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REVIEW

ANCESTRAL HIERARCHY AND CONFLICT

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Ancestral *Pan*, the shared predecessor of humans, bonobos, and chimpanzees, lived in social dominance hierarchies that created conflict through individual and coalitional competition. This ancestor had male and female mediators, but individuals often reconciled independently. An evolutionary trajectory is traced from this ancestor to extant hunter-gatherers, whose coalitional behavior results in suppressed dominance and competition, except in mate competition. A territorial ancestral *Pan* would not have engaged in intensive warfare if we consider bonobo behavior, but modern human foragers have the potential for full-scale war. Although hunter-gatherers are able to resolve conflicts preemptively, they also use mechanisms, such as truces and peace pacts, to mitigate conflict when the costs become too high. Today, humans retain the genetic underpinnings of both conflict and conflict management; thus, we retain the potential for both war and peace.

Ancestral *Pan* was the shared antecedent of humans and our two genetically closest relatives, *Pan troglodytes* (chimpanzees) and *Pan paniscus* (bonobos), and, if we look for strong social similarities shared by the two living *Pan* species and human foragers, ancestral traits are readily identified. All three live in bounded social groups and fight with conspecifics (*1*), and all three have territorial tendencies (*2*, *3*), along with a substantial amount of dyadic dominance-and-submission behavior that can erupt into serious conflict countered by active, sometimes highly effective, peacemaking (*4*). In addition, all three form community-wide coalitions that cooperatively threaten males of other groups (*5*), whereas within their communities sizable coalitions of subordinate individuals may band together to reduce the domination of higher-ranking males (*6*). Here, I rely on a behavioral phylogenetic approach (Box 1) (*7*) that allows me to conclude that such shared traits are primitive and were to be found in ancestral *Pan*. By analyzing similarities across all three descendants of ancestral *Pan*, I can make conclusions about behaviors likely to have been present in our ancestors. From this estimate of our ancestral behavior, I can explore the factors that may have led to the more uniquely human set of behaviors we find in modern *Homo sapiens*.

Comparative Hierarchies

Although all three species have social dominance behavior, there are differences worth noting (*8*). As the least aggressive, bonobos (both wild and captive) have a rather complicated social organization. Not only do they exhibit both alpha females and males, but the only small coalitions involving males occur when mothers support their sons; the alpha male stays in place because his alpha mother supports him (*9*). In contrast, small coalitions of female bonobos readily form to compete with the larger males, and as a result females generally are codominant with males (*10*). For example, subordinate coalitions often form when two or more allied females routinely (and usually quite successfully) gain primary access to food resources at the expense of competing individual males. Such behavior can escalate to the point where a sizable female coalition may wound or even possibly kill a male (*11*, *12*). Bonobos are known for having conflicts that are far less frequent and less dangerous than those of chimpanzees and more bellicose human foragers, but social dominance hierarchies are clearly present. So although they resolve many of their conflicts dyadically through sexual behavior (*10*), triadic alpha-male power interventions are also reported (*13*), and fighting does occur.

Wild chimpanzees differ in several important respects. They also have linear hierarchies among adult males, who compete strongly for their power positions; however, female hierarchies are much looser. Because females in the wild seldom form coalitions, even lower-ranking males usually can dominate the strongest females (*14*). Chimpanzee males also engage frequently in coalitions with other males, forming competitive political alliances that further their individual quests for power within the male hierarchy. However, when a pair of rivals manages to unseat an incumbent alpha, only one of the two will assume the alpha position as a new set of competitive alliances comes into play (*3*, *15*). As with bonobos, among wild chimpanzees there are small and sizable subordinate coalitions that behave antihierarchically. For example, occasionally a large coalition of males, or males and females, will actively attack and temporarily "banish" or kill an adult male (*16*–*19*).

In some captive chimpanzee groups, the balance of power between males and females is modified in the bonobo direction because the females form strong bonds and act as cohesive subordinate coalitions. In this way, they are able to challenge, manipulate, and sometimes temporarily dominate high-ranking males. However, in both wild and captive conditions, powerful alpha male chimpanzees intervene frequently in dyadic conflicts as dominant peacemakers that coerce the protagonists to separate. Individuals will also reconcile on their own, and in close conditions of captivity female third parties also manipulate male conflicts without use of force, as though encouraging the protagonists to make up (*20*).

The contemporary humans most appropriate for this evolutionary analysis are mobile hunter-gatherers who continue the "culturally modern" behaviors associated with anatomically modern

Fig. 1. Depicted by the artist is an Australian Aborigine band under attack by members of another band. There was considerable violent conflict among bands in precontact Aboriginal Australia, but there were methods of effecting truces and peace treaties as well.

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humans starting about 45,000 years ago (*21*) in the Late Pleistocene. Many scholars (*22*, *23*) have arbitrarily written off these potential exemplars because in recent times they have been so politically "marginalized"; however, I suggest that Late Pleistocene populations were similarly marginalized because of climate shifts. Thus, contemporary foragers—but just those who are economically and culturally independent and isolated from domestication and modern commerce—in fact are likely exemplars for what culturally modern humans were doing in the Late Pleistocene (*24*).

These "Late Pleistocene–appropriate" foragers live in small, multifamily egalitarian bands, and, although they certainly compete for mates and food, they are militant about not allowing male competition to develop into the kind of general dominance that is sought through alpha-male behavior in the two *Pan* species (*4*). This is because the type of antihierarchical subordinate coalition that is found in bonobos and chimpanzees emerges much more definitively in human foragers, where it results in significant reproductive leveling (*6*).

In these foragers, the virtual elimination of alpha-male behavior is possible because rebellious political coalitions are able to act efficiently on a moral basis, with a conscience-based sense of right and wrong as a political catalyst that intensifies negative group reactions against personal self-aggrandizement. In addition, both conflict and group-sponsored conflict management are vigilantly mediated by such moral concerns, which cannot be readily discerned in either chimpanzees or bonobos and therefore are likely not ancestral but derived (*24*).

In all three extant species, group males react hostilely toward males of neighboring groups, and in chimpanzees and humans lethal conflict behavior can result. However, bonobos mainly issue vocalized threats, and, although one case of possible wounding is reported (*13*), sometimes two groups may mingle (*9*). Regarding territoriality, bonobos diverge from the human-chimpanzee pattern, suggesting that intergroup conflict in ancestral *Pan* may not have been lethal often—even though chimpanzees and some human foragers systematically kill outsiders (*25*–*27*). By 45,000 years ago, however, humans had become "symbolic" and otherwise culturally modern (*21*), and surely our evolved potential for lethal conflict between bands had become substantial (*28*–*31*). Fortunately, we also had evolved ways of negotiating such conflicts when they became too costly (*4*).

Conflict and Its Resolution

In ancestral *Pan*, competitive dyadic interactions over food or mates did not necessarily provoke conflict—as long as clear roles of dominance and submission prevailed. The subordinate could simply flee, as an act of avoidance, or could stay in place and offer a submissive signal. In either case, fighting with a superior was avoided. However, because dominance hierarchies operated over time, individuals inevitably gained or lost power according to their stage of life, health, or coalitionary situation. Ancestrally, this made for circumstances in which, at times, subordinates were prone to challenge their superiors.

The result was conflict in the form of bluffing or fighting, and in fact, just like its three living descendants, this ancestor would have been well evolved to fight. As has been seen, it also was evolved to cope with conflict in that when serious quarrels erupted, if a higher-ranking individual was present, pacifying interventions could be initiated by an altruistic peacemaker (*13*, *15*, *32*–*34*). Furthermore, often the two parties might be capable of effective reconciliation (*20*) on their own. Thus, this ancestor possessed primitive patterns of conflict and conflict management that appear to have coevolved continuously for over 5 million years, as evidenced by their presence in the three descendant lineages (*35*).

Considering just the well-studied chimpanzee, conflict resolution appears to be cognitively sophisticated in that a variety of tactics are used by third parties in breaking up fights and making sure they are not resumed (*32*). In both chimpanzees and bonobos (*36*), there is also variety in the ways they reconcile their differences dyadically (*20*). Because this is also the case with humans (*33*), a flexible peacemaking approach is likely to be ancestral. Furthermore, captive chimpanzees show something like "community concern," in that female coalitions support males that act as peacemakers (*20*, *37*). Such behavior also is obvious in humans, but it is more difficult to demonstrate for bonobos, whose coalitions are not so large.

Ancestrally, it is likely that an additional type of conflict arose when subordinate coalitions formed to threaten or attack powerful, overbearing individuals that no individual group member would dare to attack alone (*4*). The resulting conflict could result in the disliked dominator fleeing or being wounded or killed. An intriguing aspect of such attacks was that they may not necessarily have been about food or mates; in all likelihood, this ancestor would have been disposed to fight over political position or power (*38*).

When such coalitional conflicts arose between allied subordinates and the alpha individuals who

Box 1. THE PARSIMONY PRINCIPLE IN BIOLOGY

One way to illuminate patterns of conflict present today is to examine their deeper background. At present, fortunately, ancestral hierarchies and the conflict they generated can be recreated with considerable reliability because such reconstructions can be based on the evolutionary biologist's specialized principle of **parsimony** (*61*, *62*).

Parsimony theory posits that over time natural selection is likely to operate as simply as possible, and the theory applies more strongly if the evolutionary time span between an ancestor and its living descendants is short. Thus, when today's humans, bonobos, and chimpanzees share a behavioral trait like conflict management, we can infer that the recent ancestor shared by all three of them at 5 to 7 million years ago (*63*) passed that trait down to each of them directly and therefore that the contemporary behaviors will have a similar underlying genetic basis. For instance, if the above three descendant species share conflict management, it is highly unlikely that their shared ancestor originally lacked this ability and that it was later acquired by all three independently.

Parsimony can be relied upon unless persuasive contrary evidence exists. Consider the fact that physically the above three species are only moderately sexually dimorphic with respect to body size. Parsimony would suggest that the same was true of their precursor, which I call ancestral *Pan* (*57*). This assumption has been challenged by an analysis of postcranial skeletal fossils for *Australopithecus afarensis*, which suggests the presence of dimorphism comparable to gorillas (*64*). This challenge has its problems, because there is no definitive evidence that *afarensis* was a member of the direct human lineage (*65*). In fact, *afarensis* may well have been a hominin descendant of ancestral *Pan* that went extinct. In reconstructing behavioral features of ancestral *Pan* that relate to conflict, it must be kept in mind that such challenges may arise and that in each case the facts must be weighed.

If a primitive trait is established ancestrally on the basis of parsimony, it follows that over time the trait would have been continuously present in the lineages that connected the three descendant species with their shared ancestor. However, the really definitive fossil referents go back only 2 million years; they include ourselves, archaic *H. sapiens*, and *H. erectus* (*21*). Although earlier fossil species include a number of candidates scholars espouse for human ancestry, such as *Ardipithecus ramidus* (*65*), ongoing debates leave even the relatively recent, tool-using *H.* (or *Australopithecus*) *habilis* as a mere possibility (*66*).

Two main rules for reconstruction help to keep the analysis conservative. First, if a major behavior pattern is found unanimously and unambiguously in bonobos, chimpanzees, and human foragers and if no evolutionary evidence exists to the contrary, the probability of its having been present in their (quite recent) shared ancestor will be very high (*1*, *3*). Second, I suggest that, if among the three extant species a trait is expressed strongly by two but weakly by the other, the ancestral assessment should be based just on the least common denominator (*24*).

normally dominated them, there were likely no pacifying interventions by third parties because this is absent today. However, overwhelming subordinate power would have made a quick and decisive end to such conflicts. These subordinate rebellions may well have provided the evolutionary basis for the egalitarian social orders that typify the life-styles of culturally modern hunter-gatherers and that in fact have continued to prevail among most tribal agriculturalists (*39*) [except when the advent of chiefdoms and civilizations has made for the rise of hierarchy (*23*)].

Thinking more broadly about sociopolitical basics of human nature, we are a species that is given both to within-group competition and to cooperation. Our innate competitiveness, coupled with the ability to fight, can lead to violence; however, we seem genetically predisposed to reduce stressful and often dangerous conflict levels. This can be accomplished by the parties reconciling, having a responsible third party intervene, or, sometimes, simply by spatial avoidance.

Human Foragers and Conflict

There is little doubt that conflict and conflict management have coevolved. Being competitive certainly has reproductive payoffs, but a capacity to end conflicts also is beneficial. It is this combination that defines much of today's political life.

Over the past 5 to 7 million years, humans have diverged from their two *Pan* congeners in several major respects that impinge on conflict and its management. First, at the level of the phenotype, we temporarily lost the alpha male role by becoming politically egalitarian (*40*). This means that we lost both a selfishly efficient oppressor and a forceful, but altruistic, peacemaker. Second, at the level of genotype, we acquired a conscience (with a sense of shame) that made us moral. This changed the very nature of our group life (*24*), for now, in addition to primitive, fearfully submissive reactions to the power of others, moral hunter-gatherers follow rules simply because group values support them. It seems we have evolved to internalize such values (*41*, *42*).

This thinking applies to all humans, but here we focus on how conflict and conflict management work in the simpler foraging bands we have been considering as later paleoanthropological exemplars. Today's evolutionarily appropriate foragers are of the type who are spatially mobile and highly cooperative and who vigilantly keep their egalitarian orders in place with only muted leadership. Because there are no alpha males to intervene authoritatively in their disputes, a serious dyadic conflict can quickly result in homicide. Indeed, the homicide rate per capita for egalitarian foragers is as high as in large American cities (*5*, *40*, *43*).

Within the community, evidence for "homicide" in adult chimpanzees and bonobos is mostly inferential but highly suggestive. For example, at Gombe alpha-male Goblin would likely have been killed by solo challenger Wilkie had not a veterinarian intervened (*16*), whereas at the Mahale field site the alpha male was photographically documented as being killed by other males (*18*). Among bonobos, a savage attack by half a dozen united females may have killed an adult male (*11*). Thus, ancestrally within-group conflict likely had at least some modest effect on adult mortality.

Aside from the important issue of morality as a derived behavior that intensifies social control and makes it more effective, in the area of conflict there are several other significant differences between humans and the two other species in our small clade. One is weapons. Bonobos and especially chimpanzees may use tools, but the use of weapons as humans do, to hunt sizable mammals, is totally absent (*44*). Bonobos and chimpanzees do have the potential to kill a smaller mammal, mainly using their canines (*45*), and this is also true of conspecific group attacks (*11*, *14*), which usually take at least several minutes for severe damage to be rendered. Human foragers use efficient hunting weapons to kill sizable mammals and members of their own species alike, and with these weapons they can do so much more quickly, at a distance, and often from ambush (*46*). These differences escalated the consequences of human conflict. Further escalation stemmed from the uniquely human propensity to lethally retaliate for the death of a close relative (*47*), a behavior that in all likelihood is not ancestral but which figures prominently in hunter-gatherer conflict. Thus, for humans the scope and consequences of serious conflict within the group would appear to be considerably greater than with ancestral *Pan*.

Another human difference is the understanding of death. When omnivorous chimpanzees or bonobos hunt, unlike dedicated carnivores, they have no evolved response that makes them into efficient automatic killers; in fact, prey may be eaten alive (*14*). When chimpanzee patrols savagely attack strangers they leave them battered and torn (*25*), but sometimes alive with some very small chance of recovery (*14*). This also is true of the one observed serious within-group attack by bonobos (*11*). In contrast, in spite of their diverse supernatural beliefs human foragers understand death as a termination of social responsiveness and muscular activity, and they inflict it deliberately. For instance, when egalitarian hunter-gatherers use capital punishment to eliminate despots, they shoot to kill (*24*).

Humans readily become lethal revenge-seekers, and chimpanzees and bonobos may at least try to retaliate for a prior aggression (*10*, *14*), so there were likely some modest ancestral preadaptations for such behavior (*47*). However, understanding how to kill with lethal weapons can lead to such motives becoming costly to groups, particularly when revenge becomes moralized as a matter of honor. On the other hand, being vindictive can be useful to a group if such a reputation keeps it from being attacked (*48*).

This holds for foragers that are given to conflict and even more so for clannish patrilocal tribal farmers (*49*, *50*). Among simpler hunter-gatherers, when a male kills another male, usually over a female, close relatives will predictably seek lethal retaliation (*40*), and the killer's only recourse is to move away. But with those foragers who do develop active, intensive raiding and warfare patterns, revenge needs also can help to motivate much larger attacks by entire groups (*51*).

Warfare is a major problem for modern humans, and most theories of warfare focus directly on resource competition (*52*). However, materialistic theories fail to fully explain the warfare patterns of forager societies (*31*, *53*). For instance, the Iñupiaq hunter-gatherers of northwest Alaska compete with some of their close neighbors for nearby natural resources, but at long distance they also conduct prolonged nonterritorial genocidal warfare against enemy bands, with surprise attacks and pitched battles motivated by retaliation (*51*). Here, I believe it is not necessary to favor one cause. A serious intergroup conflict may begin because of either resource competition or revenge, and the pattern can continue because of either factor, or both (*47*).

Managing Human Conflicts

Because adult male foragers are constantly armed as intentional killers of prey, any male dispute within a band can have drastic social consequences—particularly because our species is so prone to retaliation. On the other hand, with our large brains and language we can understand, and symbolically evaluate, the negative effects of disputes. Moral values play a direct role when band members not only condemn acts that create conflict, including killing, bullying, theft, and cheating (*54*), but extol the virtues of social harmony (*55*) and actively promote altruistic generosity that fosters cooperation (*56*). As a practical application, sharing large carcasses is so well regulated culturally that serious conflict over precious meat is routinely obviated (*57*). However, a noteworthy area that is poorly regulated socially, and which produces most of the serious conflict, is male competition over females (*40*).

Curiously, often conflictive behavior, per se, is not condemned morally. Rather, foragers appear to view most serious personal disputes as requiring an application of third-party mediation—but not individual punishment. However, it is clear that when a band suppresses morally deviant behaviors that are likely to create conflict, in effect it is preemptively reducing conflict levels as well (*58*). In evolutionary contexts this preemptive effect of social control has been little noted, but for leaderless hunter-gatherers it is very important precisely because forceful alpha peacemakers are lacking (*24*).

When dyadic conflicts do arise, powerless band members will try actively to distract the participants, facilitate negotiations, or otherwise serve as mediators (*33*). When disputes become serious, third-party intervention quickly becomes impotent, but spatial avoidance is often used by humans (*40*) if changing bands is an option. However, in

the Holocene, when many humans settled down as farmers, avoidance became too costly. This led egalitarian farmers, in their sedentary tribes, to allot some modest authority to their chosen leaders as conflict mediators. Eventually, far more authority was given to hereditary leaders as certain sedentary foragers or farmers lost their egalitarian ethos and began to form social classes. For farmers, this opened the way for the evolution of chiefdoms, kingdoms, and states, and in this way the protracted age of widespread egalitarianism ended (*23*).

The role of hereditary chiefs included an ability to mediate disputes with considerable authority (*59*); beginning about 5000 years ago, with the rise of centralized states, political leaders also had increasing coercive force to back up their mediating decisions in the form of a standing army paid for by taxation (*23*). This centralized approach to conflict management continues today in large modern societies, be they democratic or autocratic, which by their size and nature also require efficient centralized command and control. The job of managing potential major conflicts may be delegated largely to legal systems with police and courts of law, as well as to political figures who serve as mediators. But, in nations, a standing army can intervene if an internecine conflict becomes too heated. Such power interventions are not always successful, for civil wars are not uncommon. Indeed, the rebellious roots of "terrorism" would appear to be ancient.

With respect to conflict between groups, a conservative assessment of ancestral *Pan*'s patterns would limit this to the bonobo level of territorial behavior, based chiefly on threats (*13*), although a more chimpanzee-oriented model would suggest otherwise (*3*). If we look at today's humans, there has been a tendency for many hunting bands to fight ferociously with their foraging neighbors (Fig. 1) as single or regional units (*28*, *30*, *51*), whereas the sedentary egalitarian farmers who followed them are still more prone to raiding and warfare (*23*). In both cases, revenge motives can exacerbate these patterns, whereas intergroup conflicts sometimes can be negotiated through peacemaking or truces.

Virtually all nations devote significant resources to warfare readiness. In today's world, there seems to be a consistent, sizable number of small wars ongoing despite the fact that we have not experienced an active, truly global conflict since the Second World War (*59*). However, whereas a hunting band often can move away and simply avoid a predatory neighbor, our world of nations is firmly situated in space, and this ancient remedy cannot be applied (*60*). Fortunately, peace negotiations like truces and treaties that are found among warlike hunter-gatherers (*4*, *51*) also are used by nations. It would appear that, as derived behaviors, both violent, two-way intergroup conflict (*27*) and intergroup peacemaking have prevailed at least since humans became culturally modern.

Thus, humans are a conflictive species that developed its mechanisms for intergroup conflict management in the context of small hunting bands and did so without any formal political centralization. As our populations have grown, on a cultural basis we have rather quickly evolved into a species given to centralized governments. These governments try and often succeed in protecting their populaces from internal conflict and often are able to negotiate conflicts that arise between nations. This same command and control also enables us to mobilize efficiently for aggressive conventional warfare and to create weapons of mass destruction.

In the foreseeable future, the human capacity for political problem-solving will continue to be tested, with an ancient capacity for conflict management providing an important tool in international politics. The future of our own species (and surely many others) will be hanging in the balance.

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