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Article

Cell-Gazing Into the Future: What Genes, *Homo heidelbergensis*, and Punishment Tell Us About Our Adaptive Capacity

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Abstract: If we wish to understand how our species can adapt to the coming tide of environmental change, then understanding how we have adapted throughout the course of evolution is vital. Evolutionary biologists have been exploring these questions in the last forty years, establishing a solid record of evidence that conventional, individual-based models of natural selection are insufficient in explaining social evolution. More recently, this work has supported a growing consensus that our evolution, in which we have expressed extra-ordinary adaptive capacities, can best be explained by "Multi-level Selection", a theory that includes the influence of both genes and culture to support unique adaptive capacities premised on pro-social behaviours and group selection, not individual-level competition for survival. Applying this scholarship to contemporary concerns about adapting to environmental change may be quite fruitful for identifying sources of vulnerability and adaptive capacity, thereby informing efforts to enhance the likelihood for sustainable futures. Doing so, however, requires that we bridge the gap between evolutionary biology, and the social sciences study of sustainability.

Keywords: adaptation; adaptive capacity; evolutionary biology; cooperation; climate change

1. Introduction

> *The most important predictor of a Baboon infant's survival is the number of close social bonds that the mother has, not its status in the dominance hierarchy. This just might be true of you and I too* [1].

Are we headed for adaptation or extinction? This is of course an unanswerable question with any degree of certainty, because in complex systems outcomes are emergent and thus unpredictable. Nonetheless, inquiries into social adaptation are well-warranted, considering the mounting socio-economic and environmental calamities unfolding on the global landscape. While this paper is explicitly a treatise on adaptive capacity, it behoves us to point out the close association of this term to the concept of adaptation. Adaptation, a concept with origins in biology, entails responses by organisms or systems to risk or hazard, by means of the development of genetic or behavioral characteristics that enable coping with environmental changes in order to survive and reproduce [2]. As interpreted for social systems, "survival" encompasses the persistence of a socio-cultural regime. Adaptive capacity, on the other hand, refers to the ability of a given system to adapt on the basis of a set of determinants or criteria presumed to be conducive to that ability; hence assessments of adaptive capacity (current and future) necessarily entail explorations into (historic) adaptation. We can inform such inquiries, and identify opportunities to enhance the likelihood for sustainability-promoting trajectories to come to pass by delving into different areas of scholarship that explore adaptation processes. We explore one relatively un-trod pathway, into the nexus of evolutionary biology, behavioral ecology and evolutionary psychology, to highlight the emerging agreement across these fields that cooperation is the key to adaptation.

This pathway brings us immediately to a paradox of sorts—much of evolutionary biology has, for the last forty years, focused on individual-level genetic adaptation, with little to say about the adaptation of social systems or groups [3,4]. This atomized view of humans extended to sociology, aiding in the critique of functionalism, or the theory that social structures operated 'for the good of the group,' popularized by Parsons in the 1950s [5]. Well-versed extensions of this scholarship include the suppositions that, first, humans are by nature selfish, boosted by the works of a spectrum of scholars from Herbert Spencer and Gary Becker to Garrett Hardin. Second, until recently, micro-economic wisdom held fast to Adam Smith's [6] postulate that our social futures are brighter, or 'optimal,' when we each pursue our own rational self-interested desires, through the exercise of our own abilities. While this second premise is being challenged by mounting concern about over-consumption and its implications for multiple social and environmental problems, it still enjoys a large amount of cachet in western societies, best exemplified in political neo-liberalism, with its emphasis on individual property rights and liberties. As Margaret Thatcher famously announced to the world, "there is no such thing as society. There are individual men and women, and there are families." [7]

Yet over the last few decades a compelling empirical record has emerged to challenge such claims and make the case that pro-social, group-oriented behaviour is in fact far more common than these models of human nature would predict. Indeed, a recent cross-cultural psychological meta-analysis shows that the individualized (versus holistic) and independent (versus interconnected) qualities characteristic of Western, Industrialized, Educated, Rich, and Democratic populations (WEIRD) are in fact the least representative behavioural types of our entire species [8].

Recent scholarship in evolutionary biology is quite interesting indeed—it suggests not only do we humans, and other species as well, have a proclivity for group belonging, which encourages many forms of cooperation and altruism, but furthermore, this very "groupishness" may actually have been elemental to our successful adaptation to all manner of survival threats throughout the course of human history [9–16]. Research under the guise of Multi-level Selection Theory shows that natural selection operates at multiple scales (genetic, individual, and group), and that pro-social traits that are 'good for the group' tend to be selected for at the expense of selfish traits when they enhance the competitiveness of the group as a whole, even if the trait provides little or no direct benefit to an individual within the group. As Wilson and Wilson put it "Selfishness beats altruism in groups. Altruistic groups beat selfish groups. Everything else is commentary" [15].

The application of this scholarship to contemporary questions of social response to crises like climate change has not occurred to any great degree, perhaps due to the historical reliance on the individual (and gene) as the primary unit of analysis in evolutionary biology, while the group tends to be the focus of attention among social scientists studying sustainability. As we argue below, rifting this bridge will enable current sustainability-enhancement efforts to be informed by a far more complex and historically accurate view of how humans adapt to changing ecological and social environments. Our main point is simply this: our evolutionary history has given humans an unparalleled ability to cooperate, and this very ability has enabled our successful adaptation for the past 250,000 years. Adaptation to current and future social and environmental conditions therefore requires that we revitalize our unique capacity to engage cooperatively for the benefit of group survival. By studying how we evolved such a capacity, and in what contexts cooperation is most likely to flourish, we can identify those social systems with the greatest ability to adapt, and perhaps also highlight strategies for building adaptive capacity where it is found lacking.

2. Why Would Cooperation Enhance Survival? Competition Costs Energy

Cooperation is found not just in humans, but across a wide range of taxa, including ants, wasps, rodents, birds, fish, and even bacteria. In primates, mutual grooming is one of the most cited examples of reciprocal cooperation [17]. One of the clearest indications of the survival benefits of cooperation is expressed in energy expenditures. In short, competition and conflict cost energy. Male Bison of the Great Plains, for example, spend their summers grazing on the plentiful grasses. Come Autumn, all of the male bison take the mass they have built up over the summer and spend it in a month-long rut, in which males fight each other to secure access to females, leaving them to face the Winter weak and thin.

Of course we humans express this same costly sexual competition in the conspicuous consumption of status goods, but there are many other analogs for this kind of behaviour, with rewards that are arguably far less justifiable than reproductive success. Nations engage in lengthy conflicts, and spend much of their peacetime maintaining readiness for such conflicts, both of which consume an extraordinary share of resources. A case in point: Currently, twenty-two aircraft carriers float the global seas, of which the U.S. owns eleven, all nuclear-powered. Of these, five are continuously stationed along the Arabian Gulf protecting oil shipping lanes. The other six are either in transit between the Arabian Gulf and the U.S. or are awaiting deployment [16].

The male Bison and the US citizenry both pay extraordinary costs to engage in competitions in which the rewards are uncertain. Evolutionary models have shown repeatedly that the relative benefit of conflict decreases in relation to the increasing costs of conflict, and thus animals can be expected to favour restraining conflict when costs are high, and resort to less costly signaling [18]. Thus as resources become increasingly scarce and acquiring those resources becomes increasingly costly, being locked into a system of conflict and competition will only further tax a society's resource base. As the resource requirements of adaptation to ecological and climatological crises increase, the relative benefits of maintaining an energy-consumptive system premised on competition decline. Scholarship on common pool resources has offered much the same lesson: successful environmental management has much greater potential when cooperation among multiple stakeholders is achieved [19,20].

3. Getting to the Heart of the Matter: Group Selection and Cooperation

It turns out that the empirical findings of Ostrom and others [20] regarding the benefits of cooperation have a much deeper evolutionary history that stretches hundreds of thousands of years before the origins of agriculture. During the mid-1960s, the role of pro-social traits (cooperation and altruism) received a fair amount of attention from evolutionary biologists, who presumed that such traits were the result of group selection [21]—the theory that traits benefitting group survival prevail over those benefitting individuals. For example, in many bird species it was assumed that the elderly willingly sacrifice themselves in order for the group to maintain a population density below carrying capacity. The emergence in the late 1960s of Williams' [22] and then Dawkins [23] "gene's eye view of life", however, systematically dismantled this view and subsequently changed the course of evolutionary biology for several decades. Both Williams and Dawkins argued that social evolution can be explained best by the fitness-maximizing behaviours of genes, not groups or individuals. Regardless of the validity of a gene's eye view of life, which has been subject to extensive debate, Dawkins erroneously extended its logic to proclaim, "Let us try to teach generosity and altruism, because we are born selfish" (p.2). This line of reasoning became readily accepted despite the continued accumulation of empirical evidence to the contrary from developmental psychology, which has demonstrated, among other things, that pro-social tendencies are even expressed among infants [24].

The prevalence of the gene's eye view of life actually did inadvertently advance our understanding of pro-social behaviours, by inspiring inquiries into the role of genes. Biologists began with the premise that pro-social traits would only be expressed to the degree to which they increase the frequency of pro-social genes within a group [25,26]. With this in mind, researchers focused on the construction of theories that could identify the conditions under which cooperative and altruistic genes could in fact become stabilized in populations, and resist invasion by so called "defectors" or freeloaders that exploit the cooperators. On the basis of this work, models show that the conditions under which generalized pro-social behaviors could evolve are rather stringent: there must be low levels of *intra*-group conflict, and relatively high levels of *inter*-group conflict [27]. Low levels of intra-group conflict allow the group to operate in a coordinated manner, just as the component parts of organisms do. High levels of inter-group conflict, on the other hand, bind people to their own group. Inter-group conflict also tends to set clear demarcations between groups, creating the variation and competition needed for natural selection to operate at the group level. The rigidity of these conditions (and the neglect of consideration of the role of cultural evolution, discussed later) led many biologists to argue that other, more individualized or dyadic mechanisms, such as kin selection [25], reciprocity [26], and reputation [28] are the only real drivers of cooperation. With the advent of inexpensive genetic testing technology, empirical researchers are beginning to test these theories and have found many genetic correlates to cooperative behaviour in humans [29–31]. Yet, these three mechanisms simply did a poor job of explaining the high levels of cooperation observed in large complex social systems [21], especially large-scale community-oriented cooperation, and the strong desire expressed by individuals to create and maintain group-based identities.

4. The Power of "the Stick" in Stabilizing Cooperation

To explain this gap, some economists, anthropologists and biologists have recently been arguing increasingly that the observed frequency with which cooperation in large groups does indeed evolve can be explained with the inclusion of cultural factors. There are several such factors of relevance, including in particular our capacity to learn through cultural exchange, a point to which we turn later. Another, related factor that has received growing attention, is the role of punishment [9,32–36]. Game theory models [32], observational experiments [33,35], and ethnographic evidence [9,35,36] all show that punishment is a strong force inducing cooperation in large groups. Surprisingly, 'altruistic punishment' may have a genetic basis. While this may be a hard claim to sell, the reasoning is based on four lines of evidence: first, punishment is observed cross culturally in humans [36], second, it is present in other mammals such as meerkats and Naked mole rats [37], third, "policing"—a more sophisticated version of punishment—is present in many primates including chimpanzees[38], and fourth, researchers are beginning to untangle the neuro-genetic basis of 'altruistic punishment' in humans [39]. This is not to say that the propensity cannot be modulated individually or culturally but only that the tendency has an evolutionary underpinning. In short, social cooperation is maintained through the punishment of defectors, expressed as culturally-accepted sanctioning behaviours. Humans do indeed punish people who defect on social agreements regularly. This is of course the main function of our legal systems, but, arguably, even more effective are the informal expressions of norms and sanction through social interaction, reinforced by our desire to receive approval from others. Even children have a surprising proclivity to punish norm violations at a very early age [34].

Punishment is deeply intertwined with social norms, and social norms only exist because we are social learners. Our adaptive success is largely linked to the fact that we can adopt a wide array of behaviors simply by observing what other humans do, a process that unfolds much more quickly than genetic selection alone [40]. Social learning is a genetic adaptation that allows for non-genetic—namely cultural—information to spread rapidly through populations [41,42]. Punishment's ability to stabilize norms in a group is analogous to the way that mutation creates variations in organisms, and this cultural variation enables selection between groups just like natural selection operates between individuals. Selection at the group level allows for cooperative and adaptive norms that benefit groups to potentially spread across a population [43].

Yet, on their own, norms, which are simply localized behavioural and ideational patterns, have little ability to enforce otherwise costly altruistic or cooperative behaviour. The desire to follow norms is often weak in relation to the benefits that defection can offer, when unsupported by punishment.

If individuals are willing to pay a cost to abide by collectively agreed-upon forms of sanction to punish defectors, then the relative payoff that normally tempts individuals to defect is reduced. Once entrenched, punishment has two important effects. First, just as children learn the language spoken around them, children will preferentially learn norms, including punishment, from their own localized group. Learning localized norms is not just a logistical issue, but an adaptive one as a person's group probabilistically has more norms that contain adaptive information that is specific to that group's ecological and social context. Second, individuals tend to minimize interactions with members of other groups with different norms, to avoid costly coordination errors and punishment for not complying with the other group's norms. The proclivity to punish individuals and groups that violate one's own group-defined norms tends to reinforce inter-group conflict by introducing moralistic aggression into the equation. This raises an important caveat—punishment enables the stabilization of *any* kind of norm, regardless of that norm's contribution to adaptive capacity, or its ethical validity, and such cultural practices can become quite resilient in their own right [32]. The implication is unsettling and oddly familiar

5. Cooperation is the Key to Adaptation

When punishment is expressed in conjunction with other mechanisms for maintaining in-group cooperation, like kinship, reciprocity, and reputation, it can create the high levels of group-level cooperation needed for group selection to prevail [44]. In turn, punishment supports high levels of inter-group conflict through, for example, territoriality. Thus, one of the very reasons our ancestors flourished while similar species did not pertained to an adaptive complex that is dependent on social learning, which creates the necessary conditions for group selection: high levels of intra-group cooperation [9] and high levels of inter-group conflict [45]. As mentioned earlier, the group selection we observe among humans is not simply a genetic artifact; the ability of culture to operate as a vehicle for the exchange of information, including norms, is central. Cultural selection interacts with genetic selection—describing what has come to be called Multi-level Selection Theory—because in addition to the ecological environment, the socio-cultural environment is an equally central component of the context to which individuals attempt to adapt. As norms evolve, they create new socio-cultural arrangements that place new selection pressures on individuals, creating a co-evolutionary process. As punishment and pro-social norms spread through ancestral populations, our ancestors' genetic evolution responded correspondingly, and selection increasingly favoured a generalized yet parochial pro-social behaviour towards in-group members.

The importance of the process by which competition becomes suppressed at lower levels of the biological scale (genetic, cellular, individual, group), only to re-emerge at higher levels, cannot be understated. John Maynard Smith and Eros Szathmary emphasized this process in a seminal work [46] that forms the basis of Multi-level Selection Theory. Focusing on the most dramatic transitional periods in evolution, from the origins of cells, to eukaryotes, to multi-cellularity and sociality, they argue that a major transition happens whenever "entities that were capable of independent replication before the transition can only replicate as part of larger whole after it" (p. 6). In each transitional period toward greater complexity, conflict and competition became suppressed at lower levels. All of the cells in our bodies, for example, have the exact same genes in them (expressing a high degree of relatedness), and thus cooperate, allowing us to function as a single unified entity. By extension, as the size and complexity of social systems expands, so too do the cooperative networks that are forged, yet as any system expands it becomes increasingly vulnerable to selection and competition at lower levels. To exemplify the problem at hand, ethnographic evidence shows unequivocally that we reserve the most costly forms of cooperation and altruism for those closest to us [35]. Yet cooperative practices such as reciprocal gift-giving, marriage alliances, fictive kin groups, morality, and religion have supported bonding amongst otherwise geographically dispersed groups for hundreds of thousands of years, with archaeologists finding evidence of cooperation among regionally dispersed bands of *Homo heidelbergensis*, who inhabited earth as early as 800,000 years ago [47].

4. Conclusions

This work has two important messages for contemporary society. First, our evolutionary success as a species is attributed to our unique capacity for cooperation, which in turn is supported by our capacity for social learning. Second, as the complexity of systems increases, the requirements for cooperation at ever-higher scales also increase, and herein lies our contemporary challenge: as we confront unprecedented levels of socio-ecological complexity, we breach the capacities for cooperation that evolved to confront comparatively less complex systems. The evolution of post-nation-state governance apparatuses, internationalization of civil society organizations, and the internet all express extraordinary leaps in the evolution of cooperative behaviour. But the pace of our cooperative evolution may well pale in comparison to the scale of emerging social, economic and environmental crises foretold by climate models. Therefore a major strategic goal for large-scale adaptation must be achieving higher-order cooperation among component parts.

How do we apply these insights from group selection to studying contemporary problems of sustainability? First we must acknowledge that conflict exists within all individuals (and groups) between selfish- and group-oriented behaviour, and recognize that we humans have a unique capacity for both, which can be fostered in different degrees by different cultural, social, and institutional arrangements. Second, by understanding punishment’s fundamental role in stabilizing cooperation and thus increasing our adaptive capacity, we can explore how emergent forms of formal and informal punishment can stabilize adaptive norms. Take, for example, the spread of norms discouraging cigarette smoking: because smoking often happens in full view of others, punishment in the form of social disapproval reinforced more formal policy structures. On the other hand, consumption is becoming increasingly private and anonymous with the advent of internet shopping and a decline in the use (and availability) of public spaces. Stabilizing norms that punish over-consumption are difficult because of the increasing privatization of consumption.

Third, although the last 20 years of attempts at global environmental governance have engendered a growing tide of scepticism, we do have several millennia of cooperation to build on: humans for hundreds of thousands of years have been cooperating beyond a local scale, resulting in the formation of highly complex and yet stable tribes, chiefdoms, states, and international alliances. While there is little doubt that any attempt at adaptation must be local, the tightly coupled world systems we have created means that all cities, and countries are increasingly interdependent. Subsequently our ability to respond to large-scale crises at the international-scale depends on cooperation, the exchange of information, and agreement on the prioritization of those problems, although mitigation strategies may express a regional flavour. This in turn requires acknowledgement of the high levels of differentiation of attribution of responsibility, and impact. The incredibly rapid expansion of the Transition Town movement, from a single small town in the U.K. to several hundred sites across the globe in less than ten years, is an exemplar of just such adaptation-inducing processes. Transition Towns will by no means be sufficient, however. More research and practice needs to focus on: (1) identifying, and generating, conditions that support the emergence of norms that support sustainability across a multitude of social and environmental contexts; and (2) multi-scale cooperative structures that enable social learning both within and across those social contexts.

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