavior, which in turn leads to changes in neural structure that predisposes individuals to behaving prosocially (Burkart and van Schaik 2010; Burkart et al. 2009). An alternative possibility is that there is some underlying factor in such species that promotes prosociality in general, of which collective breeding is one aspect.

Human prosociality was strongly heightened beyond that of other primates living in large groups, including cooperative breeders, by virtue of the niche hominins occupied, which involved coordination in scavenging and hunting and sophisticated norms for sharing meat. This combination might account for the degree of cooperative breeding in the hominin line. As hominin brain size increased, the duration of immaturity did as well (Barrickman et al. 2008), and immatures had to learn an increasingly large number of foraging and other skills (Kaplan et al. 2000; Schuppli et al. 2012). Hominins evolved a unique system of intergenerational transfers that enabled the evolution of ever more complex cognitive abilities to support ever more complex subsistence skills (Kaplan et al. 2007). Our uniquely prosocial shared intentionality (Tomaseello et al. 2005) can be traced back to the psychological changes involved in the evolution of cooperative breeding and, additionally, hunting (Burkart et al. 2009).

Lethal Weapons and Egalitarian Political Organization from the Holocene to the Present

In the Holocene, some Big Man societies have been relatively egalitarian, such as those of highlands New Guinea, where the Big Man serves the group in outfeasting other groups and cannot transmit wealth or prestige to descendants. Other Big Man societies are fully hierarchical, with prestige and power being transmitted to future generations. The latter could have led to chiefdoms (Flannery and Marcus 2012; Service 1975).

The slow but inexorable rise of the state—both as an instrument for exploiting direct producers and for protecting them against the exploitation of external states and bands of private or state-sanctioned marauders—was a synthesis of these two types of Big Man sociopolitical systems (Andreski 1968; Gies 1984). The hegemonic aspirations of states peaked in the thirteenth century, only be driven back by the series of European population-decimating plagues of the fourteenth century. The period of state consolidation resumed in the fifteenth century, based on a new military technology: the use of cannon. In this case, as in some other prominent cases, technology becomes the handmaiden to establishing a social dominance hierarchy based on force.

In *Politics*, Aristotle writes that “there are four kinds of military forces—the cavalry, the heavy infantry, the light armed troops, the navy. When the country is adapted for cavalry, then a strong oligarchy is likely to be established

[because] only rich men can afford to keep horses. The second form of oligarchy prevails when the country is adapted to heavy infantry; for this service is better suited to the rich than to the poor. But the light-armed and the naval elements are wholly democratic. . . . An oligarchy which raises such a force out of the lower classes raises a power against itself (1952:VI:vii).”

The use of cavalry became dominant in Western Europe during the Carolingian period. The history of warfare from the Late Middle Ages to the First World War was the saga of the gradual increase in the strategic military value of infantry armed with longbow, crossbow, hand cannon, and pike, which marked the recurring victories of the English and Swiss over French and Spanish cavalry in the twelfth to fifteenth centuries. Cavalries responded by developing dismounted tactics when encountering infantry, using heavy hand weapons such as two-handed swords and poleaxes. These practices extended the viability of cavalry to the sixteenth century in the French and Spanish armies, but gradually through the Renaissance and with the rise of Atlantic trade, the feudal knightly warlords gave way to the urban landed aristocracy, and warfare turned to the interplay of mercenary armies consisting of easily trained foot soldiers wielding muskets and other weapons based on gunpowder. Cavalry remained important in this era, but even in the eighteenth and nineteenth century, cavalry was used mainly to execute the coup de grace on seriously weakened infantry.

The true hegemony of the foot soldier—and hence the origins of modern democracy—began with the perfection of the hand-held weapon, with its improved accuracy and greater firing rate than the primitive muskets of a previous era. Until that point, infantry was highly vulnerable to attack from heavy artillery. By the early twentieth century, the superiority of unskilled foot soldiers armed with rifles was assured. World War I opened in 1914 with substantial cavalry on all sides, but mounted troops were soundly defeated by men with rifles and machine guns and thus were abandoned in later stages of the war. The strength of the political forces agitating for political democracy in twentieth-century Europe was predicated on the strategic role of the foot soldier in waging war and defending the peace (Bowles and Gintis 1986), simply because conscripted armies of foot soldiers lacked the moral resolve to defend a society from whose governance they were systematically excluded.

Discussion

It is tempting to focus on the past several thousand years of human cultural history in modeling human sociopolitical organization because the changes that occurred in this period so radically and rapidly transformed the character of human society (Pagel 2012; Richerson and Boyd 2004). However, the basic genetic predispositions of humans underlying sociopolitical structure were forged over a much longer period of time, whence the million plus year perspective offered in this paper.

The framework developed here is applicable to many spheres of human social life, although we have applied it only to the evolution of sociopolitical structure. The central tool is gene-culture coevolution, which bids us to pay close attention to the long-term dynamic interplay between our phylogenetic constitution and our cultural heritage. The second important conceptual tool is the sociopsychological theory of norms. Many social scientists reject this theory because it posits a causal social reality above the level of individual actors. This position is sometimes termed methodological individualism. Methodological individualism is not a philosophical, moral, or political principle but an assertion about reality. As such, it is simply incorrect, because social norms are an emergent property of human society, irreducible to lower-level statements (Durkheim 1902; Gintis 2009). All attempts at explaining human culture without this higher-level construct fail.

In this context, we have suggested the following scenario for the long history of human sociopolitical dynamics. Our primate ancestors evolved a complex sociopolitical order based on a social dominance hierarchy in multimale/multifemale groups. Enabled by bipedalism, environmental changes made a diet of meat from large animals fitness enhancing in the hominin line. This—together with cultural innovation in the domestication of fire, the practices of cooking, and collective childrearing—created a niche for hominins in which there was a high return to coordinated, cooperative, and competitive scavenging as well as technology-based extractive foraging. This development was accompanied by the likely use of clubs, spears, and long-range projectiles as lethal weapons and also led to the spread of specialized bipedalism and the reorganization of the upper torso, shoulders, arms, and hands to maximize the effectiveness of these weapons. There was also a growth of new neural circuitry, allowing the rapid sequencing of bodily movements required for accurate weapon deployment.

The hominin niche increasingly required sophisticated coordination of collective meat procurement, the occasional but critical reliance on resources produced by others, a complementary willingness to provide others with resources, and procedures for the fair sharing of meat and collective duties. The availability of lethal weapons in early hominin society could have helped to stabilize this system because it undermined the tendencies of dominants to exploit others in society. Thus, two successful sociopolitical structures arose to enhance the flexibility and efficiency of social cooperation in humans and likely their hominin ancestors. The first was the reverse dominance hierarchy, which required a brain large enough to enable a band's rank and file to create effective coalitions that could definitively put an end to alpha male hegemony and replace this with a lasting egalitarian order. Leaders were kept weak, and their reproductive success depended on an ability to persuade and motivate, coupled with the rank-and-file ability to reach a consensus with such leadership. The second was cooperative childrearing and hunting, which provided a strong psychological predisposition toward

prosociality and favored internalized norms of fairness. This system persisted until cultural changes in the later Holocene fostered material wealth accumulation, through which it became once again possible to sustain a social dominance hierarchy based on coercion.

This scenario has important implications for political theory and social policy because it suggests that humans are predisposed to seek individual dominance when this is not excessively costly and also to form coalitions to depose pretenders to power. Moreover, humans are much more capable of forming large, powerful, and sustainable coalitions than other primates because of our enhanced cooperative psychological propensities. Such coalitions also served to reinforce the moral order as well as to promote cooperation in hunting, warding off predators, and raiding other human bands. This implies that many forms of sociopolitical organization are compatible with the particular human amalgam of hierarchical and antihierarchical predispositions that can result in either independent egalitarian bands or well-amalgamated large societies.

In particular, this implies that there is no inevitable triumph of liberal democratic over despotic political hierarchies. The open society will always be threatened by the forces of despotism, and a technology could easily arise that irremediably places democracy on the defensive. The future of politics in our species, in the absence of concerted emancipatory collective action, could well be something akin to George Orwell's *1984* or Aldous Huxley's *Brave New World*. However, humans appear constitutionally indisposed to accept a social dominance hierarchy based on coercion unless the coercive mechanism and its associated social processes can be culturally legitimated. It is somewhat encouraging that such legitimation is difficult except in a few well-known ways based on patriarchy, popular religion, or principles of liberal democracy.

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Comments

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The authors' main argument concerns the origins of egalitarian societies and nonauthoritarian leadership, the "successful political structure that ultimately replaced the an-

central social dominance hierarchy.” They suggest that this system resulted from the combined effects of two factors: the development of lethal weapons, which led to the suppression of dominance based on physical prowess, and a marked increase in cooperative activities and levels of social interdependence. These conditions would have favored the emergence of leaders able to motivate and persuade and selected for “linguistic facility, political ability, and . . . hypercognition.”

The impact of lethal weapons on the dynamics of dominance relationships must have been profound indeed. As I argued previously (Chapais 2008, 2011, 2013), weapons may have played a major role in the evolution of human monogamy from a prior state of generalized polygyny: by decreasing discrepancies in physical power between males, weapons would have substantially increased the costs of monopolizing several females and led to a more egalitarian distribution of females among males. Notwithstanding the effect of weapons, there is still a big gap between a social system featuring high levels of social interdependence and low levels of physical dominance, on the one hand, and the emergence of human leadership, on the other. Nonauthoritarian leadership stems from cooperation and is granted to leaders by followers, whereas authoritarian leadership (based on dominance) stems from competition and is imposed by dominants on subordinates. The social processes and underlying psychologies are fundamentally different. The authors are basically silent about how that crucial transition was accomplished. As will be argued here, nonauthoritarian leadership and the demise of primate-like dominance may be two consequences of a more basic phenomenon: the rise of competence-based social status (Chapais 2015).

As argued by Henrich and Gil-White (2001), highly skilled individuals in various domains (from hunting to toolmaking to shamanism) are admired, accorded privileges, preferentially copied, and spontaneously deferred to; in short, they enjoy prestige. Henrich and Gil-White proposed that attraction to experts emerged with the human cultural capacity and was selected because it enabled followers to acquire knowledge from experts. Alternatively, as I argue elsewhere (Chapais 2015), attraction to experts may have originated in the (presumably homologous) phenomenon of attraction to high-ranking individual in primates and hence in cooperative partnerships involving an exchange of services and resources between experts and group members rather than social learning benefits. Upon the evolution of cumulative culture and the ensuing proliferation of competence domains, the attractiveness of high rank would have been co-opted to generate attraction to experts and competence-based status differentials within each such domain.

Pronounced discrepancies in competence translate into marked asymmetries in the degree to which experts and non-experts may help each other satisfy their respective needs. Competence discrepancies between cooperative partners thus create dependence asymmetries, which in turn provide experts with various types of power, including passive influence (being copied), active influence (being obeyed, *sensu* Milgram

[1974]; reviewed in Blass [1999]), bargaining power, leverage (Bacharach and Lawler 1980; Chapais 1991; Lewis 2002), and dependence-based coercive power (dominance) when experts are in position to withhold knowledge, services, or resources affecting others' welfare (Chapais 2015). Thus, following the evolution of cumulative culture and the diversification of power bases, it must have been commonplace for physically weaker individuals to be more competent than stronger individuals in several domains and hence to enjoy a higher group-conferred status and higher levels of bargaining power and dependence-based dominance. In such situations, bullies trying to aggressively impose their will on skilled hunters, toolmakers, or shamans ran the risk of not only losing valuable social partners but also hurting the favorite partners of all group members and alienating the latter. At that stage in human evolution, the impact of primate-like dominance in human affairs would have been considerably diluted among several other power bases. Note that this effect is independent of whether weapons were used or not.

Simultaneously, competence-based status would have set the stage for nonauthoritarian leadership because leaders are a particular subset of experts (Chapais 2015). As noted by the authors, leaders are experts in coordination, with relevant physical, psychological, and social competences (Boehm 1993; van Vugt 2006). In that view, leadership by consent is only one particular manifestation of competence-based status. This suggests that the early political structure that replaced the primate dominance hierarchy was a system in which status was conferred by followers, competence was the key to status, and the sources of power were highly diversified. Nonauthoritarian leadership could emerge in such a context (especially after the development of weapons) whenever complex cooperative activities favored leadership-based coordination. The advent of nested, multigroup social entities in the evolution of human social organization—with their high requirements in terms of between-group and multigroup coordination (Chapais 2013, 2014)—would have rendered leadership particularly useful.

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Social Niche Construction

Two long-standing assumptions in evolutionary biology are that the genotype-phenotype map, as it is called, is simple and that the time-scale on which the environment changes is slow enough compared with behavioral change that it can be treated as static and uncoupled to behavioral dynamics (the adiabatic assumption).

It is now well understood that the first assumption is wrong for most organisms—the gene activation patterns underlying phenotypic traits are modulated by complex regulatory machinery that itself evolves—and the work of Eric Davidson and coworkers on echinoderm development stands as an excellent example (e.g., Davidson 2010). This fundamental insight also applies in the case of social-cultural evolution, where the output is social structure or institutions and the input is behavioral strategies that are modified through learning rules (transmission mechanisms; e.g., van Schaik and Burkart 2011) and regulated through conflict management and other control/robustness mechanisms (e.g., Boehm 2001; Flack, Krakauer, and de Waal 2005; Flack et al. 2006; Frank 2003).

The second assumption, which if correct would justify studying phenotypic and social development independently from evolutionary dynamics, is problematic in any system in which components (individuals, organisms, cells, etc.) can modify environmental variables and, by modifying them, change the selection pressures to which they are subject, as in ecological (e.g., Odling-Smee, Laland, and Feldman 2003) and social niche construction (Flack et al. 2006 [see also supplement]; Flack 2012b).

This modification of the environment may be to the timescale on which an environmental variable changes, its trajectory through phase space, its distribution in space, or simply its availability. By controlling these properties of environmental variables, an organism changes the selection pressure to which it, as the constructor, and its offspring are subject. This often comes in the form of a reduction of uncertainty. The increased predictability of environmental variables allows constructors to better tune their decision-making strategies and hence better adapt (Flack and de Waal 2007; Flack et al. 2013). When multiple individuals and species contribute to modification of environmental variables, the problem becomes one of collective social computation (Flack 2014; Flack and Krakauer 2011): what are the collective effects of multiple individuals estimating and attempting to control regularities in their environments, and under what conditions can this process produce predictable, regular ecological or social environments?

With niche construction, collective computation, and advances in evo-devo, we are seeing the beginnings of an evolutionary theory that can account for the origins and diversity of complex forms (for phenotypic examples, see Borenstein and Krakauer 2008; Davidson and Erwin 2006; for social examples, see Flack 2012a, 2012b, 2014) as well as for causes of gene and behavioral strategy change. The social evolution community, which tends to be very functionally oriented, has been slow to recognize these advances, as game theory, cultural evolution, and gene-culture coevolution—the primary modeling and conceptual frameworks in social evolution—have so far largely neglected the study of the feed-forward, computational, collective process producing social structure (Flack 2012a; Krakauer and Flack 2010). (Exceptions include

work on social insect societies [e.g., Page and Amdam 2007], work on collective behavior and pattern formation in animal societies [e.g., Couzin 2009], and the theoretical cooperation literature emphasizing deriving macroscopic properties from microscopic dynamics; see, for an example, the supplement of Nowak, Tarnita, and Wilson 2010.) Required now are quantitative studies of the strategies individuals use to adaptively modify the environment—whether social or ecological, how these strategies are encoded in evolutionary or developmental time and how they combine to produce in, for example, primate societies and egalitarian and other power structures (e.g., Flack 2012b; Brush, Krakauer, and Flack 2013).

The importance of this perspective is illustrated by the target article, “*Zoon Politikon: The Evolutionary Origins of Human Political Systems*,” by Gintis, van Schaik, and Boehm. The authors bring together multiple lines of evidence to argue that the temporal convergence of bipedalism, cooperative breeding, environmental changes allowing a high protein diet, and cultural innovations in the form of fire and cooking created a niche for hominins that favored coordinated, cooperative scavenging and hunting of large mammals and led to egalitarian societies. The authors make a compelling and quite simple argument, despite weaving together evidence from many sources. However, it is hard to work with in its present form because it is coarse: the feed-forward social mechanics producing egalitarian social structure are not specified, only hinted at. To develop testable hypotheses to evaluate the “*Zoon Politikon*” framework, we need niche construction models that address how a change in the accessibility of interaction strategies—whether due to an increased availability of processed protein, bipedalism, and/or cooperative breeding—changed the accessibility of egalitarian and other social structures.

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There are many attributes of *Homo sapiens* that could be said to distinguish us from all other animals—attributes that make us human—including language, sophisticated theory of mind, morality, and justice systems. To these Gintis, van Schaik, and Boehm add “a unique political dimension to human social life that, through gene-culture coevolution, became a human mental capacity intentionally to construct and reconstruct the social order. . . . The successful political structure that ultimately replaced the ancestral social dominance hierarchy [of other primates] was an egalitarian political system in which the group controlled its leaders.”

It is difficult to evaluate the long chain of causal events these authors say led from our primate ancestors to this unique mental capacity that gave rise to the political dimension of our existence, but they are surely right that there is

something special about human social relations: cooperative, reciprocal, coalitional, fluid, tribal, vindictive, and acutely reputation based.

Add to this that we are able to pool our skills and knowledge and to trade and exchange goods and services. This means we can benefit from the collective wisdom of our societies and we have a history; our communities and societies accumulate ideas, knowledge, and technology. These latter features of human society have meant that, more than any other species, our groups are vital to our life and well-being (how much of the technology you enjoy could you create on your own?), and no one individual can be said to be in charge.

This, in turn, has instilled in us a probably unique group psychology that includes the other-regarding traits Gintis et al. describe, notably, a sense of fairness and justice in our dealings with others and with our group. But these exist, I suggest, not because we are innately fair or just but as valuable brakes on our tendencies to act selfishly (because to do so risks being expelled from the group or even killed) and to avoid being taken advantage of by others.

In a word, this psychology exists to make the group work because individuals are better off with it than without it. Thus, think of emotions, such as those associated with fairness and justice, as motivational states that natural selection has built into us. They are vivid, salient, and never far from our awareness. But they are not simple and robotic in their application. We have an alarming ability to suspend or even disregard the morality that we normally extend to members of our own tribe when we confront members of other tribes or even discover traitors in our own ranks; our so-called morality, ironically, has probably led to some of the greatest slaughters of modern times.

So, the picture that emerges of our species is a complicated one. Yes, we have a sense of what Gintis et al. call “otherness,” but this probably should not be confused with being an innately angelic and kind species. More likely is that we are a shrewd and calculating species, such that our hyper-social brains and their sophisticated cognition enable us to adjust our behavior to circumstances—kind and generous when circumstances call for it, self-regarding and even brutal when we can get away with it. The countering observation—that we sometimes behave in other-regarding ways, even when not being observed or immediately rewarded—is simply a measure of how strong our emotions, as motivational states, are in getting us to behave in ways that will generally reward us.

Gintis et al. are aware of this difficult and calculating nature of our species. They paint a picture of egalitarian social-political groupings in our hunter-gatherer past, shored up, and they suggest by gene-culture coevolution that built these proclivities into us. But they recognize that these allegedly egalitarian tendencies were abandoned as soon as stored wealth became available with the advent of farming and inequalities could emerge. So, it seems that the hardwiring from gene-

culture coevolution easily came unraveled or perhaps was never there in quite the wiring diagram they suggest (to be fair to Gintis et al., it is never clear to me just what they do think has been wired into us by gene-culture coevolution).

What does seem clear, though, is that sometime in our past (my hunch is that it coincides roughly with the advent of our species around 160,000–200,000 years ago; Pagel 2012) we (somehow) acquired the cognitive skills that enabled a fluidity in our social relations, and it is this shrewdness—be cooperative and other regarding when needed, be self-regarding when that works—that really characterizes the hardwired political dimension of our cognition.

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Uniquely Human?

The authors outline the evolutionary origins of a sociopolitical human niche that is largely dependent on material culture, events such as control of fire and cooking and the consequences of these developments (biological as well as cultural). They use a phylogenetic perspective to anchor their premise, so that their hypothesis is based on the available data on nonhuman primate behavior. However, detractors may find their scenario—which includes, in addition to those traits listed above, active sharing, cooperative hunting and breeding, lethal weapons and bipedal running—as another “just so” story in paleoanthropology. Beginning with the section on the control of fire, their premise becomes more speculative and rests on multiple levels of inference. Regardless, I find it provocative, and I anticipate it will lead to further refinement of the various hypotheses.

I am particularly intrigued by the authors’ inclusion and treatment of lethal weapons and hunting. Most of my criticisms are minor but could have important implications for refining their hypotheses. In general, their chimpanzee model stems from research on the East African subspecies (*Pan troglodytes schweinfurthii*), and I believe their hypotheses would be strengthened by a more balanced assessment of *Pan* as well as inclusion of key examples from other primates (e.g., reversals in dominance systems; Sapolsky and Share 2004) and updated data on nonprimate species (e.g., wolves; Smith and Ferguson 2012).

The authors’ focus on large prey ignores the potential importance of smaller prey except during times of large-prey scarcity. The inclusion of medium-sized and small prey surely characterized the diet of early hominins as it does living humans that practice subsistence hunting, but it does not figure into the equation in bringing about a uniquely human hominin. However, my real issue is with their assertion that hunting and scavenging small animals is not cost effective

for large primates. Chimpanzees (males and females) at my Fongoli study site in Senegal hunt as well as share the meat of very small prey (i.e., *Galago*). The social implications of such sharing indicate that large-mammal hunting was not a prerequisite for behaviors that ultimately lead to the level of cooperation seen in our species. This leads me to question the hypothesis that a focus on large prey by hominins was simply cost effective.

As the authors note, chimpanzees at my study site at Fongoli, Senegal, use wooden tools to hunt their *Galago* prey in tree cavities (Pruetz and Bertolani 2007), and these tools could be considered weapons in the most primitive sense. I have been able to record wounds on *Galago* prey inflicted by such hunting tools, although this is usually difficult to assess, given the rapidity of their movement as well as the quickness with which Fongoli chimpanzees kill them (usually with a bite to the head, which is then ingested first). In a nonhunting context, the savanna chimpanzees I study, like apes elsewhere, are quite capable of accurate, overhanded throwing of projectiles (albeit from short distances and in a nonlethal context), and, while rare, stone projectiles can be used effectively against other individuals, including higher-ranking apes (and in conflicts with baboons and spotted hyenas). Similar to chimpanzees at Tai Forest, Ivory Coast (Boesch 2009), Fongoli apes have been observed to use weapons to attack leopards (Jill D. Pruetz and Boyer, unpublished manuscript). In our case, an older female with a ventral infant and an older male led the attack on a leopard hiding in a cave while the rest of the large social party looked on. These individuals were able to ultimately chase the leopard from its hiding place. Such observations make me question the point that powerful weapons would be needed to kill a predator when in fact driving them away would appear to be just as cost effective. There are a number of similar points that I found contradictory in the scenario, but reconstructing the hominin niche is understandably a complex process.

In general, I assert that most of the traits considered to be uniquely human, in fact, are likely shared with other primate species. Besides linguistic abilities of persuasion, almost every trait described could be rooted phylogenetically in our order. I appreciate the authors' assertion that, in order to better understand aspects of human evolution, anthropologists must recognize shared as well as uniquely derived traits. This necessary part of the process of phylogenetic analysis is often neglected, especially in recent years following the criticism of the chimpanzee model. However, without such a step, understanding human behavioral uniqueness becomes a guessing game and almost purely speculative. Throughout the paper, I would make additional specific criticisms regarding the authors' need to more accurately anchor their phylogenetic reconstruction of behavior using data from extant nonhuman primate species, but I applaud their efforts and anticipate that proponents and detractors alike will refine it.

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Gintis, van Shaik, and Boehm marshal an array of different lines of evidence to put forward a convincing case for the role of political life in the emergence of distinctive human social systems. In particular, they argue that the creation of potentially lethal weapons played a key role in the evolution of human egalitarian social/political systems, suppressing the potential for physical dominance and promoting prosocial tendencies. In their view, the origins of such systems lie in social changes occurring more than a million years ago, perhaps as far as 3 or 4 million years in the past, with their continuing influence being felt today.

Their argument fits with growing tendencies to trace human social systems much further back than the origins of our own species. Moreover, their perspectives align with a growing awareness that the social elements of human systems may have been much more significant in human success than the technological and that early humans may have been far more other regarding than we have assumed. Nonetheless, an emphasis on the development of weapons (an external material construction unique to humans) and the influence of weapons on the emerging moral basis to human societies is novel, adding a new element to a recent move to such perspectives, as does their appreciation of the potential antiquity of a variability of human social/political systems.

The evidence for early use of weapons to support this argument is a little more scanty than we might like. In particular, evidence for weapons is circumstantial until 500,000 years ago, when we see impact marks from spears on hunted animals at sites such as Boxgrove in the United Kingdom, and slightly later, around 400,000 years, when we see preserved weapons themselves (wooden spears) at Shoningen in Germany. Nonetheless, it is hard to imagine the appropriate preservation or extent of wear to ever give us sufficient evidence for weapons before this period. Handaxes are most clearly butchery tools unlikely to be used as killing weapons, and flakes used in ad hoc fashion are conversely unlikely to leave wear traces from use. Moreover, the most likely weapons would be wooden spears, unlikely to be preserved any earlier in the archaeological record. With evidence for early access to carcasses and potentially hunting from at least 1.8 million years ago (Bunn and Gurtov 2014) plus evidence that even spheroids at sites such as Olduvai would have been used as weapons, the antiquity of such lethal weapons seems entirely supportable, and social inferences likewise.

As the authors hypothesize, social changes appear to occur alongside economic developments not only directly through the social impact of lethal weapons themselves but also through a greater emphasis on hunting, with the need for sharing of meat and the control of fire for cooking. These

economic developments set in place a social system entirely distinct from other primates and one that fostered social sharing norms. A suite of changes including increasing collaboration, alloparenting, and hominin encephalization co-occur. While Gintis et al. are certainly not alone in linking these many different social changes and finding their basis in inferences about the social systems of the last common ancestor (Whiten and Erdal 2012), they add elements unique to humans (the use of shaped stone tools and of fire) to the equation.

If there is an area I would have like to have seen developed further, it is that of how, though acting on individuals, selection pressures acted to produce the other focus of social cognition so central to the political system proposed. Whereas biological evolution illustrates many changes of tack and even reversals, cognitive evolution seems to follow a route of increasing complexity that perhaps remains to be explained. Nowak and Sigmund (2005), for example, refer to the ratchet effect caused by indirect reputation in placing greater selection pressure on increases in intelligence. Conversely, Nesse (2007) stresses the role of displays of emotional commitment to others' interests and the possibility of runaway social selection for signals of altruism in human evolution, and I have stressed the role of material objects (the very weapons themselves) in providing lasting markers of reputation (Spikins 2012, 2015).

As with any stimulating paper addressing a complex and important issue, we are bound to find ourselves asking more questions. We are left wondering, for example, how the evolution of social tolerance toward external groups evolved in settings of potentially lethal violence (e.g., see Cieri et al 2014). Perhaps most significantly, we cannot help but ponder in particular the relevance of innate egalitarian tendencies to modern society, with its tenuous justification for impositions of dominance.

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The Deep Social Mind of Humans and the Ancestral Sociocognitive Niche

In recent years, an unprecedented richness of evidential material has become available bearing on the evolutionary shaping of the human mind, from sources as diverse as the archaeology of hominid fossils and artefacts, comparative genomics, ethnographies of recent hunting-gathering peoples, and the comparative method applied to nonhuman pri-

mates. This affords the prospect of unrivaled cross-disciplinary analyses illuminating human evolution, yet the volume of data available now exceeds the ability of any single author or team to fully assimilate and synthesize it. Nevertheless—and excitingly—a cluster of analyses sharing this aspiration has been published in recent years; they usefully overlap with Gintis et al. and with each other in scope, each incorporating perspectives and major sources of evidence lacking in the others (Boyd, Richerson, and Henrich 2011; Pinker 2010; Sterelny 2012; Tomasello et al. 2012; Whiten and Erdal 2012). Read together, this corpus offer a new depth of understanding in respect of the evolution of human nature.

Our contribution (Whiten and Erdal 2012) converges in several significant respects with the analysis of Gintis et al. in its conclusions, notably concerning the special, coupled features of egalitarianism and hyper-cooperation that underwrote the big-game hunter-gatherer niche that so significantly molded human evolution. However, our analysis incorporated other elements that we see as important omissions in that of Gintis. We inferred five major pillars characterizing human deep social mind, enmeshed in an evolutionary socio-cognitive niche (fig. 1): hyper-cooperation, egalitarianism, cumulative culture, language, and mind reading (i.e., theory of mind). Gintis et al. make no mention of the latter and only minimal reference to language. We argue that together these five pillars formed a powerfully synergistic, adaptive complex in which positive feedbacks operated between all of them (fig. 1). Mind reading, for example (attribution of states of mind, such as beliefs and desires), means that the minds of a hunter-gatherer band interpenetrate and in a significant sense form an integrated group mind that—in concert with the other sociocognitive pillars—allows the band to operate as a unitary, coherent predatory organism (in the broadest sense, including both gathering and hunting) that can more than successfully compete with professional predators, like the African big cats. There are similarly powerful reinforcing links between all of the nine paired relationships that link the five pillars we identify (fig. 1), which together justify labeling the human niche sociocognitive rather than simply cognitive (Whiten and Erdal 2012).

We agree with Gintis et al. that the legacy of our peculiar evolutionary past appears to be a social mind that incorporates a distinctive mixture of egalitarian and antiegalitarian dispositions. Our own detailed combing of 24 hunter-gatherer ethnographies consistently revealed egalitarian, generalized sharing of meat across the band together with a consistent lack of chiefs and flattened hierarchical structure (Erdal and Whiten 1996). After the hierarchies of ancestral ape societies, the vast length of this hunter-gatherer egalitarian phase—spanning many hundreds of thousands of years and active until as recently as the rise of horticulture around ~10,000 years ago—likely explains our species' capacity for charity and concern with fairness. History is replete with the hubris of dominant leaders—after storable wealth enabled them to

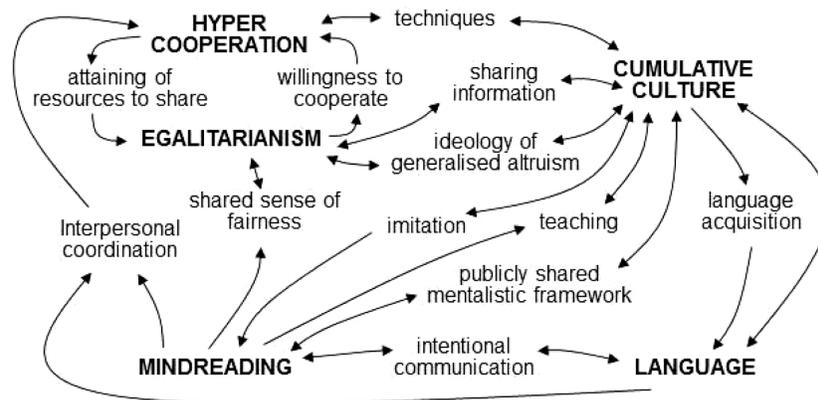


Figure 1. Five pillars of hunter-gatherer deep social mind and some illustrative positive feedbacks between them (after Whiten and Erdal 2012). Deep social mind refers to these mental attributes (hyper-cooperation, egalitarianism, cumulative culture, language, and mind reading) specifically; sociocognitive niche refers to the adaptive embedding of this complex within the hunting-gathering way of life.

consolidate control—but also with countless rebellions expressing the evolved human desire for fairness, which only collaborative resistance to domination can sustain. Democracy itself can perhaps be regarded as a cultural elaboration of this hunter-gatherer legacy. In any case, the ethnographies draw a consistent picture of group-level decision-making shaped by such elements as persuasiveness rather than the impositions of a dominating leader.

Indeed, the paper's use of a leader-follower dichotomy is inaccurate, according to our researches (Erdal and Whiten 1996). We found that simple forager bands do not institutionalize leadership, individuals remain autonomous, and whose suggestion is followed varies by situation and time, with arrogantly expressed proposals from anyone typically simply not accepted.

We also remain critical of Boehm's continued reference to reverse dominance as the social pressure sustaining hunter-gatherer egalitarianism. The ethnographies we combed described band members' resistance to any self-aggrandizing dispositions as most commonly occurring through relatively benign and subtle maneuvers, like mocking and ridicule. Rather than reversing an existing rank order, such behavior typically leveled or flattened status relationships, preventing even the most competent from gaining dominance but not imposing dominance on them. Accordingly, we advocated "counter dominance" as a more apt term for the key political tactic in egalitarian bands (Erdal and Whiten 1994), and we urge the authors to recognize more consistently the distinction we draw, as they do fleetingly in writing "dominance aspirations are successfully countered." This is neutralizing a hierarchy, not reversing it.

The rich multidisciplinary discoveries that Gintis et al. cited can now adduce and strive to synthesize are too important for

our understanding of our evolved social and political minds to be interpreted in any fashion but the most objective.

Reply

We welcome the comments on our paper "Zoon Politikon: The Evolutionary Origins of Human Political Systems," and we gratefully accept the commentators' useful observations. We here restrict ourselves to a few points worthy of additional clarification.

Bernard Chapais suggests that "nonauthoritarian leadership and the demise of primate-like dominance may be two consequences of a more basic phenomenon: the rise of competence-based social status." We do not doubt the importance of competence-based social status (Chapais 2015; Henrich and Gil-White 2001), and we understand that social norms favoring competence were likely strong contributors to human hypercognition in general and prosocial leadership in particular. However, group evaluations of leaders could not be effective before leadership based on force was overturned, and such overturning, we argued, was due to the availability of lethal weapons and interdependence. The collapse of forceful dominance may have led simply to the failure of social coordination in many bands, but at least in some hominin lines the evolutionary successful path—in response to the high returns to collaborative interactions (Tommasello 2014), probably accompanying the adoption of cooperative breeding (Burkart et al. 2009)—was an acutely developed theory of mind needed to support these interactions (Baron-Cohen 1991), along with the ability of humans

to evaluate and value exactly the sorts of technical and social competence to which Chapais refers.

Mark Pagel writes, “A sense of fairness and justice in our dealings with others and with our group . . . exist, I suggest, not because we are innately fair or just but as valuable brakes on our tendencies to act selfishly . . . and to avoid being taken advantage of by others . . . this psychology exists . . . because individuals are better off with it than without it.”

However, we never suggested that humans are innately fair or just. Rather, we said that humans have an evolved nature that is predisposed to understand the notion of social norm, to evaluate social norms according to legitimacy criteria, and to conform to social norms when they are considered legitimate. These predispositions are actualized through complex but imperfect sociocultural interactions (Bowles and Gintis 2011), and they must be protected by the sanctioning of rule violators (Boyd et al. 2010).

Moral principles doubtless serve individual fitness by inducing individuals to avoid social sanctions on selfish behavior (Gintis 2003a, 2003b). However, we know of no plausible social process whereby having a sense of fairness would protect against being exploited by others. This is because in a population of individuals who punish exploiters at a cost to themselves, a free rider can always do better by not punishing. There are cogent models in which individuals punish unfair behavior in order to establish a reputation for hard bargaining that would be useful in future interactions. But this is purely self-regarding behavior requiring no moral dimension.

Pagel claims that this moral sense exists “because individuals are better off with it than without it.” We would amend this to say that individuals have evolved a moral sense because social groups that reward prosocial behavior and punish antisocial behavior enhance the fitness of their members better and last longer than societies that do not, and in such societies, individuals with a strong moral sense have higher fitness than amoral individuals. This does not mean, however, that humans behave prosocially only because they are appropriately rewarded for such behavior. Indeed, were that the case, as we suggested in “*Zoon Politikon*,” even moral individuals would not vote in large elections and would not participate in the sorts of collective actions against tyranny from which our contemporary freedoms arose.

Pagel further suggests that

we are a shrewd and calculating species . . . kind and generous when circumstances call for it, self-regarding and even brutal when we can get away with it. The countering observation—that we sometimes behave in other-regarding ways, even when not being observed or immediately rewarded—is simply a measure of how strong our emotions, as motivational states, are in getting us to behave in ways that will generally reward us.

In other words, it is usually so strongly in one’s interest to follow socially approved behavior that it is not worthwhile

evaluating each particular social situation for one’s ability to behave selfishly with impunity because the costs of making a mistake can be very high. There are no doubt situations in which this view is plausible. For instance, one may stop for a red light even if no cars are coming and no policeman is in sight because perhaps there is a police car hidden from view. Getting caught even one time in 20 many not be worth the effort of discrimination. It is thus prudent simply to stop for a red light unconditionally. Similarly, we know that the level of tax compliance in the United States is much higher than self-interested taxpayers would choose (Andreoni et al. 1998), but doubtless some taxpayers simply want to avoid any possibility of being audited. However, in cases where serious moral choices must be made—such as harming, robbing, and killing others—this theory is implausible.

Perhaps the biggest problem is with moral actions that involve zero or very small social sanctions. This includes most forms of political participation, including voting, becoming politically knowledgeable, contributing to a campaign fund, and participating in a collective action. It also applies to moral actions that are prosocial but are not publicly monitored, such as giving to charity and being kind to strangers. Finally, the notion that men refrain from killing and raping only because they are afraid that their deeds will be detected does not describe human psychology very well. Of course, some men are quite capable of these acts, but they occur in high frequency only when the social fabric is deeply weakened.

Pagel’s emphasis on cognitive evaluation of the costs and benefits of social actions is not strongly supported by the recent emergence of strong emotional underpinnings of social actions (e.g., Haidt 2012). The internalization of prosocial norms may well serve the individual’s interest, when the damage to reputation of being detected in selfish, antisocial acts is so high that the threshold for engaging in such acts must be made very high, purely to protect the individual’s selfish interests (Gintis 2003a).

The notion of humans as shrewd but asocial creatures that respond only to sanctions and rewards is also belied by the fact that humans show all the signs of self-domestication that have been observed in species domesticated by humans. Darwin himself noticed that selectively breeding mammals for tameness leads to similar side effects in several distinct species. He then suggests that man himself “may be compared with those animals which have been long domesticated” (Darwin 1871:ch. 7). Belyaev (1979) corroborated this insight, studying captive silver foxes bred for tameness. These animals developed humanly attractive faces with short snouts, floppy ears, patches of white fur on their heads, and curly tails (Gibbons 2014). More recently, Cieri et al. (2014) documented domesticated syndrome changes in human evolution since the Middle Stone Age and Upper Paleolithic, and Wilkins et al. (2014) have proposed a general genetic model explaining the domestication phenomenon.

This is evidence for a very straightforward culture-led group selection mechanism in which an increasingly complex

division of labor and social norms that rewarded cooperation (Tomasello 2014) favored genetic changes that produced a more domesticated and prosocial human disposition.

Andrew Whiten and David Erdal write: “We inferred five major pillars characterizing human deep social mind, enmeshed in an evolutionary sociocognitive niche: hyper-cooperation, egalitarianism, cumulative culture, language, and mind reading (i.e., theory of mind). Gintis et al. make no mention of the latter and only minimal reference to language.”

Whiten and Erdal are correct, and any general model of human evolution must include language and mind reading. These factors are of foundational importance, and they nicely complement our analysis, which was rather streamlined to deal with sociopolitical issues. We would have done well to refer to their paper (Whiten and Erdal 2012), which we had not yet read.

Our analysis stresses the great potential gains from social coordination facing early hominins. Cooperative scavenging and hunting were possible because humans developed what Michael Tomasello has called collective intentionality, of which the ability to predict how others are thinking and hence how they are likely to react to contingencies is a central element. Individuals with superior ability to contribute to group goals by such flexible adaptation would be welcome members in a collaborative effort and would thereby enjoy enhanced biological fitness. Similarly, communicative facility is a highly valued personal trait in a group where complex collaboration is the key to success, and there are many paths from social value to individual biological fitness. The dramatic physiological changes in facial and tongue musculature—in the positioning of the larynx in the throat and in related instruments of vocal communication—were most likely individual adaptations to the fitness benefits of social collaboration.

Whiten and Erdal also claim that our “use of a leader-follower dichotomy is inaccurate. . . . We found that simple forager bands do not institutionalize leadership, individuals remain autonomous, and whose suggestion is followed varies by situation and time, with arrogantly expressed proposals from anyone typically simply not accepted.”

We agree with Whiten and Erdal’s findings and did not suggest otherwise. We often refer to leaders and followers, but we do not suggest that band leaders are a distinct group of individuals who maintain their status over time or that leaders are ever followed without the consent of the followers.

Finally, Whiten and Erdal are critical of Boehm’s continued reference to reverse dominance as the social pressure sustaining hunter-gatherer egalitarianism. The ethnographies we combed described band members’ resistance to any self-aggrandizing dispositions as most commonly occurring through relatively benign and subtle maneuvers, like mocking and ridicule. Rather than reversing an existing rank order, such behavior typically leveled or flattened status relationships, preventing even the most competent from gaining dominance but not imposing dominance on them.

We agree with Whiten and Erdal’s description of the relationship between leaders and followers, except that evidence from contemporary hunter-gatherer groups supports our description of followers being dominant over leaders, not in the sense that leaders are coerced against their will to lead but rather in that the incentives imposed by followers on leaders effectively counter their capacity to act against the interests of the group. The term “reverse dominance” accurately describes a situation in which the position of leaders is determined by the will of the followers. Followers dominate leaders in the sense that the position of the leader, despite the fact that he may benefit greatly from his leadership position, is continually subject to reassessment and recall by followers.

Despite the rarity of severe, weaponized sanctioning of bullies, in the long run it serves an important role in reverse dominance hierarchy. In a sample of 50 mobile hunter-gatherers chosen for their appropriateness for Late-Pleistocene modeling, Boehm (2014) found that nearly half reported incidences of capital punishment, and by far the leading cause was that a male was trying to intimidate his fellow hunters either physically or supernaturally. All of these societies were egalitarian. In fact, the Calusa of Florida stand out as the only mobile hunter-gatherers that are decisively hierarchical.—Herbert Gintis, Carel van Schaik, and Christopher Boehm

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