Chapter 20
THE DARWINIAN THEORY OF HUMAN CULTURAL EVOLUTION AND GENE–CULTURE COEVOLUTION

Peter J. Richerson and Robert Boyd

In: *Evolution Since Darwin: The First 150 Years*. M.A. Bell, D.J. Futuyma, W.F. Eanes, and J.S. Levinton (eds). Sinauer.

Darwin realized that his theory could have no principled exception for humans. He put the famous teaser, "Light will be thrown on the origin of man and his history," near the end of *The Origin of Species*. If his evolutionary account made an exception for the human species, the whole edifice might be questioned. As the *Quarterly Review*'s reviewer of *The Descent of Man and Selection in Relation to Sex* probably the long-hostile and devoutly Catholic St. George Mivart) gloated, the *Descent* "offers a good opportunity for reviewing his whole position"—and rejecting it (Anonymous, or St. George Mivart, 1871).

Darwin apparently hoped someone else would apply Darwinism to the origin of humans. Lyell (1863), Huxley (1863), and Wallace (1864, 1869) all wrote on the subject, but their work was unsatisfactory because all three had reservations about a selectionist account of human mental evolution. Darwin's views on the origin of humans did not rely entirely on selection but had a supplementary set of mechanisms consistent with a selectionist account.

Darwin eventually wrote *The Descent of Man*, a rich and sophisticated treatment of evolution, even by contemporary standards. Yet, during his lifetime, Darwin's treatment of evolution generally and of human evolution specifically had many competitors (Bowler 1988). For example, Herbert Spencer and Darwin debated the relative importance of natural selection and inheritance of acquired variation (or acquired characteristics) for evolution of the mind (Richards 1987). Each admitted that both processes were important, but Darwin thought selection was dominant, and Spencer favored inheritance of acquired variation, substantially discounting the importance of selection. Furthermore, Spencer's emphasis of acquired variation reflected his belief that evolution was the "never-ceasing transformation of the homogeneous to the heterogeneous" (Richards 1987), while Darwin was ambivalent about progress.

Despite his prestige, Darwin convinced few of his contemporaries that he had the correct theory for the origin of the human mind. He most strongly influenced the pioneering psychologists, Romanes, Morgan, James, and Baldwin, but their importance in psychology waned after the turn of the century (Richards, 1987). No twentieth century social scientist was significantly influenced by *The Descent of Man*, and eminent social scientists are hostile to Darwinism, to this day. How could a theory generate so much controversy, yet for over a century, fail to attract enough critical work to test its worth? Can a satisfactory theory of the evolution of human behavior along Darwinian lines be fleshed out, or is the endeavor fatally flawed?

The first part of this essay is an attempt to understand what sort of theory of human cultural evolution Darwin proposed in *The Descent of Man*, which is difficult for two reasons. Although, Darwin wrote clearly, he lacked important theoretical tools, especially genetics. Believing in the inheritance of acquired variation and of habits, as a special case of it, the

modern distinction between genetic and cultural evolution was foreign to him. Yet, he distinguished more conservative traits that had evolved in "primordial times" from those that had influenced more recent evolution of civilizations. For the latter, Darwin often evoked cultural explanations, though he seldom used that word in its modern technical sense. Second, scientific readers of such an iconic scientist are liable to exploit his ambiguities, citing him selectively to favor their own agenda. Any reading of Darwin is certainly influenced by our own theory of gene–culture coevolution, which we sketch in the second part of the essay.

DARWIN'S PROBLEMS WITH HUMANS

THE EARLY NOTEBOOKS

Darwin's early M and N notebooks on *Man, Mind and Materialism* clarify the importance the human species played in his thinking about evolution (Gruber and Barrett 1974). In 1838, he wrote, "Origin of man now proved.—Metaphysics must flourish.—He who understand baboon would do more toward metaphysics than Locke" (Gruber and Barrett 1974: 281). These words were written during Darwin's most creative period, shortly *before* his first clear statement of natural selection in his notebook on *The Transmutation of Species*. The passage expresses hopeful enthusiasm rather than triumph. He was actively pursuing a materialistic theory of evolution and was convinced that humans would be included. Given the scope of the theory, it could hardly be otherwise. The promise and perils of understanding human origins and behavior remained unavoidable parts of Darwin's agenda. If correct, evolutionary theory could provide powerful tools to understand human behavior, and if humans were not understandable in the terms Darwin set out, perhaps there were deep, general problems with his theory.

WHO WOULD ADDRESS HUMAN EVOLUTION?

Darwin knew that most of his contemporaries considered his theory to be dangerously radical, and he long delayed publication of even the biological part of it (Gruber and Barrett 1974). He waited a dozen years after *The Origin of Species* to fulfill his promise to discuss humans. In the Introduction to the first edition of *The Descent of Man*, he discussed his fear that publishing his views on the subject would inflame prejudices against his theory.

Natural selection is a micro-scale process in which local environments favor variants within local populations. It is not an obvious candidate for a process to generate macroevolution. As Darwin confided to his N notebook in 1838:

> "Man's intellect is not become superior to that of the Greeks (which seems opposed to progressive development) on account of the dark ages.—Look at Spain now.—Man's intellect might well deteriorate.-((effects of *external* circumstances)) ((In my theory *there* is no absolute tendency to progression, excepting from favorable circumstances!))" (Gruber and Barrett 1974: 339).

We, along with others, assert that Darwin's skepticism about evolutionary progress and his failure to incorporate it into his theory of human evolution were major reasons why his theory was not popular among his contemporaries (Bowler 1986). Even Huxley favored Spencer's

account of acquired inheritance and progress in critical respects (Bowler 1993), though Darwin speaks elsewhere more favorably of progress (Richards 1988). Ambivalence toward progress has concerned evolutionary biologists to the present day (Nitecki 1988) and certainly was not the evolutionary motor for Darwin that it is for Spencer, as the N notebook quotation shows.

Why were Darwin's contemporaries so keen on progressive theories of evolution? Almost all Victorians feared the direction in which a thoroughly Darwinian theory of human origins would lead. As the *Edinburgh Review's* commentator on *The Descent of Man* remarked:

> "If our humanity be merely the natural product of the modified faculties of brutes, most earnest-minded men will be compelled to give up those motives by which they have attempted to live noble and virtuous lives, as founded on a mistake…" (Anonymous, or W. B. Dawkins, 1871: 195)

According to Burrow (1966), a significant segment of Victorian society was skeptical about traditional religion and enthusiastic about evolution. Even the idea that humans were descended from apes did not bother these secular, Christian intellectuals. However, they did believe that human morality required natural laws. If God's Law were dismissed by the scientific as superstition, then it was crucial to find a substitute in natural laws. Spencer's law of progress included the moral sphere, and he willingly drew moral norms from his theory (Richards 1987: 203-213). His theory filled the bill, while Darwin's was ambiguous.

DARWIN'S ARGUMENT

In many respects, Darwin's *The Descent of Man* is more typical of the late twentieth century than of Victorian times. Because progress was not the centerpiece, he did not rank human minds or their moral intuitions on a primitive–advanced scale. The extent to which Darwin subscribed to what is now called the doctrine of psychic unity is often overlooked. Even otherwise knowledgeable scholars believe that Darwin shared the widespread Victorian belief that the living races could be ranked on a primitive–advanced scale (Ingold 1986). Bowler (1993: 70) remarks "*The Descent of Man* takes racial hierarchy for granted and cites the conventional view that whites have a larger cranial capacity than other races." But Darwin's (1874: 81) discussion of the cranial data, some probably influenced by racist preconceptions, is tempered by a footnote, citing Paul Broca's hypothesis that civilization should select for smaller brain size due to the preservation of weak minded individuals who ought otherwise to have been eliminated by the hard conditions of uncivilized life. Darwin also refers in the same passage to the then-recent Neandertal find and to another archaeological sample showing that some ancients had very big brains. Darwin certainly draws no conclusions about racial hierarchy from these data. Alexander Alland (1985) cited Stephen Jay Gould to claim that Darwin shared the typical Victorian idea that the dark races are primitive. This reading of Darwin is mistaken! Even such knowledgeable authors as Desmond and Moore (2009) misunderstand *The Descent of Man* in this regard.

Darwin's first published views on humans appeared in his *Journal of Researches (Voyage of the Beagle*) several years after he had first formulated natural selection but more than a decade before *The Origin of Species* and 25 years before *The Descent of Man* were published. His descriptions of the Fuegans in the *Journal* are often cited as evidence of his typical Victorian

views on racial hierarchy. He did use purple Victorian prose to describe the wretched state of the Fuegans, whom he had observed on the *Beagle*:

> "These poor wretches were stunted in their growth, their hideous faces bedaubed with white paint, their skins filthy and greasy, their hair entangled, their voices discordant, and their gestures violent. Viewing such men, one can hardly make one's self believe that they are fellow-creatures, and inhabitants of the same world" (Darwin 1845: 243).

He goes on at length in this fashion, but this is the bait, not the hook of his argument. The passage on the Fuegans begins by describing the environmental rigors of Tierra del Fuego and ends by attributing the low nature of the people to their poor surroundings rather than to inherently primitive qualities:

> "We were detained here for several days by the bad weather. The climate is certainly wretched: the summer solstice was now past (passage is dated December 25) yet every day snow fell on the hills, and in the valleys there was rain. The thermometer generally stood at 45° but in the nights fell to 38° or 40°" (Darwin 1845: 242).

Darwin continued:

> "While beholding these savages, one asks, whence could they have come? What could have tempted, or what change compelled a tribe of men, to leave the fine regions of the North, to travel down the Cordillera or backbone of America . . . and then to enter on one of the most inhospitable countries within the limits of the globe?. . . (W)e must suppose that they enjoy a sufficient share of happiness, of whatever kind it may be, to render life worth living. Nature by making habit omnipotent, and its effects hereditary, has fitted the Fuegans to the climate and the productions of this miserable country" (Darwin 1845: 246-247).

The argument is consistent with his idea that progress could come only from favorable circumstances. Thus, he is saying that any humans forced to live under such conditions, with such limited technology, would soon behave similarly. Note the reference to hereditary habits; this concept figures large in his mature ideas on human evolution.

Darwin routinely condemned White Christians' morals, for example, when he discussed slavery and the genocidal Argentinean war against the Patagonian natives in the *Journal* (Darwin, 1845). He ends the story of an Indian's daring escape:

> "What a fine picture one can form in one's mind—the naked, bronze-like figure of the old man with his little boy, riding like a Mazeppa [Ukrainian Cossack hero] on a white horse, thus leaving far behind him the host of his pursuers!" (Darwin 1845: 124).

His paean against slavery begins:

> "On the 19th of August, we finally left the shores of Brazil. I thank God I shall never again visit a slave country. To this day, if I hear a distant scream, it recalls with vivid painfulness my feelings when, passing a house near Pernambuco I heard the most pitiable moans, and could not but suspect that some poor slave was being tortured, yet knew that I was as powerless as a child even to remonstrate" (Darwin 1845: 561-563).

And ends:

> "It makes one's blood boil, yet heart tremble, to think that Englishmen and our American descendants, with their boastful cry of liberty, have been and are so guilty: but it is a consolation to reflect that we have made a greater sacrifice than ever made by any nation to expiate our sin" [Britain freed all colonial slaves in 1838] (Darwin 1845: 561-563).

Gruber and Barrett (1974) note that Darwin and his entire family shared a deep antipathy to slavery, which was not widely accepted by his contemporaries. This led, for example, to a furious argument with Captain Fitzroy on the *Beagle*. Darwin certainly thought moral progress was possible and that Europeans had achieved some notable advances, counting among them the rule of law and the enactment of just laws, including the end of slavery in the British Empire. Darwin's view of progress does not imply a racial hierarchy that would justify extermination or enslavement of the so-called lower races by the higher! We find it odd that contemporary social scientists fail to recognize that Darwin's politics, while not often as explicit as in his views on slavery, were far to the left for his day and not so different from those of today's academic left (Sulloway 1996; Desmond 1989; Richards 1987).

Of course, Darwin's (1874) best efforts on human evolution and behavioral diversity appear in his mature work, *The Descent of Man*. In Chapters 3 and 4, both entitled "Comparison of the Mental Powers of Man and the Lower Animals," he summarizes the issue: "There can be no doubt that the difference between the mind of the lowest man and the highest animal is immense" (Darwin 1874: 170). In these chapters, he struggles with the problem posed by this gap for the gradual emergence of humans from apes. His task would have been easier if he had filled the gap with the living human races, as so many of his contemporaries did. He solved the problem by proposing hypothetical continuities across the gap (as in the *Expression of Emotion in Man and Animals*) rather than bridging it with living savages.

Darwin's argument is clear in Chapter 5 of *The Descent of Man,* "On the Development of the Intellectual and Moral Faculties During Primeval and Civilized Time." In contrast to Wallace, Darwin believed that natural selection produced human mental and social capacities in *primeval* times. In particular, he posits that the foundation of human morals arose by selection on group differences:

> "It must not be forgotten that although a high standard of morality gives but a slight or no advantage to each individual man and his children over other men of the same tribe, yet that an increase in the number of well-endowed men and an advancement in the standard of morality will certainly give an immense advantage to one tribe over another. A tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to aid one another, and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection" (Darwin 1874: 178-179).

He credits "savages" with sufficient loyalty to their tribes to motivate self-sacrifice to the point of death and with the "instinct" of sympathy. His objective was to ensure that the reader understands that these moral "sentiments and faculties" are primeval and shared by the living savage and the civilized alike. The importance of sympathy in Darwin's evolutionary ethics is noteworthy, as is its role in his detestation of slavery. He cites Adam Smith's (1790) *Theory of Moral Sentiments* on the importance of sympathy. He emphasizes customs acquired by imitation to explain further moral advances. He spends several pages reviewing the tendency of advancing civilization, if anything, to weaken natural selection, and the evidence that retrogressions are common. He summarizes the argument regarding morality:

> "I have already said enough, while treating of the lower races, on the causes which lead to the advance of morality, namely the approbations of our fellow men-the strengthening of our sympathies by habit—example and imitation—reason—experience, and even self-interest—instruction during youth, and religious feelings" (Darwin 1874: 185-186).

And, in current circumstances:

> "With highly civilized nations, continued progress depends in a subordinate degree on natural selection. . . . The more efficient causes of progress seem to consist of a good education during youth while the brain is impressible, and of a high standard of excellence, inculcated by the ablest and best men, embodied in the laws, customs, and traditions of the nation, and enforced by public opinion" (Darwin 1874: 192).

Darwin's list of moral advances by the "lower races" is virtually identical to those of the highest. *Primeval* evolution endowed living savages with the same social instincts as civilized men, enabling the same improvement from "good education" and the rest. Darwin attributed the progress of morality to the strengthening of our sympathies. As we have seen in the *Journal of Researches*, on the basis of sympathy, he indicted Argentineans for killing Indians and Brazilians and Americans for holding slaves, while others defended such acts on the basis of loyalty to one's race (Richards 1987: 599-601).

The climax of Darwin's argument is in *The Descent of Man*, in Chapter 7 "On the Races of Man." He considers the two hypotheses that the races are sufficiently distinct to be different species or are alike in all-important organic respects. First, he outlines all the evidence in favor of the different species hypothesis (Darwin, 1874: 224-231)—his dispassionate tone allows the careless reader to believe that Darwin favors this alternative. However, he immediately demolishes the separate species argument in favor of the trivial differences alternative:

> "Although the existing races differ in many respects, as in color, hair, shape of the skull, proportions of the body, etc., yet, if their whole structure be taken into consideration, they are found to resemble each other closely on a multitude of points. Many of these are so unimportant or of so singular a nature that it is extremely improbable that they should have been independently acquired by aboriginally distinct species or races. The same remark holds good with equal or greater force with respect to the numerous points of mental similarity between the most distinct races of man. The American aborigines, Negroes, and Europeans are as different from each other in mind as any three races that can be named; yet I was constantly struck, while living with the Fuegans on board the "Beagle," with the many little traits of character showing how similar their minds were to ours; and so it was with a full-blooded Negro with whom I happened once to be intimate" (Darwin 1874: 231-240).

The contrast between Darwin and others, like Ernst Haeckel, who really believed that "natural men are closer to the higher vertebrates than to highly civilized Europeans," was stark (Richards 1987: 596). The behavior of people in various places does differ substantially. Darwin's explanation of these differences in Chapter 7 of *The Descent of Man* downplays differences that people today tend to attribute to genes in favor of those attributed to culture:

> "He who will read Mr. Tylor's and Sir J. Lubbock's interesting works can hardly fail to be deeply impressed with the close similarity between the men of all races in tastes, dispositions and habits" (Darwin 1874: 238).

Darwin's favorable citations of Tylor, the founder of cultural anthropology and an important nineteenth century defender of the Enlightenment doctrine of the psychic unity of all humans, are surely significant and consistent with his sympathy for savages and slaves. Tylor's (1871) postulate of the organic similarity but difference in customs is clear: "For the present purpose it appears both possible and desirable…to treat mankind as homogeneous in nature, though placed in different grades of civilization" (Tylor 1871: 7).

Darwin sometimes uses identical contrast:

> "As it is improbable that the numerous and unimportant points of resemblance between the several races of man in bodily structure and mental faculties (I do not

here refer to similar customs) should all have been independently acquired…" (Darwin 1874: 239).

Here Darwin suggests that the main explanation for differences between races is customs, not organic differences; though seeing heritable variation everywhere, Darwin would not treat humans as homogeneous. Darwin's position is difficult to understand because of his concept of inherited habits (see previous quote about the Fuegans). In the preface to *The Descent of Man*'s second edition, Darwin reiterated his commitment to the inheritance of acquired variation:

> "I may take this opportunity of remarking that my critics frequently assume that I attribute all changes of corporeal structure and mental power exclusively to natural selection of such variation as are often called spontaneous; whereas, even in the first edition of the "Origin of Species," I distinctly stated that great weight must be attributed to the inherited effects of use and disuse, with respect both to the body and the mind" (Darwin 1874: 3-4).

Darwin considered "inherited habits" to be among the most important forms of the inherited effects of use and disuse. Custom, good education, imitation, example of the best men, and his other versions of culture would tend to become hereditary. He divides traits into more and less conservative poles. Anatomy and basic features of the mind would be influenced little by the inheritance of acquired variation and mainly by selection over long spans of time; in modern terminology, these traits are highly heritable. The more labile traits are quite sensitive to environmental and cultural influences. Although they become inherited, they are susceptible to rapid remodeling by acquired habit. This feature of his theory is generally erroneous, though the discovery of transgenerational transmission of epigenetic elements has given this old idea, new legs (Griffiths 2003; Jablonka and Raz 2009). Indeed, some cultural traits are relatively conservative (Nisbett 2003) and fit Darwin's concept of inherited habits. For example, historical relationships can be traced back 6000–8000 years in languages (Atkinson and Gray 2006). Similarly, many Holocene stone tool assemblages dominated by simple expedient flakes struck from cores, as were the earliest known stone tools about 2.6 million years ago (Haines et al. 2004). The genetics of the early twentieth century were more conceptual than practical, as illustrated by its intractable quarrels over nature versus nurture. Contemporary advances in genomics are furnishing the tools to solve the difficult riddle of the interactions between inheritance and development.

Another problem with interpreting Darwin arises from his determination to minimize qualitative differences between humans and other animals. He was wary that his theory would encounter unbridgeable gaps that would imply unique processes applying only to human evolution, inevitably creating problems for his general theory. *The Descent of Man* reports many observations of animal behaviors requiring nearly human moral and intellectual faculties. Modern behavioral research shows that Darwin exaggerated the capacities of animal minds.

In particular, Darwin imagined that the ability of animals to modify their behavior by imitating others is similar to that of humans. Darwin illustrated this point with his own observations of bees imitating each other. When he observed bumble bees cutting holes in the

sides of bean flowers to steal nectar, he attributed later observations of honeybees using the same technique to imitation, with the bees using mental faculties analogous to humans (Galef 1988). Galef and other modern students of animal imitation have demonstrated such effects in many vertebrates and even some invertebrates, but nothing that approaches human capabilities for the cumulative cultural evolution of complex traditions (Whiten and van Schaik 2007). Young children are considerably better imitators than adult hand-reared chimpanzees, with a long history of being rewarded for human-like behaviors (Tomasello 1996; Whiten and Custance 1996). Accurate imitation revolutionizes social learning by increasing the number and sophistication of behaviors acquired (Boyd and Richerson 1996). Individual learning is relatively slow, costly, and produces behaviors only as sophisticated as one animal can invent. Accurate imitation permits cultural sophistication to increase through a succession of innovators, each contributing to the gradual cultural evolution of complex behaviors. Even technology as simple as a stone-tipped spear contains numerous design components that evolved step-by-step. Thus, sophisticated imitation is part of the "great gulf" that Darwin admitted separates humans from their living hominid relatives. To bridge the great gulf, Darwin tended to raise up non-humans, not cast down human races. While he is sometimes said to have biologized humans, he is more accurately guilty of having humanized animals.

THE TWENTIETH CENTURY

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

After several decades in "eclipse" (Bowler 1983), Darwin's ideas on evolution were incorporated into the foundations of biology during the first half of the twentieth century. By contrast, most leaders of the emerging social sciences virtually ignored ideas in *The Descent of Man* (Ingold 1986). In psychology and economics, for which detailed histories have been written, this was due largely to idiosyncratic events in the careers of the most prominent Darwinians (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 indicate. Social Darwinism was more in the spirit of Spencer than of Darwin. Most sociologists and anthropologists rejected 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 pioneers in the social sciences were eager to differentiate their disciplines from biology and downplay its significance. For example, the pioneering student of imitation, Tarde (1903), excluded "biological" considerations in his theory and was apparently unaware of the parallels between his ideas and those in *The Descent of Man*. Still, in 1900, the early psychologists William James, Lloyd Morgan, and James Baldwin all espoused Darwinian theories of psychology (Richards 1987).

Baldwin (1895) particularly reconciled Darwinian concepts with new findings in biology. First, he elaborated a complex theory of imitation based on observations of his own children, noting the emergence of powerful capacities for imitation in late infancy. Second, 5 years before

the rediscovery of Mendel, Baldwin 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" (Baldwin 1895: 294).

Third, Baldwin envisioned a complex interplay between biology and imitation, as the previous quote suggests. The capacity for imitation is inherently biological and emerges late in the child's first year, as more detailed recent studies have shown (Tomasello 1999, 2008). Although the impulse to imitate may override pleasure and pain, these biologically based perceptions typically affect behavior and what others imitate. In contrast, learned or imitated behaviors could lead humans (and other animals with adaptive phenotypic flexibility) to persist in environments to which they are poorly adapted biologically. Subsequent natural selection acting on heritable variation can eventually transform learned or imitated behavior into innate behavior. Baldwin termed this effect "organic selection," and it is generally known today as the "Baldwin Effect." It was actually discovered independently by Baldwin, T. Hunt Morgan, and Henry Fairfield Osborn (Richards 1987).

As will be seen, all of Baldwin's ideas resonated with late twentieth century theories of gene–culture coevolution. However, they had no immediate impact on the rapidly forming social sciences because few social scientists espoused a Darwinian perspective. The sociologist Albert G. Keller taught a version of social evolution that was truer to the Darwinian tradition than to that of his mentor Sumner, but his influence was negligible (Campbell 1965). The theories of some very influential pioneers contained elements of Darwinian processes, but they were not subsequently developed. For example, Turner (1995) argues that Durkheim's (1893) theory of the division of labor was highly Darwinian at its root, but this feature stimulated no subsequent interest.

Specific research agendas developed with the new social sciences after the turn of the century. For example, psychologists strove to sever their roots from philosophy and embrace rigorous experimental methods. Baldwin, who was a good experimentalist and observationalist in his younger days, always had a large philosophical agenda and turned increasingly toward philosophy, while his younger colleagues turned sharply in the opposite direction. His influence waned when his arrest in a Black house of prostitution ruined his career in the United States (Richards 1987). In anthropology, Franz Boas opposed all forms of theorizing, arguing that field workers should have minimal preconceptions when collecting ethnography (Harris 1979). Similarly, institutional economists, particularly Thorstein Veblen, at the turn of the twentieth century were sophisticated evolutionists, but their influenced waned and was finally extinguished (Hodgson 2004). Veblen's later career was also plagued by scandal. He had an unhappy and stormy marriage punctuated by several affairs and eventually a divorce. These contretemps cost him faculty positions at the University of Chicago and Stanford University. Physics rather than biology became the science for economists to emulate.

Another problem was that Darwin's view of evolution ebbed in the early twentieth century (Bowler 1983), just as the social sciences were emerging. When the pioneering geneticists at first discovered mutations with large effects, they rejected the Darwinian principle that selection acts mostly on continuous variation. Darwinian theory and genetics were not reconciled until Ronald Fisher's famous paper in 1918 validated the importance of Darwinian concepts in evolutionary biology (Provine 1971).

The social and biological sciences continued to diverge until mid-twentieth century. Their relationship was largely limited to sterile nature–nurture debates (Cravens 1978). Attempts to heal or at least minimize this rift included Dobzhansky and Montagu's (1947) influential argument that biology produced the substratum for human culture and that culture and biology form a unique, transcendent coevolving complex. Dobzhansky's (1962) book *Mankind Evolving* expands on this theme without ever really specifying how the coevolution works or precisely what transcendence means in this context. The position taken by Dobzhansky and Montagu (1947) was sort of a peace treaty that allowed the biological and social sciences to independently pursue their own agendas, ignoring whatever inconsistencies arose. Individuals such as Lorenz (1966) and Jensen (1969), who broke this peace in the 1950s and 60s, were unsophisticated theorists 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 the progressive evolutionary theories of Spencer. In essence, no one in the mid-twentieth century followed up late nineteenth century ideas implicit in *The Descent of Man* to create a sophisticated theory of cultural evolution that incorporated the Darwinian theory of genetic evolution. Unification of the social sciences with each other and with biology remains a work in progress (Gintis 2007).

DONALD CAMPBELL'S "VICARIOUS FORCES"

Donald Campbell, a polymath psychologist, was the first twentieth-century scientist to tackle the problem of cultural evolution seriously. He made three important arguments. First, in several papers (e.g., Campbell 1960), he proposed that all knowledge processes are related to organic evolution, captured by the idea, "blind variation and selective retention." Campbell (1965) introduced the concept of *vicarious forces* to characterize the relationship between organic evolution by natural selection and individual learning. Assuming inheritance of acquired variation, psychological forces would shape cultural variation, much as Darwin thought sympathy molded moral progress. Campbell contended that these forces vicariously act as surrogates for natural selection, because they arose by natural selection to shape phenotypes adaptively, as Darwin had argued. Second, Campbell (1965) argued that Darwinian theory should apply to any system of inheritance, including culture. Third, his (1975) article carefully distinguished Darwinian from progressive evolution, showing that there is no material basis for a concept of progress. He asserted that progressive evolutionary theory was simply a description of history without any causal process, given that Spencer's homogeneity-to-heterogeneity mechanism had been discarded.

Campbell's approach emphasizes the interplay of forces that drive cultural evolution. In genetic evolution, the most important forces to change gene frequencies are mutation, genetic drift, gene flow, and natural selection, making organic evolution a process based purely on

random variation and selective retention. Cultural evolution must be subject to analogs of these forces as well as to several vicarious forces. Not only are humans subject to natural selection, but they also change their culture by making choices as they learn. Some of the rules for making choices are inherited genetically, and then affect cultural evolution. For example, the distribution of sensory receptors in the nose and mouth may influence whether potential food items are considered pleasant or noxious. Choices of food items by individuals will in turn drive the evolution of a society's cuisine. One might expect vicarious selectors for food items to favor nutritious, healthful diets, because they have been shaped by natural selection, but they may be exploited by items like addictive drugs or overridden by cultural preferences (e.g., the consumption of peppers, which stimulate pain sensors). Culture might also drive organic evolution; for instance, evolution of adult milk-sugar (lactose) digestion has evolved within the last few thousand years in milk-consuming human populations (Simoons 1978). Simoons apparently discovered the tip of an iceberg (Hawks et al. 2007), as agricultural has greatly changed the diets, disease exposure, and social life of many human populations, driving a major coevolutionary response over the past 10,000 years.

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 was apparently unaware of the late nineteenth century Darwinian social scientists, such as Baldwin and Veblen. Subsequently, several other evolutionary research programs applied to humans followed pioneering contributions by Cavalli-Sforza and Feldman (1973), E.O. Wilson (1975), and Alexander (1979). They became heavily politicized in the famous sociobiology debate (Segerstråle 2000). Today, Darwinian social science is tolerated, if reluctantly in some quarters, and is a very active field spread across the social sciences and human biology (Laland and Brown 2002). The importance of cultural evolution in human organic evolution is an important debate in the field. One view 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 these parasites' support. A third view, to which we subscribe, is that in humans, genes, and culture play more or less equally important roles in a coevolutionary system.

A THEORY OF GENE–CULTURE COEVOLUTION

DARWINIAN PRINC IPLES APPLIED TO CULTURAL EVOLUTION

The way that culture might make us theoretically interesting, as opposed to merely taxonomically unique, is if it 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. 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 is that learning by imitation or teaching is analogous to acquiring genes from parents (Baldwin 1895; Campbell 1965, 1975). In both cases, a determinant of behavior is transmitted from one individual to another, and it is

important to consider the population as a whole in analyzing either. As individuals acquire genes or culture, they sample a large population of potential parents and cultural models. Then, evolutionary processes operate on individuals, favoring some cultural and genetic variants and disfavoring others. A population's next generation typically differs from the previous one. As many generations pass, changes accumulate and evolution occurs. Population genetic theory is a formal system that scales up effects on individuals in the short run to longer-term changes within populations. Its basic methods are equally applicable to culture, and evolutionary theory should function in the social sciences in a manner similar to that which it does in biology (Cavalli-Sforza and Feldman 1981). This analogy undoubtedly caused Darwin's failure to make as sharp a distinction between genes and culture as twentieth century biologists did. Both inheritance systems are historical population processes that frequently result in adaptive diversification of behavior.

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 are required to make genetic models mimic culture, and cultural models need to be linked with genetic models to understand the coevolution of genes and culture. These tasks have only begun, but fascinating processes have already been uncovered. Consider a few of the main differences between genes and culture and their evolutionary implications (reviewed by Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Richerson and Boyd 2005; Mesoudi 2007; Henrich 2008).

First, an individual is not restricted to sampling just their two biological parents to acquire a cultural trait. Dozens of other people in one's social network may be surveyed as well, and the one individual whose behavior seems best by some standard is chosen as the source of a cultural variant. This process can give inordinate weight to teachers, leaders, or celebrities and generates variation among groups much more rapidly than genetic evolution can.

Second, we are not limited to imitating people of our parental generation; peers, grandparents, and even ancient prophets can influence cultural evolution. Imitating peers, in effect, shortens the generation time in cultural evolution. Traits spread among peers may be harmless fads, important skills, or pathological behaviors. Hunt and Chambers (1976) studied heroin addiction, which spreads mostly among close friends. Parents observe that kindergarten children bring home viruses and bad habits alike! These pathways for cultural transmission likely have not been closed by selection on genes or culture, because the cost of catching a cultural pathogen is outweighed by the benefit of adaptive vicarious selectors to acquire useful traits from people other than one's parents.

Third, individuals acquire and discard items of culture throughout life. One is stuck with one's genes, though *expression* of genes can be modified throughout life. In contrast, culture is acquired gradually, traits acquired early can influence those adopted later, and later enthusiasms displace previous traits. The flexibility to pick and choose allows great scope for vicarious selection in cultural evolution and creates what we call "biases" (Richerson and Boyd 2005) and Cavalli-Sforza and Feldman (1981) called "cultural selection."

Fourth, variations acquired during an individual's lifetime are readily passed on to others by coupling the common animal ability to learn to imitation. Animals without imitation lose

what the parents have learned, and the young must relearn each generation. With culture, the results of learning in one generation can be passed on to the next and accumulate over generations. Coupling individual learning to the cultural system allows new non-random variation to be introduced into the cultural system.

Exploring these differences has just begun. Culture is about as complex as genes, making it a tremendous task. No one has devised a precise comparison, but the number of words a high school graduate knows may be a few tens of thousands—that is, about the same as the number of protein-coding genes in our genome. One hundred fifty years after publication of *The Origin of Species,* evolutionary biology remains a vibrant field; cultural evolution is perhaps a half-century behind.

EVOLUTION OF HUMAN UNIQUENESS

Formal models of cultural evolution can be used to study the evolution of the cultural system itself. There are three major differences between humans and our close primate relatives that are basic to understanding human evolution, using the Darwinian framework. Humans have (1) a greater capacity for imitation and the associated massive use of culture; (2), much symbolism and stylistic variation (e.g., many languages) of no obvious practical use; and (3) larger to significantly larger social groups, with relatively high levels of cooperation, coordination, and division of labor. How and why have these differences arisen? Theoretical models can provide some interesting tentative answers.

ESTIMATES OF THE BASIC BENEFITS AND COSTS OF A MASSIVE CAPACITY FOR CULTURE

Why do humans have such a large capacity for culture? The standard answers are 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 humans made the breakthrough to a qualitatively superior mode of cultural adaptation. Landau (1991) showed that all accounts of human origins, *even by professional paleo-anthropologists*, have the structure of folk hero stories. The human species had to perform tasks and overcome obstacles before reaching fully modern form. Even such deep-dyed Darwinians as Lumsden and Wilson ~~(1981: 330–331)~~ remarked that humankind "overcame the resistance to advanced cognitive evolution by the cosmic good fortune of being in the right place at the right time~~.~~" and that "~~T~~the eucultural (complex human culture) threshold could at last be crossed" (Lumsden and Wilson 1981: 330–331). The breakthrough hypothesis is plausible if we assume that special, costly cognitive machinery is necessary to imitate complex traditions (Boyd and Richerson 1996). However, such capacities could not easily increase when they are rare, even if complex traditions had been a great adaptive advantage. In other words, mutations that create the ability to learn complex culture could not be advantageous until such complex traditions already existed!

Comment [LA1]: If you want to make it one citation, we need to have one sentence. Edit okay?

Given the great span of time available, the absence, until recently, of complex capacities for imitation suggests the hypothesis that the costs of elaborate cultural capacity usually outweigh the benefits. If there are intrinsic barriers to the evolution of such capacity, it is surprising that complex culture has only evolved once in the history of life. Perhaps Darwin's

"favorable circumstances" recently create the potential for the benefits of a large culture capacity to outweigh its costs.

Simple evolutionary models that link the capacity for individual learning to a capacity for imitation can be used to model the inheritance of acquired variation. They illustrate how culture can have real advantages in some environments (Boyd and Richerson 1985). Suppose individuals inherit some economically important trait by imitating their parents—for example, knowing how much subsistence to derive from hunting versus gathering plants. Individuals must combine traditional knowledge acquired culturally with that acquired by their own experience. We assumed that they use a weighted average. If tradition and individual learning were equally important, the traditional diet is 50% animals, but experience indicated that 90% was best. Then, individuals might end up collecting enough plants to make up 30% of the diet in the first generation, 20% in the second, 15% in the third, and so on. We also investigated similar models in which genes and learning, but not culture, were used to decide what to do.

Under what circumstances should cultural tradition be emphasized over individual experience plus genetic transmission? The answer depends upon two interacting factors: how the environment is changing and the economics of information acquisition and transmission. We assumed that the genetic system is less prone to random transmission errors (mutation) than is cultural transmission and that individual learning is fairly costly or error prone (closely related variables, since learning could always be improved with more time and effort). If the environment is changing very slowly, a fixed genetic rule is superior to any combination of learning and imitation. Selection acting on a conservative inheritance system can track slow environmental change, and the greater errors of learning and imitation are a fitness burden. In contrast, in very rapidly changing environments, any form of transmission from parents is useless—their world is simply too different from their children's. Instead, individuals do best by depending entirely on experience. In intermediate environments, some mixture of individual and social learning is typically the most adaptive system. Culture's greatest advantage is in environments that are changing substantially over tens of generations but not too rapidly within any one generation. By making individual learning cumulative, a cultural system of inheritance can track changing environments more rapidly than genes while reducing the need for costly individual learning.

Assuming that individual learning is costly compared to imitation, the model's results recover Darwin's intuition: inheritance of acquired variation has distinctive advantages in variable environments. Empirical support exists for this result. The origin of culture in humans is associated with the increasingly fluctuating climates of the last few million years (deMenocal 1995; Potts 1996; Vrba et al. 1995; Richerson et al. 2009). 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 interrupted by numerous, short warm intervals of about 1,000 years' duration. The last glacial was more variable than the Holocene at the 10-year limit of resolution in the ice core record, depending upon depth in the core (Ditlevsen et al. 1996). Similar but less intense variation also occurs in three earlier glacials (Martrat et al. 2007). According to our simple model, individual and social learning might be advantageous in this sort of world. Culture may be as much a means of coping with the

deteriorating Pleistocene environment as a cosmic breakthrough of progressive evolution. As more and longer high-resolution cores become available, the climate hypothesis will be tested with greater rigor. For example, it predicts that hominin brain size increases will follow increases in millennial and sub-millennial climate variation. Whether or not this prediction is accurate remains to be seen.

However, if our model is correct, many animal lineages should have become increasingly cultural during the Pleistocene. In fact, many bird and mammal lineages with simple social learning systems manifested trends for increasing brain size when environmental variability increased during the Miocene to the late Pleistocene (Jerison 1973). Brain size in both birds and primates is associated with innovative behavior and social learning. Thus, 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 Neandertals and the anatomically modern, tropical African humans apparently both evolved very large brains after diverging 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). Richerson et al. (2009) argue that small population size of both species probably limited their cultural complexity. Small, isolated living populations also produce very simple toolkits (Henrich 2004). Perhaps much inheritance of acquired variation in many species is carried by epigenetic inheritance systems (Jablonka and Raz 2009). Suppose that specific capacities are necessary for the transmission for complex culture. If these capacities are rare, no complex culture will exist ~~to be acquired~~ for individuals to acquire, and thus these capacities will provide no adaptive advantage. If so, some piecemeal innovations might have allowed the human lineage to reach a threshold frequency at which the capacity would be advantageous to the individual. What costs might these piecemeal innovations have incurred? Inferring the causes for any lineage's unique evolutionary history is challenging (Nitecki and Nitecki 1992), but science must explain why only the human species has complex culture, despite frequent occurrence of simple social learning in other species. Washburn (1959) proposed that bipedal locomotion made hands free to specialize for tool-making, setting humans on the path to the capacity for complex culture.

Other Complex Benefits and Costs of a Massive Capacity For Culture

Further clues about 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 multiple models is useful to find a better one to imitate. High frequency of a trait among replicate models often indicates a successful trait. As in the model for simple learning plus imitation, these advantages are most useful in variable environments.

On the cost side, imitating people other than parents exposes individuals to the possibility of acquiring pathological cultural traits. Deleterious cultural traits are unlikely to evolve if cultural transmission follows the conservative parent-to-child pattern. Few heroin addicts, for instance, survive to raise children. Natural selection acts against such cultural variants, but addicts can attract peers before the most harmful consequences emerge. With non-parental transmission, natural selection *on cultural variation* can favor the evolution of cultural fragments that act much like viruses, as in Dawkin's famous selfish meme idea (Goodenough and Dawkins

1994; Blackmore 1999). Much as microbial pathogens invade the body by attaching to receptor molecules on the host cell's surface, pathological cultural variants often subvert biases that normally act to favor adaptive behavior. Addictive drugs subvert the pleasure systems in the brain. Natural selection acting on parentally transmitted culture and genetic variation alone could reduce the chances of acquiring such traits, but only by sacrificing the potential benefits from imitating superior non-parents. Parental advice, formal instruction, and mass media propaganda are cultural defenses against pathological cultural variants, just as medicines augment defenses against pathogens.

A massive, sophisticated system of culture is an excellent adaptation; witness the spread of humans from tropical homeland into the Arctic and New World. But loosely speaking, the coevolutionary complexity of coordinating two inheritance systems means that the cultural system even now is far from perfect. We pay for cultural flexibility with a susceptibility to diverse cultural pathologies. *Humans are built for speed, not for comfort*.

The problems created by a second inheritance system are not necessarily as obviously harmful as heroin addiction. Many otherwise puzzling patterns of human behavior may be a by-product of the cultural system. For example, many wealthy societies have recently experienced sustained reductions in birth rates that are now often below replacement (Coale and Watkins 1986). Borgerhoff Mulder (1987) and Irons (1979) have argued based on case studies in East Africa and Iran, respectively, that wealth is efficiently converted into children in traditional rural societies, as we would expect from fitness considerations. Why do modern and modernizing societies behave so contrary to the expectation that wealth should be translated into greater fitness?

Such societies have expanded non-parental routes to transmit culture, which should multiply the pathways by which pathological cultural variants can spread (Newson et al. 2007). (We mean pathological from the perspective of Darwinian fitness and do not mean to suggest that the demographic transition is 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, such as teaching, are influential in socializing the young. Competition for these roles is keen, and preparation for them imposes delayed reproduction. Those who sacrifice marriage and a large family for a career they value are likely to succeed and to influence their pupils', subordinates', and employees' values and aspirations. Western society with "careers open to talent" seems to have fostered the spread of low fertility norms through cultural means of transmission (Newson and Richerson 2009).

Symbols

Do models of cultural evolution offer insights into the existence of elaborate, apparently functionless symbols as costumes, artistic creations, and complex supernatural belief systems, which, along with other aspects of culture, distinguish the human species? Social groups are usually symbolically marked. For example, modern research universities, bastions of rationality, have a seal, a motto, elaborate graduation rituals, and sports teams that engage in ritualized combat. Even the faculty exhibits remarkable affection for the symbols and rituals of academia. Campbell (1969) noted the similarity of academic disciplines to ethnic groups.

To investigate this problem, we 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 benefit from imitating 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 can serve as an adaptive marker (McElreath et al. 2003; Boyd and Richerson 1987). In a spatially variable environment with migration, using symbolic criteria can reduce imitation of individuals with inappropriate cultural adaptations.

THE ORIGIN OF COOPERATION AND COMPLEX SOCIETIES

The ethnic unit, like human culture, has no close parallel in other species. Altruism in large sophisticated societies of bees, ants, and termites has classically been attributed to inclusive fitness (Hamilton's 1964). The workers in canonical insect colonies are all siblings, and each colony contains only few reproductives. African naked mole rats, the mammal with the most complex social organization aside from humans, form colonies comprising a reproductive queen and numerous 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 may be important in many species (Hölldobler and Wilson 2009). Among our primate relatives, cooperation appears to be largely restricted to close relatives and to partners engaging in reciprocal altruism.

To judge from simple contemporary societies (Johnson and Earle 2000), Upper Paleolithic societies comprised three levels of social organization: the family, the co-residential band, and sets of bands that routinely intermarried, spoke a common language, and shared a set of myths and rituals. Members of this largest unit, often called a tribe, maintain relatively peaceable relations with each other and routinely cooperate. Again, by analogy with simple contemporary societies, there was probably no overall formal leader or council. Rather, forceful, able men probably acted as semiformal headmen of bands. Inter-band affairs were probably regulated by *ad hoc* negotiations dominated but not controlled by the headmen.

Several hypotheses have been proposed to explain human cooperation. Alexander (1987) supposed that human intelligence allows extensive reciprocal altruism and indirect reciprocity involving assistance to others who may be several steps removed from anyone who can help you in return. However, it is difficult to scale 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 group selection (Panchanathan and Boyd 2004). Something like Darwin's proposal for selection among tribes perhaps accounts for human abilities to cooperate (Richerson and Boyd 1999; Sober and Wilson 1998).

Most evolutionary biologists, including Darwin and Hamilton, are skeptical that selection between groups of unrelated individuals is effective (Williams 1966; but see Wilson and Wilson 2007). As with any form of natural selection, group selection must proceed through the differential survival or reproduction of entities that differ for heritable traits. Reproduction of groups must ordinarily be slower than that of individuals, and group death must be infrequent compared to individual death. Migration among groups can also erode differences among them. Any successful group dominated by altruistic individuals may evolve toward selfish qualities

because non-cooperators enjoy the benefits of altruism without paying its costs. Inside the group, non-cooperators will increase. Neighboring human societies have far more cultural than genetic variation (Bell et al. 2009), suggesting that the cultural inheritance system is a likelier target for group selection.

Several properties of cultural inheritance make it more responsive to group selection than genes. First, as already noted, a few influential teachers in each group can create great variation among them. The impact of great ethical teachers, like Moses, Christ, Confucius, and Mohammed, on a whole series of civilizations, is evidence for the power of this effect (Cavalli-Sforza and Feldman 1981).

Second, the tendency of newcomers to conform will minimize the homogenizing effects of migration on variation among groups (Henrich and Boyd 1998). As long as migrants are a minority and are not disproportionately influential, resident culture will limit the cultural impact of minority migrants. The assimilation of many immigrants to the United States and to British–American culture is testimony to the power of this effect.

Third, cultural symbols are a potent source of variation among groups (McElreath et al. 2003). Ritual, religious belief, and language isolate groups. They 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, and important aspects of culture, such as the ethical norms, are often embedded in rich symbolic belief systems.

Finally, selection on cultural groups can be rapid because cultural death and reproduction do not depend upon biological death and reproduction. Defeated groups are often absorbed by the victors or by other friendly groups. In simpler societies, defeat in war typically produces more captives and refugees than dead. Successful societies also attract imitators and uncoerced immigrants who assimilate into a society and build its population (Boyd and Richerson 2009), so a culture could expand without any overt conflict at all (Boyd and Richerson 2002). Cultural group selection may thus be rapid.

Once such a system begins to evolve, selection on genes will have a difficult time opposing cultural evolution. Practices that penalize deviation from social conventions would tend to exclude genotypes that resist conformity to culturally prescribed behavior. 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). Similarly, 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).

DISCUSSION

The Descent of Man contains a sophisticated theory of human biocultural evolution. Darwin's ignorance of the basis for inheritance may turn out to be prescient if trans-generational epigenetic inheritance turns out to be important. His treatment of culture inheritance foreshadows late twentieth century developments rather exactly. We think Darwin actually understood cultural evolution well and made it his model for organic inheritance. Failure to appreciate his project in *The Descent of Man* has misled many modern readers, including sympathetic and knowledgeable

ones. Historians of science have made some headway in explaining why his theory failed to influence the emerging social sciences in the early twentieth century, leading the social sciences to fall decades behind the biological sciences in evolutionary matters. But, much remains to be told.

Human culture may have originated as an adaptation permitting rapid evolution in a noisy Pleistocene environment. The costs of culture include the complexity and clumsiness of a coevolutionary system in which genes and culture are often collaborators but sometimes antagonists. Human ultra-sociality is a super adaptation that underpins our ecological dominance of Earth, yet it is much less perfect than the ultra-sociality of the ants, bees, and termites. In one of our models of gene–culture interaction (Boyd and Richerson 1985), each system of inheritance tends to pull behavior in the direction that favors its own transmission. As one system obtains a small advantage, the other escalates to correct it. 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.

ACKNOWLEDGEMENTS

We thank Doug Futuyma and Mike Bell for organizing the wonderful conference that resulted in this contribution. Thanks also to our fellow participants for making the conference so stimulating and enjoyable. Two anonymous reviewers and Mike Bell much improved our chapter.

LITERATURE CITED