

*Una teoría darwinista
de la coevolución gen-cultura*
A darwinian theory of gene-culture coevolution

PETER J. RICHERSON¹ AND ROBERT BOYD²

University of California Davis¹ and UCLA²
pjricherson@ucdavis.edu (EEUU)

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RESUMEN

Darwin estaba convencido de que el éxito de su teoría de la evolución dependería de su capacidad para dar cuenta de la conducta humana. Las ideas expuestas en *Descent of Man* fueron ampliamente discutidas por sus contemporáneos, aunque no eran las únicas teorías evolucionistas a finales del siglo XIX. Las tesis específicas de Darwin y las de sus principales seguidores tuvieron poco impacto sobre las nacientes ciencias sociales a comienzos del siglo XX. Las ciencias biológicas y sociales continuaron divergiendo hasta la segunda mitad del siglo XX. En los sesenta, Donald T Campbell, un psicólogo social americano, publicó los primeros trabajos teóricos dedicados a aplicar los principios evolucionistas al desarrollo de las culturas. Desde el pionero trabajo de Campbell han surgido varios programas evolucionistas de investigación dirigidos a explicar la cultura humana. En este ensayo esbozamos nuestra propia teoría de la coevolución gen-cultura.

A pesar de su prestigio, Darwin sólo convenció a unos pocos de sus contemporáneos de que poseía la teoría correcta sobre los orígenes de la mente humana. Su influencia más poderosa la ejerció sobre los pioneros de la psicología: Romanes, Morgan, James y Baldwin; pero su influencia sobre la psicología se desvaneció a comienzos del siglo XX (Richards, 1987). Ninguna ciencia social del siglo XX ha sufrido la más mínima influencia de *Descent of Man* y hasta ahora mismo muchos eminentes científicos sociales siguen siendo completamente hostiles hacia el darwinismo. ¿Cómo es posible que, durante más de un siglo, una teoría pueda engendrar tanta controversia y sin embargo no produzca una reflexión crítica capaz de evaluar sus méritos? ¿Podemos articular to-

davía una teoría satisfactoria de la evolución de la conducta humana en términos darwinistas o tal empresa se halla abocada fatalmente a un fracaso?

PALABRAS CLAVE

Boyd&Richerson, coevolución gen-cultura, darwinismo, ciencias sociales, Donald T Campbell.

ABSTRACT

Darwin believed that his theory of evolution would stand or fall on its ability to account for human behavior. The ideas in the *Descent of Man* were widely discussed by his contemporaries although they were far from the only evolutionary theories current in the late 19th Century. Darwin's specific evolutionary ideas and those of his main followers had very little impact on the social sciences as they emerged as separate disciplines in the early 20th Century. The social and biological sciences continued to diverge until the late part of the twentieth century. In the 1960s, Donald T. Campbell, an American social psychologist, published some of the first theoretical work that adapted principles of evolutionary theory to the problem of the evolution of cultures. Since the pioneering work of Campbell several research programmes on evolutionary approaches to human culture have been developed. Here we sketch our own theory of gene-culture co-evolution.

Despite his prestige, Darwin convinced only a few of his contemporaries that he had the correct theory of the origin of the human mind. His strongest influence was on the pioneering psychologists, Romanes, Morgan, James, and Baldwin, but their importance in psychology waned drastically after the turn of the 20th Century (Richards, 1987). No 20th Century social science derives any significant influence from the *Descent of Man*, and to this day, eminent social scientists are quite hostile to Darwinism. How can it be that a theory can generate so much controversy, and yet not attract enough critical work to test its worth for over a century? Can we flesh out a satisfactory theory of the evolution of human behavior along Darwinian lines, or is the enterprise really fatally flawed?

KEY WORDS

Boyd&Richerson, Gene-culture Coevolution, Darwinism, Social Sciences, Donald T Campbell.

1. DARWIN'S EVOLUTIONARY THEORY USED IN BIOLOGY AND NEGLECTED IN THE SOCIAL SCIENCES

Darwin's ideas on evolution were incorporated into the foundations of biology in the first part of the 20th Century. In the meantime, most of the intellectual leaders of the newly emerging social sciences almost entirely ignored the ideas in the *Descent of Man* (Ingold, 1986). In the cases of psychology and economics, where detailed histories have been written, the reason for the neglect of Darwinism was substantially due to idiosyncratic events in the careers of the most prominent Darwinians in these disciplines (Hodgson, 2004; Richards, 1987). The so-called Social Darwinism that influenced turn-of-the-century sociology and anthropology was thoroughly Victorian in its moral naturalism and progressivism, as the confident recommendations for social policy of its followers illustrate. Social Darwinism was more in the spirit of Spencer than of Darwin. Most sociologists and anthropologists distanced themselves from Social Darwinism, probably because they found its political uses abhorrent (Hofstadter, 1945; Campbell, 1965), although Bannister (1979) argues that Hofstadter's famous critique of Social Darwinism substantially mythologizes it. Myth or truth, other social-science pioneers were eager to differentiate their disciplines from biology and downplayed the significance of biology for the social sciences. For example, the pioneering student of imitation, Tarde (1903), set aside «biological» considerations in developing his theory, and was apparently completely unaware of the parallels between his ideas and those expressed in the *Descent of Man*. Still, in the year 1900, psychology still carried an influential tradition that was quite directly derived from Darwin (Richards, 1987). William James, Lloyd Morgan, and James Baldwin all espoused evolutionary theories of psychology based upon Darwin's ideas.

Baldwin's theory was especially advanced in reconciling the Darwinian legacy with the emerging genetics. First, Baldwin (1895) elaborated a complex theory of imitation. Baldwin grounded elaboration of the concept on his observations of his own children, noting the emergence of powerful capacities for imitation in late infancy. Second, even as early as 1895, five years before the rediscovery of Mendel, Baldwin (1895: 294) drew a sharp distinction between the «machinery of heredity» and imitation:

(T)here is instinctive tendency to functions of the imitative type and to some direct organic imitations; but those clear conscious imitations which represent new accommodations and acquirements are not as such instinctive, and so come later as individual acquirements.

Third, Baldwin envisioned a complex interplay between biology and imitation, as the above quote suggests. The capacity for imitation is a part of biological development that emerges late in the child's first year of life, much as more detailed modern studies show (Tomasello, 1999, 2008). Moreover, he portrays imitation as affected by the individual's experience of pleasure and pain. Sometimes the impulse to imitate is so strong as to override pleasure and pain, but the-

se biologically derived senses typically have their effect on behavior and hence on what will be imitated subsequently by others. On the other side of the coin, learned or imitated behaviors could lead humans (and other animals with adaptive phenotypic flexibility) to persist in environments to which they are organically ill adapted. Subsequently, natural selection acting on the machinery of organic inheritance can eventually make the learned or imitated behavior innate. Baldwin termed this effect «organic selection.» Today it is generally referred to as the «Baldwin Effect.» It was actually an independent discovery of Baldwin, T. Hunt Morgan, and Henry Fairfield Osborn (Richards, 1987).

As we shall see, all of Baldwin's ideas have resonated in late 20th Century theories of gene-culture coevolution. However, they had no immediate issue for the same reasons that other evolutionary influences on the rapidly evolving social sciences fell into disuse around the same time. Few social scientists truly espoused a Darwinian perspective. The sociologist Albert G. Keller taught a version of social evolution that was truer to the Darwinian tradition than his mentor Sumner, but his subsequent influence was negligible (Campbell, 1965). Some pioneers whose influence was great may have had elements of Darwinian processes in their theories, but these were not subsequently developed. For example, Turner (1995) argues that Durkheim had a highly Darwinian mechanism at the root of his theory of the division of labor, but this feature stimulated no subsequent theoretical or empirical work in the modern Darwinian style.

As the new social sciences developed, specific research agendas developed in them. For example, psychologists after the turn of the century worked to sever their roots from philosophy and embrace more rigorous experimental methods. Baldwin, a good experimentalist and observationalist in his younger days, but whose philosophical agenda was always large, turned increasingly in a philosophical direction while his younger colleagues turned sharply in the opposite. It did not help that his career in the US was ruined by a scandal (Richards, 1987). In anthropology, Franz Boas reacted negatively to all forms of theorizing, wanting field workers to have minimal preconceptions when collecting ethnography (Harris, 1979). Turn-of-the-20th Century institutional economists, particularly Thorstein Veblen, were sophisticated evolutionists, but their influence waned and was extinguished (Hodgson, 2004). For economists, physics rather than biology became the science to emulate. Veblen's later career was also plagued by scandal.

Part of the problem was that Darwin's own view of evolution reached a low ebb in the early 20th Century. The pioneering geneticists at first discovered mutations with large effects and quarreled with Darwinians who held to selection working on continuous variation. Not until Ronald Fisher's famous paper in 1918 did the reconciliation of Darwin and genetics begin and his star rise again in biology (Provine, 1971).

The social and biological sciences continued to diverge until mid-century, and relationships between them tended to be limited to sterile nature-nurture debates (Cravens, 1978). Various attempts were made to heal or at least manage

this rift. One of the most influential formulas was Dobzhansky and Montagu's (1947). They argued that biology produced the substratum on which human culture was built, that culture and biology remained a coevolving complex, and that cultural evolution is unique and transcendent. Dobzhansky's (1962) book *Mankind Evolving* expands on this theme without ever really specifying how the coevolution works or just what transcendence means in this context. His and Montagu's (1947) position was really in the nature of a peace treaty between the biological and social sciences that allowed each to independently pursue its own agenda, ignoring the inconsistencies that arose as a result. The breakers of this peace in the 1950s and 60s, such as Lorenz (1966) and Jensen (1969), were not sophisticated theorists and were trapped in the nature-nurture debate. Evolutionary thinkers in the social sciences, such as White (1959), Carneiro (1967), and Lenski and Lenski (1982), remained wedded to progressive evolutionary theories owing more to Spencer than to Darwin. In essence, in the mid-20th Century no one followed up the late 19th Century ideas implicit in the *Descent of Man* to create a sophisticated theory of cultural evolution to link up with the Darwinian theory of genetic evolution. The project of unifying the social sciences with each other and with biology is still a work in progress (Gintis, 2007).

After a long hiatus, Donald Campbell, a polymath psychologist, was the first to seriously tackle the problem of culture. He made three important arguments. First, in a series of papers culminating in his (1960) article, he argued that all knowledge processes had a fundamental kinship with organic evolution, summarized in his slogan «blind variation and selective retention.» His (1965) book chapter fleshed out this idea with the concept of vicarious forces to characterize the relationship between organic evolution by natural selection and knowledge processes in the narrower sense of individual learning and related processes. Given the inheritance of acquired variation, psychological forces would shape cultural variation, much as Darwin thought sympathy was conducive to moral progress. These forces are vicariously acting as surrogates for natural selection because they arose by natural selection to shape phenotypes adaptively, again exactly as Darwin had argued. Second, in the 1965 chapter, he provided a clear argument for why Darwinian theory ought to apply to any system of inheritance, including culture. Third, in his (1975) article, he carefully distinguished between Darwinian and progressive evolution, and showed that a century of work had failed to identify any sort of scientifically respectable process to underlie a concept of progress. Progressive evolutionary «theory» was simply a description of historical trajectories in terms of stages, lacking any causal process, given that Spencer's homogeneity-to-heterogeneity mechanism was no longer plausible.

Campbell's approach encourages us to think in terms the interplay of «forces» that drive cultural evolution. In the case of genetic evolution, the most important evolutionary forces, processes that are capable of changing gene frequencies and causing evolution are mutation, genetic drift, gene flow, and natural selection, making unvarnished organic evolution a process based purely on

random variation and selective retention. Cultural evolution must be subject to the analogs of these four forces, but is also subject to several kinds of vicarious forces. People are not only selected willy-nilly by natural selection, they also change their culture by making conscious and unconscious choices as they learn for themselves or from others. Some of the rules for making choices are inherited genetically, and then affect cultural evolution. For example, the way sensory neurons with different properties are distributed in the nose and mouth play a large role in whether potential diet items are considered pleasant or noxious. Choices of diet items by individuals will in turn drive the evolution of a society's cuisine. Normally, we might expect that vicarious selectors for diet will favor nutritious, healthful diets because they have been shaped by natural selection. However, some evolved selectors may be exploited by items like addictive drugs, and others may be overridden by cultural preferences, as in the inclusion of pain and heat sensor stimulating peppers in many cuisines. Culture might also drive organic evolution, as in the case the evolution of adult milk sugar digestion during the last few thousand years in the human populations that consume milk (Simoons, 1978). Simoons apparently discovered the tip of an iceberg (Hawks et al., 2007). Agricultural innovations in the early Holocene greatly changed the diets, disease exposure, and social life of many human populations, apparently generating a large coevolutionary response.

In essence, Campbell forcefully reintroduced Darwinian ideas to social scientists after a lapse of some 60 years. He did not trace specific parallels in his scheme to Darwin and Baldwin and was probably unaware of the degree of parallelism, especially in Baldwin and Veblen. Subsequently, several more or less distinctive research programs in evolutionary approaches to humans developed, following pioneering contributions by Lucca Cavalli-Sforza and Marc Feldman (1973), E.O. Wilson (1975) and Richard Alexander (1979). These contributions were heavily politicized in the famous sociobiology debate (Seigerstråle, 2000). Today Darwinian social scientists are reluctantly tolerated by their colleagues. By now this is a very active field with several active research programs spread across the social science disciplines and in human biology (reviewed by Laland and Brown, 2002). The degree to which cultural evolution plays an active role in human evolution is among the important debates in the field. One view, held in various forms by many, is that selection ultimately falls on genes, and thus that genetic vicarious selectors strongly constrain cultural evolution. Another view, championed most effectively by Susan Blackmore (1999), is that memes are cultural parasites that have driven the evolution of human brains and other genetically coded aspects related to the support of these parasites. A third view, to which we subscribe, is that in humans genes and culture have more-or-less equally important roles to play in a coevolutionary system.

2. DARWINIAN PRINCIPLES APPLIED TO CULTURAL EVOLUTION

The way that culture might make us theoretically interesting, as opposed to merely taxonomically unique, is if culture affects the evolutionary process in fundamental ways. Many evolutionary social scientists have been keen to apply the main theoretical and empirical results of evolutionary biology, such as Hamilton's inclusive fitness rule, to human behavior (either now or in the past). Contrariwise, using the formal, mathematical, experimental, and observational methods of Darwinian biology to study cultural evolution has turned out to be an effective way to understand the distinctive processes of cultural evolution and the coevolution of genes and culture. The argument for applying Darwinian methods to culture, well articulated by Campbell (1965, 1975) and in more turgid prose by Baldwin (1895), goes as follows: Learning from someone else by imitation or teaching is similar to acquiring genes from parents. A potentially important determinant of behavior is transmitted from one individual to another in both cases. It is important not to ignore the population as a whole in analyzing either case. As individuals acquire genes or culture, they «sample» a large population of potential parents and cultural models. Then, evolutionary processes operate on individuals, discriminating in favor of some cultural and genetic variants and against others. The population that exists for the next generation to sample typically differs subtly from the previous one. As many generations pass, changes accumulate and evolution occurs. Population genetical theory is a large set of formal machinery for scaling up what happens to individuals in the short run to what happens to populations in the long run. Its basic methods are as applicable to culture as to genes, and evolutionary theory ought to do the same work for the social sciences as for biology (Cavalli-Sforza and Feldman, 1981). This analogy between genetic and cultural evolution is undoubtedly what led Darwin fail to make a as sharp a distinction between genes and culture as 20th Century biologists did. Both inheritance systems are population level, historical processes that frequently result in the adaptive diversification of behavior.

3. BASIC PROCESSES OF GENE-CULTURE COEVOLUTION

The task implied by Baldwin's and Campbell's argument is not trivial because there are many differences between genetic and cultural transmission. Substantial modifications in genetic models are required to make them mimic culture, and cultural models need to be linked with genetic models to understand the coevolution of genes and culture. Only a beginning has been made on these tasks, but already a rich and fascinating set of processes have been uncovered. Consider a few of the main differences between genes and culture and their evolutionary implications (see Cavalli-Sforza and Feldman (1981) and Boyd and Ri-

cherson (1985) for amplification and Richerson and Boyd (2005), Mesoudi (2007) and Henrich (2008) for recent reviews of the field).

First, we are not restricted to sampling just two «parents» when acquiring a cultural trait. We often survey dozens and choose to imitate one individual whose behavior seems best to us by some standard or another. This can give inordinate weight to teachers, leaders, or celebrities if many people choose to imitate them. One charismatic figure can establish a new sect with hundreds or thousands of members in a single lifetime. This effect will generate variation between groups much more rapidly than is possible in the case of genetic evolution.

Second, we are not restricted to imitating people of our parental generation; peers, grandparents, and even ancient prophets can be direct sources of our culture. The case of imitating peers is, in effect, a shortening of the life cycle of an item of culture. Such behaviors are more than a little like microbes; they can spread rapidly from individual to individual. Some such traits are harmless fads, some are important skills, and some are quite pathological. Hunt and Chambers (1976) studied heroin addiction as a pathological cultural character. It spreads mostly among close friends, much like a venereal disease does. Parents observe that kindergarten children bring home nasty viruses and bad habits alike! These transmission pathways have likely not been closed by selection on genes and/or culture because the risk of catching cultural pathogens is counterbalanced by using adaptive vicarious selectors to acquire useful skills, attitudes, and beliefs from people other than our parents. Language facilitates the very wide and rapid spread of some ideas.

Third, we acquire and discard items of culture throughout our lives. One is stuck with the genes one inherits at conception, though of course the expression of genes can be heavily modified throughout life. Not so with culture. Our culture is acquired gradually, with plenty of opportunity for early-acquired items to influence those adopted later, and for later enthusiasms to result in the discarding of previous ideas. Many of us change hobbies, occupations, religions, or political beliefs substantially over a lifetime. It is this relatively free ability to pick and choose that allows such scope for vicarious selection in cultural evolution. Vicarious selection comes in many forms that we call «biases» (Richerson and Boyd, 2005) and which Cavalli-Sforza and Feldman (1981) called «cultural selection.» The only trouble with «cultural selection» as a term is that it is liable to confused with natural selection on cultural variation, a process that we think is quite important in cultural evolution; (see below and Blackmore, 1999).

Fourth, variations that we acquire for ourselves are readily passed on to others. In culture, the common animal ability to learn is coupled to a system of imitation. In animals without some form of imitation, what parents learn is lost, and the young have to relearn each generation. With culture, the results of learning in one generation can be passed on to the next, and cumulative improvements over the generations by the inheritance of acquired variation are possible. The coupling of individual learning to the cultural system allows to non-random new variation to be introduced into the cultural system,

The task of exploring just these differences has only just begun. Some sense for the magnitude of the task can be had by noting that culture is roughly as complex a system as genes. No one has devised a precise comparison, but the number of words a high school graduate knows is said to be a few tens of thousands, on the same order as the number of protein coding genes in our genome. One hundred fifty years after the publication of the Origin evolutionary biology remains a vibrant field. The study of cultural evolution is perhaps a half century behind that of organic evolution.

4. EVOLUTION OF HUMAN UNIQUENESS

One interesting set of questions to study with formal models of cultural evolution is the evolution of the cultural system itself. There are three major differences between humans and even our close primate relatives that are basic for understanding ourselves in the Darwinian framework: (1) a greater capacity for imitation and the associated massive use of culture; (2), much symbolism and stylistic variation (e.g., many languages) in culture of no obvious practical use; and (3) larger to much larger social groups with relatively high levels of cooperation, coordination, and division of labor. How and why have these differences arisen? Some interesting tentative answers to these problems emerge from the theoretical models.

Estimates of the Basic Benefits and Costs of a Massive Capacity For Culture

The question of why humans came to have so large a capacity for culture is the most fundamental question. The standard answers are very strongly flavored by non-Darwinian progressivist evolutionary ideas. Almost everyone assumes that human culture is an intrinsically superior method of acquiring and transmitting non-genetically heritable adaptations. The question is not why humans came to have culture, but how and when we made the breakthrough to our qualitatively superior mode of cultural adaptation. Landau (1991) has shown that all accounts of human origins, even by professional paleo-anthropologists, have the structure of folk hero stories. The human species was set tasks and had to overcome obstacles to eventually triumph upon reaching fully modern form. Even such deep-dyed Darwinians as Lumsden and Wilson (1981) are led to speak of humankind's «cosmic good fortune of being in the right place at the right time» to the breakthrough adaptation of advanced cognitive abilities. «The eucultural (complex human culture) threshold could at last be crossed.» The breakthrough hypothesis is plausible if we assume that special, costly, cognitive machinery is necessary to imitate complex traditions (Boyd and Richerson, 1996). Such capacities could not easily increase when rare, even if having complex traditions

had been a great adaptive advantage, because even if some lucky mutation created the ability to learn complex culture, there will be no complex traditions to imitate until a population of such imitators existed!

Given the great span of time available for the evolution of complex capacities for imitation, and their non-existence for all but the latest slice of it, we should also consider the hypothesis that the costs of having an elaborate cultural capacity usually outweigh the benefits. Even if there are intrinsic barriers to the evolution of the capacity for complex culture, it is surprising that it has only evolved once in the whole history of life on earth. Perhaps only a highly «favorable circumstances» in an unusual environment leads to the benefits of a large culture capacity to outweigh these costs.

Simple population-genetics-style models that link a capacity for individual learning with a capacity for imitation create a basic model of the inheritance of acquired variation. They illustrate how culture can have real advantages in some environments, but not in all (Boyd and Richerson, 1985). Suppose individuals inherit some economically important trait by imitation from their parents, say how much subsistence to derive from hunting versus gathering plants. Individuals compare this traditional knowledge with what individual experience suggests is the correct strategy. Individuals then have to combine the traditional knowledge acquired culturally with that acquired by their own experience. We assumed they use a weighted average. If tradition and individual learning were equally important in the decision, and if the traditional diet is 50% animals, but experience indicated that 90% was best (say in some new environment), individuals might end up collecting enough plants to make up 30% of the diet in the first generation in the new environment, 20% in the second, 15% in the third, and so on. We also investigated similar models in which genes and learning (but no inheritance of acquired variation) were used to decide what to do.

Under what circumstances should there be a significant weight to cultural tradition, as opposed to depending only on individual experience plus genetic transmission, as most animals apparently mostly do? The answer depends upon two interacting factors: how the environment is changing, and the economics of obtaining and transmitting information. Let us make the reasonable assumption that the genetic system is less prone to random transmission errors (mutation) than the cultural tradition. Let us also assume that individual learning is either fairly costly or fairly error prone. (These two variables are closely related because learning could always be made more accurate by devoting more time and effort to it.)

Given these assumptions, if the environment is changing very slowly, a fixed genetic rule is better than any combination of learning and imitation. The reason is that selection acting on a conservative inheritance system tracks slow environmental change very well, and the greater errors inherent in learning and imitation are a considerable fitness burden. At the opposite end of the scale, in very rapidly changing environments, any form of transmission from parents is useless; their world is simply too different from their children's. In such an en-

vironment, each individual does best by depending entirely on experience, since only individual learning has a better than random chance of producing the currently advantageous behavior. In intermediate environments, some mixture of individual and social learning is typically the most adaptive system. The largest advantage to culture comes in environments that are changing substantially on the time scale of tens of generations, but not too rapidly within any one generation. A cultural system of inheritance, by making individual learning cumulative, can track changing environments more rapidly than genes, yet economize substantially compared to the costs associated with individual learning.

Given the assumption that individual learning is costly relative to imitation, the results of the model recover Darwin's intuition: the inheritance of acquired variation has distinctive advantages in variable environments. Empirical support exists for this result. The origin of human culture, and of large brained animals generally, is associated with the increasingly fluctuating climates of the last few million years (Richerson, Boyd, and Bettinger, 2009; deMenocal, 1995; Potts, 1996; Vrba et al., 1995). Really sophisticated human culture arose during the last few hundred thousand years under the strongly fluctuating Ice Age climates of the Middle and Late Pleistocene. The last glacial period (70,000-10,000 years ago), for which ice cores from Greenland give an especially good picture, was punctuated by many short warm episodes of about 1,000 years duration. The last glacial was more variable than the Holocene right down to the limits of resolution of the ice core record ten years or less, depending upon depth in the core (Ditlevsen, Svensmark, and Johnsen, 1996). This sort of variation, though less intense, occurs in 3 earlier glacials as well (Martrat et al., 2007). This is the sort of world in which both individual and social learning might be of advantage according to our simple model. Culture is, perhaps, as much simply a means of coping with the deteriorating environment of the Pleistocene as a cosmic breakthrough of progressive revolution. As more and longer high resolution cores become available the climate hypothesis will be tested more rigorously. For example, it predicts that hominin brain size increases will be preceded by increases in the millennial and sub-millennial component of climate variation.

However, clearly something is still missing from the picture. The model is very general, and the fluctuations of the climate are a global phenomenon. If the model is correct, ought not many lineages of animals to have become cultural during the Pleistocene? They may in fact have. Many bird and mammal lineages show trends of increasing brain size during the increasingly variable environment from the Miocene to the late Pleistocene (Jerison, 1973), and many have simple social learning systems. Brain size in both birds and primates is correlated with innovative behavior and social learning. The emerging picture is that humans are merely the upper tail of the distribution in terms of cognitive and cultural responses to increasing climate variation (Laland and Reader, 2010). Interestingly, the West Eurasian Neanderthals and the Tropical African Anatomically Modern Humans apparently both evolved very large brains in parallel after they diverged from a smaller-brained common ancestor (Klein, 2009). A strong possibility

exists that Neandertals also independently innovated symbolic artifacts about 50,000 years ago (Zilhão et al., 2010). Many Anatomically Modern populations also did not make durable symbolic or exhibit other supposed signs of behavioral modernity. Richerson et al. (2009) argue that many populations of both species were probably small, so small that cultural complexity was limited. Living populations are known to produce very simple toolkits when small and isolated (Henrich, 2004). Perhaps much inheritance of acquired variation in many species is carried by epigenetic inheritance systems (Jablonka and Raz, 2009). If there is an intrinsic barrier to complex culture of the useless-when-rare sort, what piecemeal innovations might have eventually allowed our lineage to work up to the threshold where enough individuals were capable of complex traditions for a capacity for such to be favored directly? What costs might these piecemeal innovations have incurred? We are on the horns of an explanatory dilemma. We must account for an evolutionary innovation that causes the extraordinary success of the only species to have it. Our account must explain why our species has complex culture, and why no others do, despite presumably preadapted systems for simple social learning being rather common. Reconstructing the evolutionary history of any lineage is a challenging problem not least because they are a string of singular events. For discussions of the relationship between ordinary science, in which replication is possible, and historical reconstructions, where it is usually absent, see the essays in Nitecki and Nitecki (1992).

More Complex Benefits and Costs of a Massive Capacity For Culture

Further clues for the value of high capacity for culture emerge from the features of human culture. The capacity to use many people in addition to parents as models is a good example. On the benefit side, surveying many models is useful to find a better one to imitate. If Dad is a lousy hunter and Mom makes shabby baskets, we can seek a better mentor. The commonness of a trait among replicate models will frequently be a good guide to whether to acquire it or not; often the most common way of doing things is the local optimum. As with the case of the simple learning plus imitation model, these advantages are most useful in spatially and temporally variable environments.

On the cost side, imitating people other than parents exposes populations to the possibility that pathological cultural traits can arise. We have already mentioned some examples. How can such things as heroin addiction arise? Cultural traits that give rise to seriously deleterious behavior are unlikely to evolve if cultural transmission follows the conservative parent to child pattern. Not enough heroin addicts survive and raise children. Natural selection acts against such self-destructive cultural variants. However, if the addicts can attract peer friends during the early phases of addiction, before the most harmful consequences are manifest, the behavior can spread from victim to victim regardless of the ultimate harm done. With non-parental transmission, natural selection on cultural

variation can favor the evolution of fragments of culture that act very much like viruses as in Richard Dawkin's famous selfish meme idea (Goodenough and Dawkins, 1994; Blackmore, 1999). Microbial pathogens typically invade the body by attaching to specific receptor molecules on the surface of a host's cells. These are the analogs of the vicarious selectors for and against cultural variants created by senses of pleasure and pain, normally adaptive bits of our psychology that pathological cultural variants use to invade our minds. Natural selection acting on parentally transmitted culture and on genes could reduce the chances of acquiring such traits but only by foregoing the benefits of being able to imitate superior non-parents. We do use cultural defenses with varying success to try to defeat pathological cultural variants just as we use medicines to cope with pathogens. Most parents try to inculcate a fear of addicting drugs in their children. Formal instruction and mass media propaganda buttress their efforts.

A massive, sophisticated system of culture is a wonderful adaptation for responding to spatial and temporal variation, and the human species' ability to survive during the Pleistocene and spread from its tropical homeland into Arctic regions and the New World is testimony to this flexibility. In the Holocene, following the evolution of agriculture, we became explosively successful. But, to speak loosely, the coevolutionary complexity of managing two inheritance systems means that the cultural system even now is far from perfect. We pay for cultural flexibility with a susceptibility to the evolution of cultural pathologies of various kinds. Humans are built for speed not for comfort.

The problems that arise from a second system of inheritance are not necessarily as obviously harmful as heroin addiction. Many otherwise puzzling patterns of human behavior are plausibly a by-product of the evolutionary activity of the cultural system. Take the modern small family. Recent Western societies, beginning in France in the early part of the 19th Century, have undergone sustained reductions in birth rates (Coale and Watkins, 1986). Today many developed nations have extremely low birth rates, often below replacement. Many developing countries have rapidly falling birth rates. Borgerhoff Mulder (1987) and Irons (1979) have argued strongly from case studies in East Africa and Iran, respectively, that traditional rural societies have the opposite pattern, as one would expect if natural selection acting on genes were responsible for decision-making rules. People ought to convert wealth into Darwinian fitness— children. Why do Moderns behave so contrary to the prediction that everyone should transform wealth into greater fitness?

Modern societies have greatly expanded non-parental routes of transmission of culture and this ought to act to multiply the pathways by which pathological cultural variants can spread (Newson et al., 2007). (Pathological from the perspective of genetic fitness; we do not mean to suggest that the demographic transition is a bad.) Urbanization brings people into contact with many non-kin, diluting the influence of family members who have a kin selected interest in family members' reproduction. Specialized non-parental roles have arisen, such as

teaching, which are influential in socializing the young. Competition for these roles is keen, and preparation for them requires extending education into the prime reproductive years. Those who value a career and cheerfully sacrifice early marriage and a large family to obtain it are more likely to be successful, and successful career seekers are likely to influence their pupils', subordinates', and employees' values and aspirations. The modern society with «careers open to talent» pioneered by Napoleon has, it seems, permitted the spread of low fertility norms due to a process we would call natural selection if the norms were genetic instead of cultural (Newson and Richerson, 2009).

Symbols: The Origin of Modern Humans

What of the large scale of human societies and our elaborate use of symbols, such as elaborate costumes, artistic creations, and complex supernatural belief systems, which have no intrinsic function outside of cultural communication? Do models of cultural evolution give any insights into the evolution of these attributes, which, along with culture itself, differentiate our species from its ancestors?

These two features are empirically closely associated. Social groups are usually also symbolically marked. Take two examples likely to be familiar to readers. Even that quintessential bastion of rationality, the modern research university, has a seal, a motto, elaborate graduation rituals with special colorful dress, and, in the United States, even sports teams to represent it in ritualized combat with other universities. Even among faculty, there is a surprising amount of sincere affection for the symbols and rituals of academia. Campbell (1969) noted the similarity of academic disciplines to ethnic groups.

To address this problem, we have constructed theoretical models in which individuals use marker traits to assess whom to imitate. (Note the analogy to mate choice sexual selection.) In the first instance, people might gain an advantage by choosing to imitate others who are economically successful and have large families. Prestige and success in survival and reproduction are empirically frequently correlated, as Irons (1979) showed. Models also demonstrate that apparently adaptively neutral, symbolic characters like language differences can serve as an adaptive marker (McElreath, Boyd, and Richerson, 2003; Boyd and Richerson, 1987). In a spatially variable environment with migration, using similarity of language, dress, or other symbolic criteria to bias imitation is a good way to avoid imitating those whose adaptation to a different environment that makes the behavior less fit in your environment.

Stone tools with unmistakable stylistic variation and purely artistic productions arrived suddenly in Europe with the Aurignacian tradition, beginning 35,000 years ago, though precursors have been found earlier in Africa (Henshilwood et al., 2004). The long, less well documented sequence of perhaps gradual changes in Africa, stretching back some 280,000 years, leads up to the Au-

rignacian level of stylistic sophistication according to some authors (McBrearty and Brooks, 2000). Other authors see ephemeral bouts of sophistication in Africa rather than a steady progressive trend (Marean et al., 2007; Jacobs et al., 2008). Bettinger (1991) argues that this so-called Upper Paleolithic Transition represents the first evidence of ethnic groups. The origin of symbol use is accompanied by a substantial increase in human technical sophistication, and the spread of humans to cold-temperate and subarctic habitats. Local variations in technology as well as symbols apparently permitted people to adapt more finely to more kinds of environments than was possible by Neanderthals and other ancient humans. Ethnic markers make marked groups «pseudo-species» that can preserve fine local adaptations in the face of a flow of ideas from other environments. Ecologically, humans constitute a spectacular adaptive radiation albeit one based primarily on cultural rather than genetic variation.

The Origin of Cooperation and Complex Societies

The ethnic unit, like human culture, has no close parallel in the animal world. There are many large, sophisticated societies among such groups as bees, ants, and termites. Altruism in such cases has classically been attributed to kinship, in accordance with Hamilton's (1964) inclusive fitness rule. The workers in canonical insect colonies are all siblings, and each colony consists of a few reproductives and many non-reproducing workers. A similar situation pertains in African naked mole rats, the mammal with the most complex social organization aside from humans, which consist of colonies headed by a reproductive queen and comprising highly inbred and closely related workers (Sherman et al., 1991). The discovery of insect colonies with moderate to low relatedness within colonies (Pedersen et al. 2006) has given rise to the suggestion that colony level selection is important in at least some interesting cases (Hölldobler and Wilson, 2009). Among our close relatives, the apes and monkeys, cooperation appears to be largely restricted to close relatives and partners engaging in reciprocal altruism.

To judge from contemporary simple societies (Johnson and Earle, 2000), three levels of social organization would have characterized Upper Paleolithic societies: the family, the coresidential band, and a collection of bands that routinely intermarry, speak a common language, and have a common set of myths and rituals. Members of this largest unit, often called a tribe, generally maintain relatively peaceable relations with each other, and routinely cooperate in subsistence, defense, and other activities. Relations between tribes vary, much like relations between nations, from close alliance to traditional enmity. The whole linguistic-cultural group consisted of a few hundred to a few thousand people (by analogy with modern hunter-gatherers) in contrast to modern ethnic groups that range up to many millions of people.

Compared to many agricultural societies of the last 10,000 years, the sop-

histication of political organization of ancient ethnic groups was limited. Again drawing analogies with contemporary simple societies, there was probably not an overall formal leader of the group, probably not even a formal council. Rather, forceful, able men probably acted as semiformal headmen of bands, subject to considerable pressure of opinion from other adult members of the band. Inter-band affairs were probably regulated by ad hoc negotiations dominated but not controlled by the headmen.

A number of hypotheses have been proposed to explain human cooperation. For example, Alexander (1987) supposed that human intelligence allows us to greatly extend the range of a mechanism for supporting cooperation known as reciprocal altruism to indirect reciprocity, in which you help someone who has helped someone else, who may be several steps removed from anyone who can help you in return. The problem comes in scaling this process up to larger groups. Models show that reputation and punishment can help stabilize indirect reciprocity, but the solution to collective action problems seems to require additional process like equilibrium selection at the group level (Panchanathan and Boyd, 2004). Many of us suspect that something like Darwin's proposal for selection at the level of tribes lies at the heart of human abilities to cooperate (Richerson and Boyd, 1999; Wilson and Sober, 1998).

Most evolutionary biologists, including Darwin and Hamilton, are normally skeptical that selection between groups of unrelated individuals is effective (Williams, 1966; but see Wilson and Wilson, 2007). The problems with large-scale group selection are straightforward. As with any form of natural selection, group selection must proceed through the differential survival or reproduction of entities that differ for traits that are both heritable and variable among them. In the case of selection at the level of tribes, reproduction of groups must ordinarily be slower than the reproduction of individuals, and group death must be infrequent compared to the death rates of individuals. Also, it is hard to maintain variation among groups if there is very much migration between them. If we start somehow with a group dominated by altruistic individuals it is susceptible to evolving toward a selfish one because a few non-cooperators will enjoy the benefits of altruism without paying its costs. Inside the group, non-cooperators will increase rapidly.

What if we imagine that cultural rather than genetic variation is the subject of group selection? Several common properties of cultural inheritance make it a much more plausible candidate for group selection than genes.

First, as we have already noted, if only a few influential teachers exist in each group, much variation between them is likely to be created. On the largest scale, the tendency of great ethical teachers like Moses, Christ, Confucius, and Mohammed, to put a stamp on a whole series of civilizations, is evidence that this effect is real (Cavalli-Sforza and Feldman, 1981).

Second, the conformist «When in Rome» imitation rule has a strong tendency to minimize the effects of migration on the variation between groups (Henrich and Boyd, 1998). Even if migrants are fairly common, so long as they

do not approach half the population of a group and are not disproportionately influential, resident culture will have an advantage over that of minority migrants; resident culture will be over-represented due to the conformity of old-stock individuals and second-generation migrants alike to the commoner norms. The assimilation of many immigrants to the USA to British-American culture is testimony to the power of this effect.

Third, the symbolic aspects of culture are a potent source of variation between groups (McElreath et al., 2003). Ritual, religious belief, and language isolate groups. Symbolic systems act to protect groups from the effects of migration, much as in the case of conformity, because people ordinarily tend to admire, respect, and imitate individuals displaying familiar symbolic traits. Cultural chauvinism is all but universal. Directly important aspects of culture, such as the ethical norms that are the basis for patterns of altruism and the basic form of social organization, are often embedded in richly symbolic belief systems.

Finally, selection on cultural groups can often be fairly rapid because cultural death and reproduction do not necessarily depend upon the biological death and reproduction of people. Defeated groups often are incorporated into the victorious society, or by friendly groups not involved in the conflict. In simpler societies, defeat in war typically results in more captives and refugees than dead. Successful societies also attract imitators, so that a culture could expand without any overt conflict at all (Boyd and Richerson, 2002). This form of cultural group selection is potentially very rapid. Successful societies also attract uncoerced immigrants who assimilate to a society and build its population relative to less successful groups (Boyd and Richerson, 2009).

Thus, human-scale societies may have evolved because peculiar properties of the cultural inheritance system lend themselves to group selection (Bell et al., 2009). Originally, processes like conformity may merely have functioned to reduce the risk of adopting foreign traits that are less likely to be useful than indigenous ones in an environment that varies from place to place. Group selection, and resulting indiscriminate altruism from the genetic point of view, may at first have been a by-product of adaptation to a spatially varying environment.

Once such a system begins to evolve, selection on genes will have a difficult time acting in opposition to the situation. To the contrary, social norms enjoining the punishment of deviations from social institutions would tend to select out genotypes that were resistant to following culturally prescribed behavior. Indeed, cultural environments can clearly exert strong coevolutionary forces on genes. The development of agriculture, for example, seems to have launched a wave of strong selection on genes (Hawks et al., 2007). Human «social instincts,» as Darwin called them, plausibly evolved by gene-culture coevolution. Primitive culturally transmitted social customs would select for the innate capability to follow social rules which would in turn allow the evolution of more sophisticated customs (Richerson and Boyd, 1999).

5. DISCUSSION

Human culture perhaps originated as an adaptation permitting rapid evolution in a noisy environment of the Pleistocene. The costs of culture include the complexity and clumsiness of a coevolutionary system in which genes and culture are often collaborators but sometimes antagonists. Our ultra-sociality is a sort of super-adaptation that underpins our ecological dominance of the earth, yet it is much less perfected than the ultra-sociality of the ants, bees, and termites. In one of our models of gene-culture interaction (Boyd and Richerson, 1985, pp. 194-197), each system of inheritance tends to pull behavior in the direction that favors its own transmission. As one system gets a small advantage, the other escalates to correct, and vice versa. This system comes to rest only when the cost of psychic pain becomes a significant selective disadvantage. This result is reminiscent of Sigmund Freud's model of humans painfully torn between an animal id and a cultural superego as the price of civilization.

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