Abstract:
The question of whether a given trait qualifies as an adaptation must be answered on a case-by-case basis. Nevertheless, a strong case can be made for species as primarily adapted to their environments. A similar argument can be made for human cultures as primarily adapted to their environments at the group level. The reason that human cultures are primarily adaptive at the group level is because the capacity for culture is itself a group-level adaptation. Establishing a consensus on human cultures as primarily adapted at the group level will enable human cultural diversity to be studied in the same way as biological diversity.

SOCIAL EVOLUTION FORUM

Human Cultures are Primarily Adaptive at the Group Level

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Introduction

A recent conference on cultural evolution sponsored by the Ernst Strüngmann Foundation affords an opportunity to assess the state of the art for this subject (http://www.esforum.de/forums/esf12_cultural_evolution.html). Forty-five scientists were present, representing a melting pot of disciplines and nationalities, making the event as close to a world congress on cultural evolution as one can get.

The participants were divided into four groups that met over a period of five days to address the topics of *Cultural Evolution of the Structure of Human Groups*, *Cultural Evolution of Technology and Science*, *Cultural Evolution of Language*, and *Cultural Evolution of Religion*. The results will appear as a volume published by MIT press, but one conclusion emerged loud and clear: Human cultures are primarily adaptive at the group level.

This conclusion might seem shocking to some, given the long history of controversy over the topics of cultural evolution and group selection, separately and in conjunction with each other. It might also seem suspect coming from me, a lifelong proponent of group selection. Nevertheless, not only did it represent the consensus view of all four groups—a claim that the

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participants are free to dispute—but it can also be justified by analogy with species as biological entities that are primarily adapted to their environments. In this article, I will first outline the case for biological species and then make the parallel case for human cultures.

If I am correct, then the consensus that emerged at the Ernst Strüngmann forum represents a watershed event for the study of cultural evolution as a whole. In the past, there has been a profound lack of agreement on whether cultural change counts as an evolutionary process, the degree to which cultural traits are adaptive, the processes by which they become adaptive, or the unit(s) of adaptation, which might be individuals, groups, or the cultural traits themselves. If a consensus can be reached on human cultures as primarily adaptive at the group level, then the future study of cultural evolution can start to build upon this foundation, rather than questioning whether it can serve as a foundation at all.

Why Biological Species are Primarily Adapted to Their Environments

When evolutionary biologists study any given trait in any given species, they must test a number of major hypotheses. Is the trait an adaptation that evolved by natural selection? If so, did it evolve by virtue of increasing the fitness of genes relative to other genes within the same organism, individuals relative to other individuals within groups, or groups relative to other groups relative to the total population? If it is not an adaptation, then why does it persist in the population? Was it adaptive in the past but not the present? Is it a byproduct of another adaptation, in the same way that a spandrel is a byproduct of an arch (Gould and Lewontin 1979)? Did it increase in frequency by virtue of being located close to a beneficial mutation (Hedrick 1982)? Or is it a neutral trait that drifted into the population without having any effect on survival and reproduction?

In the analysis of single traits, there is nothing privileged about an adaptationist hypothesis; all of the hypotheses must be evaluated on a case-by-case basis. Nevertheless, we can still robustly say that species are primarily adapted to their environments. Pick any species, study the traits that are required for it to survive and reproduce in its environment, and the list of traits will be very impressive indeed. We can begin with the processes required for life to exist in any species. Then we can proceed to the long list of traits required to survive and reproduce in any particular environment.

Any species could serve as an example, but I will choose the hemipteran insect *Aquarius remigis*, commonly called the water strider. It is adapted to live on the surface of water, where it scavenges and preys on other invertebrates. The vast majority of insects do not have the traits required to

move on the surface of water, which is why they become prey for water striders when they inadvertently fall in. Water strider feet are so hydrophobic that they can support the weight of 16 water striders and their ultra-structure is being studied to create waterproof fabrics for human use (Feng et al. 2007). Water striders use ripples on the surface of water as a source of information, in the same way that we use sound waves traveling through the air. They also use ripples as a medium of communication with each other (Wilcox 1979). A short list of adaptations required to survive and reproduce include the avoidance of predators, overwintering, dispersal, competition with members of the same sex, and mating with members of the opposite sex (e.g., Preziosi and Fairbairn 1996, 2000) . It becomes mind-boggling that so many adaptations can be packed into such a small creature, as I recount for a general audience in a chapter of my book *The Neighborhood Project* (Wilson 2011) titled "The Parable of the Strider," where details and additional references can be found.

Every species has a similar story to tell, right down to microbes and viruses. Surviving and reproducing is not a simple matter–the minimal set of required adaptations is very extensive indeed. Thus, the study of any given biological species can begin with the knowledge that it is primarily well adapted to its environment; otherwise it would not be there. This does not mean that each and every trait is adaptive, or that the adaptations are easy to identify. There will be examples of drift, hitchhiking, and environmental mismatch. Most adaptations produce byproducts. A given adaptation hypothesis might be rejected in favor of another adaptation hypothesis, in addition to non-adaptation hypotheses. That is why all of the major hypotheses must be evaluated for any given trait on a case-by-case basis. Nevertheless, *the overall inquiry is guided by the search for functional organization*, which is justified by the fact that the species must be impressively adapted to its environment to even be there.

Biological species are primarily adaptive, but not necessarily at the group level. The water strider provides an example of a species that is primarily adaptive at the individual level. Most of its adaptations, such as its hydrophobic feet, evolve by virtue of causing individuals to survive and reproduce better than other individuals in their immediate vicinity. Considerations of "for the good of the group" or "for the good of the species" need not be invoked. An important exception concerns the mating behavior of males, which differ greatly in their aggressiveness toward females. In a series of experiments, Omar Eldakar and his colleagues showed that aggressive males outcompete docile males in their immediate vicinity, but that groups with docile males are more productive than groups with aggressive males—the classic group selection scenario. Conditional movement creates enough variation among groups for docile males to be maintained in the population by between-group selection, despite their selective disadvantage within groups

(Eldakar et al. 2010). This example underscores the fact that the level(s) of selection for any particular trait must be determined on a case-by-case basis for any given species. Water striders are primarily adapted to their environment at an individual level, with some exceptions.

Other species are primarily adaptive at the group level, notably eusocial insect species such as wasps, ants, bees, and termites (Holldobler and Wilson 2008) . In these species, most traits evolve by virtue of increasing the fitness of colonies relative to other colonies, not by virtue of increasing the fitness of individuals relative to other individuals within the colonies. As a result, the colonies become highly cooperative units, even qualifying as 'superorganisms.' Some traits do evolve by within-colony selection in the eusocial insects, but these tend to disrupt the functional organization of the hive (Ratnieks et al. 2006). A chapter of *The Neighborhood Project* titled "The Parable of the Wasp" serves as a companion to "The Parable of the Strider" to stress the comparison between levels of selection for a general audience.

It is important to stress that my multilevel account can also be framed in terms of inclusive fitness theory and other theoretical frameworks such as selfish gene theory. These frameworks should be regarded as different 'languages,' 'perspectives,' or 'accounting methods' that are inter-translatable, a principle called 'equivalence' that I have described in a previous *Social Evolution Forum* (Wilson 2012). Once we appreciate the concept of equivalence and cultivate an ability to translate between frameworks, much of the controversy that seems to surround the topic of multilevel selection evaporates.

To summarize, virtually all research on biological species takes an impressive degree of overall functional organization for granted, even if any given trait must be evaluated on a case-by-case basis. This is what I mean by saying that species are primarily adapted to their environments.

The Parallel Case for Human Cultures

The statement "Surviving and reproducing is not a simple matter–the minimal set of required adaptations is very extensive indeed" applies as forcefully to human cultures as to biological species. Robert Boyd and Peter Richerson have emphasized this point for cultures that live in challenging climates such as the arctic (Richerson and Boyd 2005, Boyd et al. 2011). The knowledge required to build a sea kayak or clothing protective against frigid weather, when all of the tools must be made in addition to the objects made with the tools, is mind boggling when one pauses to consider it. Yet, these are only two items in a long list that is required to survive and reproduce in the arctic; others include building a shelter, hunting and gathering techniques, navigating long distances, social conventions within the group, and conduct toward other

groups. The adaptedness of any given belief or practice must be determined on a case-by-case basis, but the basic adaptedness of the culture as a whole can be taken for granted; otherwise it would not be there.

This point can be made as strongly for human cultures as for biological species on the basis of existing information. It is best appreciated by stepping back to consider the raw fact that while we are genetically a single species, our cultural diversity enables us to occupy all climatic zone and to occupy hundreds of ecological niches–an adaptive radiation comparable to the dinosaurs, birds, and mammals (Pagel and Mace 2004).

What's new, going beyond the raw fact of cultures adapted to their environments, is our emerging knowledge of how we evolved our capacity for cultural evolution. It all revolves around cooperation. In other primate species, members of the same group cooperate to a degree but they are also each other's chief rivals for status, resources, and mates. The lack of cooperation and trust limits the ability of group members to learn from each other in a cumulative fashion and to transmit their learned behaviors across generations.

Small human groups are much more cooperative than primate groups, thanks largely to the their ability to suppress bullying and other self-serving behaviors, a kind of social organization that evolutionary anthropologist Christopher Boehm calls "reverse dominance" (Boehm 1993, 1999, 2011). If members of a group can't succeed at the expense of each other, then their main avenue of success is to succeed as a group, compared to less cooperative groups. The competition might be direct, as in warfare, or indirect, as in producing more offspring that emigrate to other groups or form new groups. In the language of multilevel selection theory, reverse dominance suppresses within-group selection and magnifies variation among groups (especially through the establishment and enforcement of norms), making between-group selection the dominant evolutionary force.

Hunter-gatherers cooperate to raise their children, to hunt and gather, to defend themselves from predators, to regulate their social interactions within groups, to trade with other groups, and to raid and defend themselves against other groups. We are familiar with this list of physical activities. More novel is to think of the *mental* activities required for cumulative cultural evolution as forms of cooperation, starting with an awareness of the interests of others that is far more highly developed in humans than in our closest primate relatives (Tomasello 2009). Even something as simple (for humans) as a shared symbol is a communal activity. In short, the entire package of traits that are so distinctively human, such as cooperative physical activities, cumulative cultural evolution, and our capacity for symbolic thought, are all examples of cooperation that evolved due to the shift in the balance between levels of selection. Something close to Christopher Boehm's reverse dominance scenario came first, and everything else followed.

Symbolic thought is an especially important capacity for open-ended cultural evolution. There is a nearly infinite variety of imaginary worlds, just as there is a nearly infinite variety of genotypes in sexually reproducing species. Each imaginary world motivates a suite of behaviors, creating a 'symbotype'—phenotype relationship similar to the familiar genotype-phenotype relationship. In short, symbolic thought provides a cultural inheritance system that rivals the genetic inheritance system in its combinatorial diversity (Jablonka and Lamb 2006, Wilson et al. 2013). This goes a long way toward explaining how our ancestors were able to expand their range to include the entire planet, adapting to all climates and hundreds of ecological niches, in just a few tens of thousands of years. Emile Durkheim (1912/1995:233) wrote that "at every moment of its history, social life is only possible thanks to a vast symbolism." Modern evolutionary science is proving him right.

The origin of agriculture resulted in a positive feedback loop between the production of resources and the scale of society that continues to this day. The increasing scale of society is also a matter of multilevel selection. Cultures vary widely in their ability to function at a large scale. The most cooperative spread by conquest and/or productive superiority. They are also copied on the basis of their success. Yet, all societies are vulnerable to factionalism and self-serving strategies that disrupt cooperation at the societal level. Recorded history provides a detailed fossil record of multilevel cultural evolution, as documented by books such as *War and Peace and War*, by Peter Turchin (2005).

Perspectives on culture are incredibly diverse, from Durkheim's functionalism to Derrida's postmodernism. Even when we restrict our attention to modern evolutionary perspectives, evolutionary psychology pays scant attention to transmitted culture (Wilson 2010) and the concept of memes portrays cultural traits as free agents, as likely to harm as to help their human hosts (Blackmore 1999). It is therefore remarkable that the 45 scientists at the Strüngmann Forum were in such agreement on the account of human cultural evolution that I have outlined above (audio interviews with members of the four groups are available at http://www.thisviewoflife.com/index.php/magazine/articles/major-forum-clarifies-nature-of-cultural-evolution1). The best way to demonstrate their consensus is to let them speak for themselves. Here are some excerpts from group one's preliminary report, which was circulated and discussed on the last day.

> What we call small-scale societies are still huge cooperative endeavors compared to the scale of cooperation in other vertebrates.
>
> The identification of a minimal set or sets of predispositions necessary for small-scale societies to arise then gives us building blocks

necessary for thinking about the cultural evolution of large-scale societies.

We now turn to three requirements/necessary conditions that…could produce SSS (Small-Scale Society) cooperation. These are (1) Increasing returns to scale in group size; (2) Control of defectors and (3) Cultural group selection/assortativity.

Increasing returns to scale is a prerequisite for cooperation to evolve, but essentially, all this means is that there should be some benefits to cooperation…The hard problem is how does cooperation evolve, given that exploiters will appropriate these benefits causing the cooperation to dissolve.

The products of human cooperation have to be protected by monitoring and enforcement systems. These systems start with norms, and the importance of norms is recurrent throughout this chapter.

At this point we are armed with some idea of the behavioral predispositions that are necessary for the evolution of small-scale society and cooperation. The cultural evolutionary perspective then allows us to hypothesize how those features can be exploited in the transition from small- to large-scale societies.

We can identify two evolutionary "engines" in (1) cultural group selection and (2) within-group processes which will produce change in social structure and allow transitions between levels of complexity.

Cultural Group Selection (CGS) where between-group competition favors societies that are more effective in production and/or warfare. Larger and more complex societies with more efficient social institutions can arise through such between-group selection. Between-group selection can result through warfare…,through differential population growth…, through immigration into more successful societies…, and through adopting the social institutions of successful groups.

Social change can also arise endogenously, from within-group processes that generate variation. Endogenous change can result from prosocial preferences like a regard for equitable or fair or parochial outcomes that has resulted from a longer history of cultural group selection. Such preferences, combined with abilities for persuasion, leadership, or deliberation—can allow societies to adopt norms that are consistent with these preferences. Democracies, or jury systems, may be the result of preferences shaped by cultural group selection (like fairness and peer sanctioning, respectively). It is important to note that on longer time-scales, these institutions will persist only if they lead groups that have adopted these social arrangements to fare better than other groups. However, on shorter time scales, some of the change that we see

> in human societies can be the result of people tinkering with their social institutions in accordance with their preferences, rather than due to between-group selection itself.

Notice that even the within-group processes discussed in the last passage are largely the result of psychological processes shaped by past between-group selection and are ultimately winnowed by ongoing between-group selection over the long term.

The Case of Religion

The artifacts that we associate with technology, from the first hand tools to hand computers, are straightforwardly utilitarian. Many artifacts are used by individuals for their personal benefit, but a whole culture is required for their evolution. Language is likewise eminently utilitarian and a group-level process, even when it is used by individuals for their personal gain. Thus, it is not surprising that the second and third groups largely agreed with the group-level functional account of the first group.

Religion is another matter. It fascinates the scientific imagination precisely because it does not seem utilitarian. How can all that hocus-pocus increase the fitness of either individuals or groups? Durkheim thought otherwise. His definition of religion ("a unified system of beliefs and practices relative to sacred things … which unite in one single moral community called a Church, all those who adhere to them") emphasized its great "secular utility," as he put it (Wilson 2002). Yet, other theories abound that portray religions as primarily dysfunctional, such as sociologist Rodney Stark's economics-inspired theory that religions involve the invention of Gods with whom we bargain for that which we can't have (e.g. Stark and Bainbridge 1987).

The modern study of religion from an evolutionary perspective began at the turn of the 21st century with books such as Religion Explained (Boyer 2001), In Gods We Trust (Atran 2002), Breaking the Spell (Dennett 2006), The God Delusion (Dawkins 2006), and my own Darwin's Cathedral (2002). The authors agreed on the basic hypotheses that needed to be tested about religion, but differed sharply on the ones that they favored. Some interpreted religions as primarily adaptive for human individuals and groups, while others interpreted them as primarily byproducts or as parasitic memes that are as likely to be harmful as helpful for their human hosts.

Research on religion from an evolutionary perspective has burgeoned since the appearance of these books and the Ernst Strüngmann Forum provided an opportunity to assess progress. There was a strong consensus among members of the religion group that the major elements associated with religion, such as counterfactual beliefs (including but not restricted to supernatural agents), a

sense of the sacred, and costly activities (including but not restricted to rituals), are typically functional at the level of the religious community, despite first appearances. Essentially, Durkheim was right in basic outline, even though the modern study of functionalism differs from the earlier tradition of functionalism in many respects.

As with the study of biological species, all of the major hypotheses are still relevant and must be evaluated on a case-by-case basis for any given element of a religious system, but the overall inquiry can be guided by the search for functional organization. The study of byproducts provides a good example. Just as many biological adaptations are derived from previous adaptations or byproducts (e.g., the bones in our ears are derived from reptile skull bones), many elements of religion are derived from biological adaptations that evolved without reference to religion (e.g., kinship terminology or the tendency to infer agency from events). They quality as byproducts as far as genetic evolution is concerned, but the question of whether they qualify as adaptations vs. byproducts in cultural evolution requires a separate determination. Enough empirical research has been conducted, using a variety of cross-validating methods, to conclude that the adaptations and byproducts of the past have been woven into religious systems that are impressively functional at the group level (Atran and Henrich 2010). The hypothesis that religion writ large is a functionless byproduct has been authoritatively rejected.

The study of cultural parasites provides another example. It is theoretically possible for a cultural trait to spread, disease-like, without benefiting either human individuals or groups. It is a legitimate hypothesis that must be evaluated on a case-by-case basis. A religion called Millerism provides a candidate example (Numbers and Butler 1993), as I describe for a general audience in a chapter of *The Neighborhood Project* titled "The Natural History of the Afterlife." Miller was a Baptist farmer in New York State during the 19th century who became convinced that the return of Jesus was imminent. The movement he started would have remained localized and unknown to history, were it not for the advent of print media such as newspapers and pamphlets, which caused Miller's 'meme' to spread viral-like around the world. Thousands of people made decisions in preparation for the second coming that were not useful for them, either as individuals or groups. The movement quickly collapsed in boom-and-bust fashion, which is typical of disease epidemics. Millerism therefore qualities as a good candidate for an empirically documented cultural parasite.

The story does not end there, however. After the collapse of Millerism, a number of splinter groups clung to the belief that Christ's return was imminent and modified some of their other beliefs to accommodate the fact that he did not return on the day predicted by the Millerites. One of these splinter groups became 7th Day Adventism, one of the fastest growing religions in the world

(Numbers 1976). Unlike Millerism, 7th Day Adventism harnesses the psychologically motivating belief in Christ's imminent return to sustainable practices on earth, at both the individual (e.g., healthful eating habits) and group (e.g., schools and hospitals in addition to churches) levels.

This example illustrates how history provides a detailed fossil record of cultural evolution that allows the major hypotheses to be evaluated on a case-by-case basis, similar to the branch of the biological sciences known as paleontology. By now, many historical examples of religion have been analyzed from an evolutionary perspective, using quantitative in addition to qualitative methods (e.g. Voland and Schiefenhövel 2009, Wilson 2005). The evidence for the group-level functionality of most enduring religions is very strong, with dysfunctional examples such as Millerism constituting a minority.

Multilevel selection theory predicts an ongoing tension between beliefs and practices that enable the group to function as a whole with beliefs and practices that benefit some members of the group at the expense of others. This tension has a temporal component; groups that start cooperative can fall apart as self-serving strategies take root and spread from within. The conflict between levels of selection is amply preserved in the historical record for religions, as for non-religious social institutions (Wilson 2002). The conclusion that most enduring religions are functional at the group level is therefore not a claim that within-group selection never happens, but rather that between-group selection is a strong force in religious cultural evolution, thanks in large part to mechanisms that effectively suppress factionalism and self-serving strategies within the group.

The historical evidence is supported by evidence from different sources. A growing psychological literature demonstrates that when people are primed with religious cues (e.g. unscrambling words such as 'church' compared to unscrambling non-religious words), they become more cooperative (Shariff and Norenzayan 2007). Field and laboratory studies show that some of the most costly aspects of religion, such as time-consuming and pain-inflicting rituals, can be understood as credibility-enhancing displays (Bulbulia and Sosis 2011,Henrich 2009).

Another important conclusion that emerged from the religion group was that most of the major elements associated with religion also extend to other cultural systems. A theory is needed to explain why we are so prone to accept counter-factual beliefs of all sorts, not just belief in supernatural agents. Likewise for a sense of the sacred and costly credibility-enhancing displays. A well-known Atlantic Monthly article by Harvey Cox titled "The Market as God" (Cox 1999) demonstrates how a cultural system that few people associate with religion—free market capitalism—has all the trappings of religion.

In short, group 4 (on religion) affirmed the conclusions of group 1 (on the structure of human groups) as strongly as group 2 (on technology and science)

and group 3 (on language). Human cultures are primarily adaptive at the group level.

Why a Consensus Matters

A consensus, by definition, involves leaving some alternatives behind and concentrating on a reduced set of possibilities. A consensus is never final. Group selection provides an outstanding example of a possibility that was excluded by a consensus that formed in the 1960's, only to force its way back into consideration, as the Ernst Strüngmann Forum made abundantly clear.

Even though a consensus is never final, it is still important—even essential—for scientific progress. A lack of a consensus, when one is warranted, is a kind of paralysis that prevents a field of inquiry from moving forward. Consider the diversity of opinion about culture that currently exists across academic disciplines:

- A dominant position throughout the 20th century, which is still common in some quarters, is to regard the study of culture as outside the orbit of evolutionary theory altogether.
- The study of cultural evolution has a complex history in anthropology, leading to many different conceptions in the minds of different anthropologists. The tradition of functionalism, for example, was seldom associated with evolution, as strange as that might seem against the background of modern evolutionary theory.
- Evolutionary theory in the biological sciences is highly gene-centric. The idea that evolution requires an inheritance system, and that other inheritance systems exist in addition to the genetic inheritance system, needs to become more prominent within mainstream evolutionary biology (Jablonka and Lamb 2006).
- When we restrict our attention to contemporary evolutionists interested in human evolution, the version of evolutionary psychology associated Cosmides and Tooby (1992) pays scant attention to transmitted culture (as opposed to what they call evoked culture), as previously mentioned.
- When we restrict our attention to contemporary evolutionists interested in cultural evolution, the consensus reached at the Ernst Strüngmann forum is an important advance over other conceptions of cultural evolution, such as memes as primarily atomistic free agents, religion writ large as primarily maladaptive, and so on.

The study of culture becomes paralyzed when it means so many different things to different people. Reaching a consensus that human cultures are primarily adaptive at the group level will enable human cultural diversity to be

studied in the same way as biological diversity—and will result in the same kind of scientific progress.

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Commentaries

Martin Hewson. *Consensus and Dissensus on Cultural Evolution: A Commentary on David Sloan Wilson*

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David Sloan Wilson detects signs of an emergent consensus around a broad notion of evolution which encompasses both genetic and cultural history and which recognizes as driving forces selection among groups, individuals, and genes.

I hope so. Movement in that direction would be welcome. The comprehensiveness of Wilson's view of evolution is highly attractive. For students or

general readers, faced with the many fragments of specialized knowledge and the rival claims of numerous specific theories, Wilson's synthesis offers the possibility of the general understanding that so many seek. Scholars too need a broad conception of evolution if they are to find some way to overcome the barriers of the specialized disciplines. A hallmark of Wilson's approach is its quest for balance. For all his emphasis on the evolutionary success of groups, Wilson balances this with awareness that groups are prone to breakdown into self-serving fragments. Though he stresses the selective pressure of competition between groups, he acknowledges similar pressures within groups too.

But, even if there is movement in that overall direction, I expect there will continue to be dissensus and debate over key issues.

One is adaptation. The moral connotations of the word adaption in human affairs are so strong that it will most likely continue to be a bone of contention. It is not too controversial to call cooperation, technology, or language adaptations because they are generally regarded as positive. Much more controversial would be any attempt to name warfare, or imperialism, or racism as adaptations. Consider religion. Wilson points out that his explanation of religion as an adaptation that binds people together in groups has been generally supported in the Strüngmann Forum discussions. Yet, by contrast, the 'New Atheists' (Richard Dawkins, Daniel Dennett and others) remain loathe to describe religion as adaptive. This is not because they are unaware of its binding effects but because the term adaptation connotes something of practical value. It may be noteworthy that in the excerpts Wilson cites from the Strüngmann Forum, the word adaptation is absent.

Another likely point of debate concerns the question of just how cooperative is the human species. The overall tenor of Wilson's discussion of cultural evolution is mildly progressive and optimistic. Wilson's brief overview of human history begins with humans evolving to be much more cooperative than chimps, mentions next the advent of symbolic thought as an instance of growing cooperation, and interprets the main significance of agriculture as an opportunity for the most cooperative groups to spread. The overall direction of cultural evolution could well be summarized as "growing collaboration." If so, the future portends yet more coordination, maybe towards a world community of some kind. But, this judgment is likely to remain controversial. It might be pointed out that Wilson tends not to dwell on the darker episodes in human history. In any case, future debate will probably continue to grapple with striking the appropriate balance between the pro- and anti-cooperative traits of humans.

In pursuit of a new consensus over cultural evolution, its directions and its driving forces, I hope that we will see a follow-up to the Strüngmann Forum which provides a comparable overview of the state-of-the-art beyond the

domains of social structure, technology, language, and religion to include other areas such as the evolution of the arts, marriage, civilizations, or war. Even if a broad consensus does arise, there is little danger that debate will subside over collateral issues concerning the shape of human history, the question of progress, and the prospects of the future. It is a sign of the importance of Wilson's ideas that they prompt such fundamental questions.

Mark Pagel. *Adapted, Yes, but for Whom or What? A Commentary on David Sloan Wilson*

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David Sloan Wilson's essay *Human Cultures are Primarily Adaptive at the Group Level* is helpful in calling attention to the fundamental role that the human social group has played throughout our evolutionary history. But Sloan Wilson is mistaken, in my view, in seeming to use the phrase "primarily adaptive at the group level" to mean that humans have acquired a suite of social and psychological dispositions for promoting the fitness of their groups even if it means suffering a cost to their own fitness.

There is agreement that there is something important to explain. Human beings are distinguished among all animals for having forms of cooperation that, on the face of it, pose a challenge to conventional Darwinian accounts of evolution. We routinely help others, we share our knowledge and skills, we give up seats on trains, pay taxes, hold doors for people, give money to charities, and even sometimes risk our health and well-being to fight wars.

The challenge to Darwinism is to explain how such apparent altruism can evolve when there are people who are only too happy to benefit from your aid but have no intention of returning it. This question is often answered by drawing on an analogy to the social insects – the ants, bees, wasps and termites – or even to the skin cells in your body.

Individual ants quite willingly, indeed sometimes enthusiastically, go to their deaths in support of their queen, and skin cells in your body do not have to be coaxed into giving their lives to protect you from the harmful rays of the sun. These actors' high genetic relatedness to each other makes selfless

altruism a good strategy for promoting copies of their genes that reside in others.

But humans are different – the multiple actors in the great 'bodies' we call our societies are not like cells in a body, nor even like a colony of ants. Indeed, the wonder of human cooperation is that we somehow manage to make our style of altruism work even among non-relatives. We have moved beyond the mere *eusociality* of the social insects to an *ultrasociality*, this term acknowledging that we cannot explain our actions as strategies for promoting copies of our genes in relatives.

Sloan Wilson is one of the leading proponents of 'group selection' as a way to explain this fascinating dilemma of human behavior. The idea is that our groups have been as important to our survival and well-being throughout our evolutionary history as an ant's colony has been to it. As a consequence we have been molded by natural selection to do things that advance our 'colonies' even if it means suffering a cost to our individual fitness.

Our groups have been important to our success as a species – a point that is difficult to overemphasize. But have we really evolved to be willingly subservient to them? Is this what it feels like to *you* to be a human? This is really one of the most fundamental questions we can ask of our nature. Are we fundamentally 'good' or are we fundamentally self-interested?

In seeking answers to these questions, it is vital not to fall into the trap of assuming that what appears to be selfless group-level altruism and cooperation can only emerge from the sort of group-selection Sloan Wilson envisages. There can be selection between groups but this need not imply 'group selection' in the sense that Sloan Wilson uses it. In my book *Wired for Culture*, I discuss several alternative propositions that explain how apparent group-level altruism can evolve because it has returned individual benefits, not group ones at the expense of individuals.

In the simplest case, imagine you inhabit a group of two and that by helping each other you can achieve more than twice as much as the two of you working alone. Now ramp this scenario up to a larger group. The behaviors might range from cooperation in acquiring food to fighting battles with other groups. The returns from cooperation mean that what looks like altruism, is really a form of enlightened self-interest. Selfishness can never be widespread because groups with lots of selfish players cannot compete against cooperative ones.

Another scenario I call 'enhancement selection' and it seems to capture some of the more psychologically and socially nuanced, charming and puzzling aspects of our behavior. What if, by virtue of being useful to the group in some way, you enhance your reputation, becoming widely known as the kind of person others like to have around. Perhaps you are a good hunter willing to share the meat you bring back, a good warrior, or you might simply be good at making arrows or navigating on the open seas. If as a consequence of your

good deeds you attract kindnesses from others, then your apparent altruism can be more than repaid, and what looks like altruism is really in your best interest.

The appeal of this scenario is that once 'altruism' becomes a way of acquiring a good reputation, the problem of how to get altruism to evolve is subverted: if being altruistic attracts altruism from others, then people will actually compete to cooperate. In fact, we will become altruism 'show-offs', falling all over ourselves in an attempt to convince others of our worth. Our ultrasocial nature becomes the altruistic equivalent of a peacock's tail, except where the peacock uses his tail to acquire a mate, we use our altruism to secure the spoils of cooperation.

This can explain the peculiar and repeated acts of altruism that most of us display throughout a typical day. All those doors we hold open, seats we give up, coins we drop into charity boxes and cats we rescue from trees are ways that we display our 'long tails' of altruism. The wonderful irony is that, as a self-interested tactic, this kind of 'altruism' can happily take its seat alongside all the other self-interested things we do, like cheat on taxes, exceed speed limits, lie to people, or pay huge sums of money to have our children educated. It is hard to explain these in the 'nice' world of Sloan Wilson's style of group selection – you certainly wouldn't see ants behaving like this.

So, yes, many of our distinctly human traits are adaptations that make it more likely our groups will be successful, but they need not be 'adaptive at the group level' in the sense that I think Sloan Wilson has in mind here. There might be an emerging consensus about the former, but certainly not about the latter, and it would be mischievous to suggest otherwise.

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Matthew R. Zefferman. *Should the Consensus be Essentialist and Adaptationist? A Commentary on David Sloan Wilson*

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Wilson describes a growing consensus concerning the role of culture in human evolution. While not everyone is yet a member (he excepts advocates of memetics and evoked culture), I am heartened by much of what Wilson describes. I readily join this consensus when it holds that cultural inheritance is an important tool that has allowed humans to thrive in wide variety of environments; that the properties of cultural inheritance can better explain human cooperation, including altruism, in larger groups than can be explained by genetic inheritance alone; that group-level selection is a useful way to think about human cultural evolution, especially because many important group-level traits are not easily reducible to individual-level fitness calculations; and that many of these group-level traits can be considered adaptations in that they help groups of humans survive in their environment. However, I would like to sound a couple notes of caution.

First, it can be problematic to describe groups as competing 'cultures.' This may seem like a semantic quibble, but in this case terminology has the potential to lead us astray. For example, calling groups "cultures" gives the impression that groups are to be defined primarily by their common cultural traits. However, if our goal is to explain the distribution of cultural traits within and between groups, defining groups based on their distribution of cultural traits introduces endogeneity to our analysis. This issue can be avoided if, as in Sober and Wilson (1999, 92-98), groups are defined by *interactions* in relation to traits, instead of by the traits themselves.

For example, suppose two villages are involved in separate collective action problems, such as maintaining an irrigation system. In each village, a significant fraction of individuals are contributors and significant fraction are free-riders. In a multilevel cultural selection model, the "groups" should be defined at the scope of the collective action problem, in this case the villages, because this defines the scope of each individuals' influence on others' payoffs. The groups would not be defined as the set of cooperators and the set of free-riders because free-riders do not affect the payoffs of free-riders in another village in relation to their free-riding trait. Similarly, if each village was made up of recent immigrants from two different backgrounds, the relevant groups

would still be defined by the village-level collective action problem and not by the origins of the village members.

Furthermore, characterizing groups as "cultures," can also encourage essentialist thinking, i.e., discounting the importance of both within-group cultural variation and between-group cultural similarity. Essentialism has left the ethnographic record mostly bereft of the individual-level data necessary to build empirically-grounded theoretical models (Richerson and Boyd 2005, 246-253). This problem is more easily avoided if groups are not thought of as discrete "cultures," but as sets of individuals who frequently interact with each other and have distributions of cultural traits that influence those interactions.

A second note of caution concerns what seems, to me, like an overly strong adaptationist emphasis. There are many flavors of adaptationism and it is important to identify which is under consideration. When Wilson states that "human cultures are primarily adaptive at the group level," this seems to be a statement of what Godfrey-Smith (2001) calls "empirical adaptationism." Empirical adaptationists posit that selection is the most dominant force governing the distribution of traits. While recognizing that the origins of individual traits must be examined on a case-by-case basis, Wilson seems to imply that selection at the group level is the most dominant force governing the distribution of cultural traits as a whole. This begs the question "most dominant compared to what?"

My sense is that this is still an open question and my concern is that if the consensus is to focus primarily on group-level adaptations, we may miss important group-level cultural traits that are not adaptations and many cultural traits that are more easily understood as a mix of group-level and individual-level selection. Consider intergroup warfare, which at first glance looks like a classic group-level cultural adaptation. Individuals put themselves at great risk and successful groups have the potential to gain wealth, territory and other resources. However, a closer look complicates the view that warfare is a group level cultural adaptation.

Warfare's status as an adaptation is partially undermined by frequency-dependence between groups. Warfare can spread if war-like groups are more successful than peaceful groups. However, as in the classic Hawk-Dove game (Maynard Smith and Price 1973), the more warlike one's neighbors, the more costly it is to fight and eventually, it may pay to become peaceful. Frequency dependence and balancing selection diminish the utility of adaptationist explanations. For me, it is much more parsimonious to consider how group structure influences the distribution of traits, than it is to consider whether that distribution, or some subset of that distribution, can be considered a group-level adaptation.

Furthermore, participating in warfare can be quite costly for individuals and they may, with some frequency, shirk fighting. Even in the most warlike

groups when shirkers are actively punished, selection at the individual level drives some individuals to not participate (e.g., Mathew and Boyd 2011). If participation in warfare is an adaptation at the group-level, is non-participation in warfare an adaptation at the individual level? Which of these forces is more dominant? If fifty-one percent of individuals shirk, is it useful to conclude that culture is primarily adaptive at the individual level? Again, I think it is a more promising approach to consider all relevant forces, selective and otherwise, at different levels of analysis when thinking about the distribution of cultural traits. A strong focus on group-level adaptations may critically limit the effectiveness of our investigations.

In conclusion, I agree with the spirit of this growing consensus and my comments are merely an attempt to shift the emphasis. I strongly agree that recognizing the importance of group-level cultural selection is essential to understanding the distribution of cultural traits. However, I worry that the larger goal of understanding how the combination of selective and non-selective forces operate on cultural traits at different levels of analysis could be hindered by overreliance on essentialist and adaptationalist thinking.

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Stephen K. Sanderson. *A Commentary on David Sloan Wilson*

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David Sloan Wilson has been perhaps the strongest advocate for group selection for several decades now. The article under consideration here is an attempt to show that human cultures have been created by and evolve by a form of group selection, presumably cultural group selection. I am afraid that I don't find anything in this article convincing at all. It mostly consists of a series of assertions for which no evidence is provided. Since space is short, I shall take up just a few of Wilson's arguments. In my discussion I shall think of group selection as behavior that has been selected "for the good of the group."

1. *Widespread human cooperation is to be explained primarily by group selection.* Certainly humans are a highly cooperative species and in every society there is an enormous amount of cooperation. But I see no reason why group selection is necessary to explain this. Groups are aggregates of individuals who are pursuing their own interests, which are both somatic and reproductive. But to achieve these interests they have to cooperate in numerous ways. Wilson gives the example of the difficulties of survival in the Arctic, pointing out the many forms of technology that are required, much of which can only be produced by cooperative efforts. No problem there. But the cooperation is easily explained by standard gene-level (or individual-level) evolutionary theory. What individual living in such an environment would be so foolish to think that he or she could somehow survive on his own? This would be well-nigh impossible. Of course members of Inuit groups cooperate, otherwise they would be driven to extinction as individuals. Cooperation doesn't require selection at the level of the group. Ordinary individual selection will do just fine. (Sometimes I think that the group selectionists believe they are the first scholars to discover that there is such a thing as human cooperation.)
2. *Religion fascinates social scientists because it seems not to be utilitarian.* I have not read many works on the sociology or anthropology of religion that take such a perspective. Indeed, I can't think of a single example. Quite the opposite is the case. Nearly all social-scientific theories of religion stress its benefits, with different theorists proposing different benefits. Wilson is keenly interested in religion, indeed wrote a whole book on it (*Darwin's Cathedral*) in

which he tried to explain it by group selection. Many years earlier Durkheim proposed one of the most famous theories of religion ever developed. He argued that religion is really the worship of society and thus binds individuals together. Its function is to provide social cohesion. This is a type of group selection argument. Wilson believes that Durkheim got it basically right. I would claim, however, that he got it basically wrong. I have formulated a list of ten major criticisms that I will be developing in a book on religion that I am currently writing. Be that as it may, the really shocking thing Wilson says in his discussion of religion is that Rodney Stark, a leading sociologist of religion, "portrays religion as primarily dysfunctional." Stark is rolling over in his grave at this very moment. The last person on earth who would make such a claim is Stark. He uses the well-known sociological theory known as exchange theory to explain how people use gods in order to gain rewards that are otherwise unavailable in daily life. Religion is not dysfunctional, but highly functional, and it is individuals that religion is highly functional for. Exchange theory is a highly individualist theory and Stark is a strong anti-Durkheimian. He is also, in my view, the best sociologist of religion since Max Weber.

3. *Cultural evolution is a product of group selection*. Group selectionists talk a lot about cultural evolution, but in a very constricted way. Usually they have in mind just very small bits of it over very short periods of time. But let's think about cultural evolution – I prefer to call it social evolution – on a long-time scale, the 10,000 years since the Neolithic Revolution. Social evolutionists are generally agreed that over this period of time there have been remarkably similar evolutionary trajectories all over the world. In terms of subsistence technology, we see a shift from hunting and gathering to horticulture (shifting cultivation), from horticulture to intensive agriculture, and from intensive agriculture to modern industrial capitalism. In terms of political life, we see an evolution from bands, to tribes, to chiefdoms, to states. Societies have grown much larger with much denser populations and greater complexity. It's pretty much the same story wherever you look. We know that it is those societies smallest in scale that exhibit the highest levels of cooperation. But what happens when societies evolve? A big thing is increasing status differentiation and social stratification along with increasing concentration of power in the hands of a few. Hunter-gatherer societies are highly egalitarian and status competition is frowned upon and strongly policed. In horticultural societies we see the development of status competition that is lightly policed, if at all. In some of these societies "big men" hold large feasts to show how skilled they are. Some of them grow big

inedible yams that they present to status rivals, who must respond with yams of equal or greater size or else lose status. Among the Kwakiutl of the Northwest Coast, chiefs held potlatches in which they gave their goods away, daring other chiefs to give their own goods away or lose status. Once we get to full-fledged chiefdoms, a major line of division opens up between a powerful chiefly class and the rest of the population. This class is capable of exercising a lot of coercion over everyone else. Once states are achieved, the level of coercion becomes much greater still. Chiefdoms and states can extract tribute from most of the population, and coerce a lot of young able-bodied males to fight in wars of conquest against other societies. Most of these men are not interested in fighting. They are given no choice. What kind of cooperation is that?

4. *Inter-societal selection*. The point about conquest is especially important because it is about one group defeating another. On the surface that looks like group selection. But is it? I would say no. It isn't a matter of a whole society against another, but of the most powerful members of a society conquering another in order to gain the spoils. Do they want to share these spoils with the rest of the society? Not really. They may share some to keep the population relatively quiescent, but mostly they keep the spoils for themselves. That's largely what preindustrial states and preindustrial warfare are all about. And what allows one group to defeat another is such things as bigger armies, superior military technology, more effective military strategies, and so on. It isn't really about cooperation. But none of this is for "the good of the group." It is for the good of those who are running the group. The sociologist Gerhard Lenski called this sort of thing inter-societal selection. I can't see that it is any sort of group selection in Wilson's sense.
5. *Consensus*. Wilson stresses that the 45 participants in the Strüngmann Forum all agreed that group selection is a vitally necessary concept. He seems to be implying that, because of this consensus, and because they agree with him, *they must therefore be right*. But who are these 45 people and what are their backgrounds? It would be quite easy to organize another forum and invite 45 different people (or even 1,045 people) all of whom agreed that group selection is a wobbly concept that explains nothing. To be fair to Wilson, consensus in science is necessary, as Thomas Kuhn pointed out years ago. Research can march forward more efficiently this way. But the entire history of science is a story of consensus formed, consensus lost. Unfortunately, Wilson seems to want a *permanent* consensus, since he used that phrase in the title of an earlier article. The idea of a permanent

consensus is dangerous because such a consensus can easily descend into dogma, and dogma doesn't advance the cause of science.

In conclusion, I would just say I think Steven Pinker got it almost exactly right in his essay "The False Allure of Group Selection." Of course there are cultural traits that may benefit the group as a whole. But all this can mean is that these traits benefit all of the individual members of a group. And of course there are individuals in societies who may display altruism (e.g., suicide bombers, men who volunteer for the military and are only too happy to fight for their country in faraway lands). But if one looks around I don't think genuine altruism is the sort of thing one finds at a high level of frequency in human in any human society. And Pinker tells us why.

Michael E. Hochberg and Harvey Whitehouse. *To Understand Present Day Cultures We Must Study the Past: A Commentary on David Sloan Wilson*

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David Sloan Wilson's essay provides ample fodder for provocative discussion on cultural evolution. Are cultural traits adaptations, and if so, at what level(s) of selection? These questions can only be resolved on a case-by-case basis but that will mean we also need to know much more about how cultural traits and groups change over time. It can be misleading to offer hypotheses to explain present day group behaviors without considering forces molding the past. We cannot assume that the same underlying processes affecting emerging groups in the distant past are still at work in those groups today. Below we use religious traditions as examples of cultural groups more generally but our arguments would be equally applicable to secular polities or financial corporations.

It is possible that religions emerge and flourish because they are adaptive for their members or for religious groups or both. Those that persist as a consequence may undergo further growth and perhaps indefinite evolution, but the cultural transformations that have resulted in the major religions we see today may not have been selected in a Darwinian sense. Even if they are, then present day selection might not operate at the same level as in the past.

Once a religious tradition is established, individual decisions and behaviors continue to influence group dynamics as a (metaphorical) 'tug-of-war': group governance seeks to maintain (or perhaps increase) numbers of adherents, whereas individuals seek fulfillment as members, perhaps leaving the group if the perceived benefits of defection outweigh the costs. If a religious tradition were to go extinct as a consequence this is not necessarily because of competition between religious groups. A group could simply lose members without any distinctive outside influence. Successful groups that continue to grow and (perhaps slowly) evolve will express emergent behaviors that do not stem from selection in the distant past. Rather, they are evolving 'survival machines,' much like invasive species or (and no deeper parallels intended) cancer.

It is possible that the rate at which religious groups expand or contract can be predicted largely by internal factors. For example, a simple rule of thumb may be that the longer a tradition has been established the harder it becomes to lose due to the 'weight of tradition' (and all that implies psychologically). On this view, established religions with deep histories do continue to evolve, but the institutions change their functions over time not as a consequence of between-group competition, but only because the needs of the tradition change as the system matures. In this scenario, we are left with a time course in the life-cycle of a human group: initially requiring Darwinian selection on culture towards increased expectations of individual survival and/or productivity (which may be tied to group performance and competitive ability), but through time, involving more diffuse forces that continually shape the group, and depend less and less on survival of the fittest and more on group maintenance through internal adaptation to more complex environments (internal and external).

Cultural group selection may be a more prominent feature of warring groups. When tribes or states go to war the fates of individuals may become closely entwined with those of the group. Sedentarism and territoriality may contribute to these processes. But even in these circumstances, processes of cultural group selection are likely to be complex, since the characteristics of prevailing polities will depend on among other things, history, bordering states, local environments, cultural composition, etc.

We can actually test these hypotheses empirically. In much of the debate responding to David Sloan Wilson's essay the question of evidential support is somewhat neglected.

Historians, anthropologists and evolutionary biologists can combine forces to study past and present religious cults, or hunter-gatherers that either make or don't make the transition to sedentarism. They can study insurgencies and nation states. They can investigate .com startups and established firms and industries. There is a trove of simple questions waiting to be answered. What

are the characteristics of groups that survive and those that do not? What are the individual and group level traits associated with different demographic trajectories, such as membership or employment? Is there good evidence for competition being reduced and/or cooperation being fostered within groups? What are the associated traits (individual, group)? Do these nascent groups, once gaining a foothold "reproduce", spawning spatially distinct daughter groups? Are traits transferred to new groups with high fidelity (otherwise said, what is trait heritability)? For the oldest of these groups where histories are sufficiently detailed, did they experience a 'transition' in their past that permitted them to go from a cult or emerging status to one that is more established, and in so doing, grow in membership number? Finally, and critically, does this transition process occur via measurable Darwinian processes, and if so, at what level(s) does it occur?

Joseph A. Bulbulia,[1] Simon J. Greenhill,[2] Quentin D. Atkinson,[3] Russell D. Gray.[3] *First Shots Fired for the Phylogenetic Revolution in Religious Studies: A Commentary on David Sloan Wilson*

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Wilson's target article illustrates how evolutionary hypotheses are advancing the science of complex cultural systems. We agree. The following extends the conversation to consider the benefits of evolutionary methods**.** We restrict our review to computational phylogenetic methods as these are being used to test evolutionary hypotheses about religions.

Why cultural phylogenetics?

Offspring resemble their parents because offspring share parental genes. Computational phylogenetic modeling of genetic lineages has enabled researchers to test hypotheses about the timing, sequence, and rate of

evolutionary change in genetic sequences, advancing understanding about how complex biological systems evolve and function (Yang and Rannala 2012).

In humans, offspring also resemble their parents because offspring acquire parental culture (Boyd & Richerson 1985; Sterelny 2005). Consider languages. A child raised in a community of exclusive Canadian speakers will not utter 'rot' for 'red,' though matters differ in German-speaking communities. Yet the resemblance between 'rot' and 'red' is not arbitrary. Both languages trace their origins about 1,500 years ago to Old High German. The properties of cultural evolution enable the modeling of cultural lineages using Bayesian approaches developed to model genetic lineages. A compelling virtue of phylogenetic approaches is their capacity to deal with the statistical non-independence of culturally acquired traits—'Galton's problem'—which invalidates standard statistical tests (Mace & Pagel, 1994). Comparative phylogenetic methods account for variation explained by shared ancestry, avoiding Galton's problem (Felsenstein, 1985). Preliminary applications to the evolutionary study of culture have produced striking results (Mace, Holden et al. 2005, Pagel 2009, Gray, Atkinson et al. 2011). Phylogenetic studies have explained the ancestral roots of modern languages (Atkinson 2011), social influences on rates of word change (Pagel, Atkinson et al. 2007), the evolution of grammars (Dunn, Greenhill et al. 2011), and the geographical location of ancestral language homelands (Bouckaert, Lemey et al. 2012). Applications have been far-reaching, bringing new understanding to ancestral migrations in the Pacific (Gray, Drummond et al. 2009), the rise and fall of social complexity (Currie, Greenhill et al. 2010), and the evolution and diffusion of social norms (Fortunato, Holden et al. 2006, Jordan, Gray et al. 2009).

Cultural Phylogenetics and Religious Cooperation

Can computational phylogenetic methods be used to test functional hypotheses about religion? Evolutionary researchers hypothesize that religious cultures are exquisite designs for cooperation, which both motivate and signal cooperative intentions. In a recent article, Luke Matthews used computational phylogenetic methods to test model for religious cooperation that he calls "recognition signaling" (Matthews 2012). According to recognition signaling, culturally acquired traits enable religious partners to discriminate between cooperators who belong to a group and defectors who might imitate belonging. Discrimination is possible because it is difficult to simultaneously acquire knowledge of many religious characters at one time [for a similar model see (Mahoney 2008).] Cultural phylogenetics is appropriate for testing recognition signaling predicts the model predicts that religious group schisms will be associated with an increase in religious character change. The expected increase in character change arises from the demands of religious brand

differentiation. By hypothesis, the more traits that distinguish religious groups, the easier for members to identify who belongs. Matthews tested recognition signaling's prediction for increasing differentiation at historical schisms by first producing a database of sixty-four religious characters that existing Christian denominations might have or not have. Examples of such characters are whether a denomination supports iconography, whether the sick are anointed, and whether Jesus is believed to have been immaculately conceived. The histories of Christian denominations are known, which enabled Matthews to reconstruct their phylogenetic ancestries on exact trees. Matthews then used comparative phylogenetic methods to model rates of change in religious characters over time. Correlational analysis empowered Matthews to evaluate whether higher rates of change occurred at schism events. Matthews found that the rate of change in culturally acquired religious traits tended to become faster precisely at the point where religious groups divide. In line with the recognition signaling hypothesis, diversification in characters tended to occur near historical schisms.

Importantly, Matthews identified the religious characters for his study in consultation with a religious studies expert, and his phylogenetic tree was populated with data gathered from historical texts. Rather than consigning historians to unemployment, cultural phylogenetics reveals their central importance for addressing basic scientific questions about how religious cultures work.

Cultural Phylogenetics and Religious Violence

The extent to which religious people acquire religious traits from "horizontal" influences is an empirical question that comparative phylogenetic methods can help to answer. In the case of language evolution, cultural phylogenetic methods have proved remarkably robust to horizontal transmission (Currie, Greenhill et al. 2010). Yet perhaps the transmission properties of languages and of religions differ. To better disentangle the contributions of inherited influences from those of horizontal influences, Matthews and colleagues conducted a second study examining sixteenth century Anabaptist groups (Matthews, Edmonds et al. 2012). The authors identified forty-four characters in eighteen Anabaptist groups, and coded these characters using binary variables (has or does not have the character). Phylogenies were developed for this period from known schism events in Anabaptist denominations. Comparative phylogenetics enabled the team to estimate the amount of character change along each branch of these known phylogenies. Forty-seven leaders were identified from historical sources, and leader networks were reconstructed. The authors were especially interested in the dark side of within-group religious cooperation: between-group religious violence. To

examine how attitudes to violence and religious orientations are transmitted, the team used logistic regression mixed models to compare the effects of inherited culture and of leader networks for practical and abstract religious orientations.

Results were intriguing. The best-fitting models showed that phylogenetic inheritance was a better predictor of denominational attitudes to violence, yet leader networks were a better predictor of similarities in theological beliefs and practices. Although this is a small study, which was restricted to a relatively brief episode in religious history, the team's finding suggests that religious violence might be subject to adaptive lag. Strategies from a violent past appear to be transmitted to contexts where they might prove harmful or even lethal. This finding repeats the important point that evolutionary approaches to religion do not imply that religions are always and everywhere functional (Richerson and Boyd 2005, Wilson 2008, Sosis 2009). That attitudes to violence are vertically transmitted may also hold important lessons for peacemakers. Instead of wiretapping the lines of religious leaders, the intelligence community might better spend their time consulting historians about the violent histories (Matthews, *pers. comm.*)

Conclusion

As Wilson argues, evolutionary hypotheses must be tested on a case by case basis. Though evolutionary hypotheses for religion abound, they are only beginning to be put to the test (Bulbulia and Slingerland 2012). To fully understand the role that religion plays in the emergence of human societies we need to trace religious, social, and environmental variation between societies, and assess the functional role that religion played over the course of human history. Cross-cultural comparisons of religions, moreover, must account for the statistical non-independence of cultural traits (Galton's problem). Computational phylogenetics affords a powerful toolkit for addressing evolutionary questions about religion precisely because computational phylogenetics relates the historical and functional properties of religious cultures using statistically appropriate methods. Preliminary applications have proved encouraging, showing that religions harbor exquisite functional designs for within-group cooperation. Yet early findings also reveal constraints on these designs. Religious conflict might be inherited from a denomination's past. Far from rendering classically trained historians of religion obsolete, computational phylogenetics discloses their central importance. Early studies herald the beginnings of what we believe will amount to phylogenetic revolution in the study of religious cultures. By testing evolutionary hypotheses for religion using phylogenetic methods, a ubiquitous, ancient, and still mysterious dimension of the human condition is slowly divulging its secrets.

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David Sloan Wilson. *Reply*

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Thanks to Peter Turchin and Michael Hochberg for creating and managing the Social Evolution Forum, which has become an excellent arena for high-level discussion. Thanks also to my colleagues who took the time to write commentaries and to readers who responded with their comments. In addition to this general reply, I have also provided comments in the 'response' section of each commentary.

Equivalence check: Superficially, it appears that two commentators (Pagel and Sanderson) agree with my assessment about cooperation but not about group selection, while the others (Hewson, Zefferman, Hochberg and Whitehouse, Bulbulia, Greenhill, and Gray) are more accepting of group selection. In fact, Pagel and Sanderson are just as accepting of group selection when terminological issues are resolved. In a previous essay published in the Social Evolution Forum (Wilson 2012), I focused on the concept of equivalence, whereby scientific frameworks are *different* but *worthy of coexistence*. Equivalence requires an ability to understand and translate between frameworks, similar to translating between languages. Scientists who insist on employing only one framework run the risk of committing errors comparable to "I don't speak Russian; therefore everything stated in Russian is wrong."

This kind of error is on display in the comments by Pagel and Sanderson. The 'language' of multilevel selection is easy to speak. It involves identifying where fitness differences exist in a multi-tier hierarchy of units. I clearly indicate my use of the multilevel framework in my target essay, as in this passage concerning the evolution of any given genetic trait: "...did it evolve by virtue of increasing the fitness of genes relative to other genes within the same organism, individuals relative to other individuals within groups, or groups relative to other groups in the total population?"

Pagel and Sanderson are either unable or unwilling to speak this language. Consider this passage by Pagel: "In the simplest case, imagine that you inhabit a group of two and that by helping each other you can achieve more than twice as much as the two of you working alone. Now ramp this scenario up to a larger group. ...The returns from cooperation means that what looks like altruism, is really a form of enlightened self-interest."

Pagel is not speaking the language of multilevel selection theory. If he did, he would see that there are no fitness differences among cooperators within single groups in his example. The fitness differences exist at the group level—groups of cooperators contribute more to the total gene pool than groups of non-cooperators or solitary individuals. If cooperation is cost-free, then the trait is neutral with respect to within-group selection and evolves by between-group selection given any variation among groups. If cooperation involves any private cost, then cooperators are less fit than non-cooperators within groups, which between-group selection must overcome for cooperation to evolve in the total population.

Or consider this statement by Sanderson: "Of course there are cultural traits that may benefit the group as a whole. But all this can mean is that these traits benefit all of the individual members of a group". Sanderson is not speaking the language of multilevel selection. If he did, he would see that there are no fitness differences among individuals within groups. Natural selection requires fitness *differences*, and fitness differences at the group level are required for the cooperative trait to evolve in the total population in his own example.

I do not insist that my colleagues speak the language of multilevel selection in their own work. I appreciate that terms such as "self-interest" and "altruism" can be defined in numerous ways; e.g., in terms of absolute fitness rather than relative fitness within groups. But before I brand their results as wrong, I do an equivalence check by translating their examples into my preferred framework. This is what Pagel and Sanderson fail to do in their commentaries.

I invite readers to do an equivalence check for all of the examples in all of the comments on my target essay. By my reckoning, not only do Pagel and Sanderson agree with me on the importance of cooperation, but they also agree with me and the other authors on the importance of between-group selection, as defined within the framework of multilevel selection theory. As Peter Turchin comments on Pagel's use of the phrase "groups as collective survival vehicles" in his book *Wired for Culture*, "That's group selection!"

On groupishness: Group selection does not favor altruism or cooperation per se. It favors any proximate mechanism that causes groups to differentially contribute to the gene (or meme) pool of the total population. Some of the mechanisms appear altruistic in the conventional sense of the word and require substantial individual cost to benefit the group. Other mechanisms might appear selfish in the conventional sense of the word, and need not require much or even any self-sacrifice. Some forms of competition among individuals within groups also benefit the group and will be favored, rather than suppressed by group-level selection. Complex social interactions often

result in multiple stable equilibria, which are internally stable by definition. Selection among equilibria results in well-adapted groups that are also internally stable, unlike the internal instability characteristic of altruism. I have emphasized these points in other publications but not sufficiently in my target essay, especially when I stated "it all revolves around cooperation." I therefore agree with Peter Turchin in his response to Pagel that 'groupishness,' not 'cooperation,' is the best general term for describing the products of group selection.

These points are part of the consensus exhibited at the Ernst Strüngmann forum and are appreciated by some of the commentators but not others. The only evidence that Pagel and Sanderson will accept for group selection is the kind of self-sacrificial altruism found in social insect colonies. All other mechanisms that benefit groups are interpreted as "enlightened self-interest" and are assumed to be explicable without invoking group selection. The only way to evaluate this claim is to perform an equivalence check on a trait-by-trait basis. Please see my response to their individual comments for more.

On the rewards and punishments that support groupish behavior: Human social groups bristle with mechanisms that punish bad behavior and reward good behavior. When these mechanisms are in place, behaving prosocially becomes individually advantageous and behaving antisocially becomes just plain stupid. Nevertheless, we still need to explain how the rewarding and punishing mechanisms evolve. Causing others to promote the common good is usually itself a common good that requires time, energy, and risk on the part of the rewarding and/or punishing individual, which economists term a second-order public good.

These points are part of the consensus exhibited at the Ernst Strüngmann forum and are appreciated by some of the commentators but not others. Consider the example of reputation discussed by Pagel. Good deeds increase one's reputation and bad deeds decrease one's reputation, so individuals who care only about their reputation will perform good deeds. But what are the traits required for others to bestow a high or low reputation upon a given person? Do *these* traits evolve based on relative fitness advantages within groups, or do they require between-group selection?

On distinguishing between psychological and behavioral definitions of altruism: The distinction between proximate and ultimate causation in evolutionary theory requires separate definitions of altruism based on psychological motives (proximate) and phenotypic consequences (ultimate). If we imagine a 2×2 table with psychological altruism and selfishness as rows and behavioral altruism and selfishness as columns, all four combinations are possible. This should be common knowledge among all evolutionists, so it is discouraging that some of the commentators appear to conflate psychological

and behavioral definitions. Consider the following passage by Sanderson: "The point about conquest is especially important because it is about one group defeating another. On the surface that looks like group selection. But is it? I would say no. It isn't a matter of a whole society against another, but of the most powerful members of a society conquering others to gain the spoils. Do they want to share the spoils with the rest of society? Not really." Sanderson is comparing apples and oranges when he uses psychological motives to argue against the fitness differences of traits within and among groups. This example is problematic in other respects that I address in my response to Sanderson's commentary.

On consensus: Sanderson questions the significance of the consensus exhibited at the Ernst Strüngmann forum, even given that it took place. I agree with Sanderson that it is silly for anyone to claim that a given position is true because X people endorse it, no matter what the value of X. Nevertheless, science is not a frictionless pendulum of ideas. Results are established that are durable enough to be called facts, and these tend to become widely accepted. The earth is round and very old. Continents drift. To these we can add the fact that many traits evolve on the basis of the differential fitness of groups, despite being selectively disadvantageous within groups, as these terms are defined in multilevel selection theory. What's new is that large numbers of scientists are accepting this fact at face value and do not regard equivalent descriptions as a denial of the fact.

On using consensus and equivalence to guide empirical research: The commentaries by Hochberg and Whitehouse and Bulbulia, Greenhill, and Gray are especially welcome because they show how the consensus exhibited at the Ernst Strüngmann forum can be used to guide empirical research. I wholeheartedly agree about the importance of history as a fossil record of cultural evolution, which is often so rich that it puts the biological fossil record to shame. Narrative histories often provide sufficient detail to evaluate how new cultural forms originate and spread in competition with alternative forms. An important book in this regard is Robert Bellah's (2011) *Religion in Human Evolution: From the Paleolithic to the Axial Age* (an audio interview that I recently conducted with Bellah is available here) Quantification, including the phylogenetic methods described by Bulbulia, Greenhill, and Gray, adds additional power. Please see my response to their individual commentaries for more. The most important general point is that the entire theoretical and empirical toolkit that is used to study biological diversity can be used to study cultural diversity. We can look forward to the same kind of integration for the study of culture during the 21st century that took place for the biological sciences during the 20th century (and continuing).

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