

The Coevolution of Warfare, Punishment, and Culture in *Homo sapiens*

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Suppose astrophysics textbooks explained that the standard theory in physics works well for explaining the paths of the other planets, but fails in explaining the path of our own planet, the Earth. Physicists might pragmatically and successfully continue to use the standard theory, while bickering about why it fails for our own planet.

Thankfully, that is not the case in physics. But unfortunately it is the case in social evolution, the field of evolutionary biology addressing the nature of social behavior in animal and plant societies. Despite an empirically successful theoretical revolution begun in the mid-20th century (1,2) that has explained and predicted counter intuitive aspects of social behavior in animal and plant societies (the “other planets”), there is yet no consensus explanation for the hypertrophied cooperative nature of our own species, *Homo sapiens*. In this issue of PNAS (3), evolutionary anthropologists Sarah Mathew and Robert Boyd use a study of warfare among contemporary Turkana pastoralists of East Africa to support one model of how costly, large-scale human cooperation evolved.

One of the triumphs of 20th century evolutionary biology was the successful explanation of self-sacrificial behavior. Why do animals and plants sometimes sacrifice personal safety and reproduction for the benefit of other organisms? The principle answer, kin selection, has allowed us to explain both why the most extreme forms of altruism are usually limited to close kin, as well as why eusocial animal societies—bees, ants, termites—exhibit reproductive division of labor, in which only a fraction of the population reproduces (4,5).

The embarrassment to this theory is *Homo sapiens*, which cooperates in the largest groups of any mammal, in violent conflict involving thousands of individuals, without reproductive division of labor. Among animals, most costly self-sacrifice is limited to close kin, and is therefore usually confined to small groups. Where it involves large groups, as in ants and other social insects, substantial genetic variation between colonies makes this behavior consistent with kin selection (5). In contrast, modern human societies participate in large-scale organized warfare, in which individual fighters suffer substantial mortality risks, while their actions benefit a large territorial population that is barely genetically differentiated from the enemy. Kin selection models predict that self-sacrifice of this kind cannot evolve, instead requiring smaller groups or additional assumptions (6). The stakes here are high, as the theory of social evolution has made sense of topics as diverse as intragenomic conflict and interspecific mutualism, as well as the evolution of eusociality. Its failure so far to produce a consensus explanation of our own species' sociality is a blemish on an otherwise meritorious record.

There are two families of competing explanation for large-scale cooperation in human societies, and the report by Mathew and Boyd in this issue (3) supports one of them. The first invokes kin selection in past social environments, and is termed the *evolutionary mismatch hypothesis* (7,8). An evolutionary mismatch is a trait that was adaptive in past environments, but which is no longer adaptive in changed environments. For example, unlimited

desires for fat and sugar are possibly adaptive in environments in which fat and sugar are in limited supply. But in modern industrial environments, fat and sugar are cheap and abundant, and these desires lead to overconsumption and negative health consequences. Applied to human cooperation, the mismatch hypothesis argues that, for most of our evolutionary history, humans lived in small residential groups comprising close kin. In such groups, kin selection would favor mechanisms that could sustain generalized cooperation and violent conflict between groups. In other words, genetic group selection among small foraging bands in the Pleistocene favored self-sacrifice for the benefit of foraging bands. In modern social environments, the hypothesis states, our psychology mistakes large territorial groups like nation states for groups of close kin.

The second explanation also invokes group selection, but focuses on socially learned contributions to human behavior. This *cultural group selection* (7,9) framework argues that the asymmetry in how culture and genes are transmitted among individuals can lead to natural selection for culturally—rather than genetically—transmitted beliefs that promote self-sacrifice on behalf of large cultural groups. There are three parts to the cultural group selection idea.

First, the keystone of the theory is the proposition that individually adaptive social learning heuristics, such as prestige and conformist biases, can evolve under genetic evolution. These biases help individuals acquire locally adaptive culture, in the face of substantial mixing among human groups. Modeling studies find that selective learning biases evolve essentially whenever cultural learning evolves, as it has in *Homo sapiens*. Laboratory and field evidence suggest that these biases exist and are strong (7,9).

Second, cultural learning biases can, as a side effect, lead to reduced cultural variation within and increased cultural variation between communities, even in the presence of substantial mixing of peoples. Either immigrants re-socialize by acquiring local behavior through social learning or natives avoid learning from immigrants. Physical bodies and their genes move freely between cultural groups, keeping genetic variation between such groups low. Because genetic variation between these groups remains low, kin selection predicts very little costly cooperation within such groups. Strong learning biases, however, may maintain cultural variation despite migration (9). While anthropologists rarely collect the individual-level data needed to estimate variation within and between cultural groups, crude underestimates suggest there is much more cultural variation than genetic variation between ethnic groups, on the order of 30 times as much (10).

Third, group selection among cultures operates statistically just like kin selection: if there is sufficient variation among groups, selection favors adaptations at the group level. In kin selection, the groups are descent groups, and common descent maintains variation among them. In cultural group selection, the groups are defined instead by cultural processes. Groups that happened to have pro-social norms have an advantage competing with other groups, leading to a form of multi-level selection operating on cultural variation. While cultural group selection could work when cooperative groups exterminate uncooperative groups, the process does not require differential extinction of this kind. Instead, pro-social norms could spread either by the recruitment of people into successful groups or by the copying of institutions between groups (9).

How does punishment factor into these theories? Punishment here refers to costly enforcement of norms, often by third-parties who have suffered no direct harm. In the mismatch hypothesis, punishment is either a product of complex societies or an adaptation for cooperation within small bands of kin. In cultural group selection models, punishment coevolves with pro-social norms,

stabilizing these norms and increasing variation among groups (7,9,11). That punishment occurs does not necessarily support cultural group selection over a mismatch hypothesis. Instead, punishment targeted at failures to cooperate in very large symbolic groups, even in the absence of political integration, is consistent with cultural group selection.

Mathew and Boyd use a study of warfare among contemporary Turkana pastoralists to address the contest between these two broad models of human sociality. The Turkana are a Nilotic people, numbering perhaps one-half million, now living in arid and anarchic northwest Kenya. Turkana make their living by nomadically herding zebu cattle, camels, and goats. Cattle raiding is and long has been commonplace among Turkana and other pastoralist groups in the region.

The Turkana are an important test case for cultural group selection, because they are not politically integrated in any formal way beyond small, seasonal collections of households. There is no coercive state to enforce participation in warfare—the Turkana are not a nation and have no formal leadership. Therefore if participation in warfare is maintained by punishment and the benefits of warfare accrue to the Turkana as a whole, this case supports cultural group selection. If instead individual gains from raiding are all that is needed to maintain warfare in this context, or war parties are formed from descent groups, this would not support cultural group selection.

Mathew and Boyd analyze interview and family history data from 118 Turkana men and 88 distinct raids. They make two claims. First, punishment supports costly, cooperative warfare among the Turkana, even in the absence of coercive formal institutions. Second, the scale at which cooperation is supported is the Turkana ethnic group, not kin groups. The Turkana participate in dangerous warfare—both raiding and retaliation for raids—in groups of hundreds of men from diverse descent groups. Many are strangers. Raiding also carries substantial costs. During his reproductive years, a Turkana man is more likely to die from warfare than from all other causes combined. While there are benefits of joining a raid that help offset these risks—a raider can acquire as many as 10 cattle per raid—the benefits of deterrence against raids from other ethnic groups accrue to all Turkana regardless of participation. Furthermore, even those who join raids have incentives to retreat early or otherwise engage in acts of “cowardice” that reduce risks of death. The Turkana punish such acts with beatings, fines, and social exclusion, and even third parties who are not present at a raid discriminate against cowards. That such punishment is necessary speaks to the inadequacy of the spoils of war—stolen cattle—for maintaining warfare. Participation is costly, even after accounting for plunder, and the Turkana strategically employ punishment to maintain it. This punishment notably benefits the entire Turkana ethnic group and is enforced throughout it. The Turkana hold a strong injunction against raiding co-ethnics for cattle. If cultural group selection were responsible for the evolution of cooperation and punishment, then we should expect cooperation and enforcement to be bounded by cultural groups, rather than genetic descent groups. This appears to be the case among the Turkana.

While an important advance, this report will not settle the debate. Finding that punishment helps to maintain cooperation among Turkana does not exclude other mechanisms. Reputation and reward are also implicated and may act synergistically with punishment. Human cooperation is so variable in form, extent and mechanism that no single human population is representative of the whole species (7,12).

Additionally, there are few explications of mismatch hypotheses. Most descriptions of evolutionary mismatch are written by supporters of cultural

group selection (7). Further confounding the issue, some of the most compelling versions of cultural group selection also argue for a kind of mismatch—a cultural remapping of “social instincts” evolved for life in smaller groups. Groups having institutions that manipulate these instincts in pro-social ways may spread their institutions via cultural group selection (13). Some clarity is needed. The literature on cultural group selection contains a number of mathematical and simulation models that algorithmically specify the cultural processes and demographic conditions that may support and maintain large scale cooperation. A parallel literature for mismatch hypotheses has yet to develop, but the field would benefit from it.

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