Built For Speed, Not For Comfort

Darwinian Theory and Human Culture

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Running head: Darwinian Theory of Human Culture

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Abstract

Darwin believed that his theory of evolution would stand or fall on its ability to account for human behavior. No species could be an exception to his theory without imperiling the whole edifice. 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. Not until the late 20th Century were concerted, sophisticated efforts made to apply Darwinian theory to human behavior. Why such a long delay? We argue that Darwin's theory was rather modern in respects that conflicted with Victorian sensibilities and that he and his few close followers failed to influence any of the social sciences. The late 20th Century work takes up almost exactly where James Baldwin left off at the turn of the Century.

I. Introduction

Darwin believed this theory applied to humans, and devoted the *Descent of Man* to developing an account of human evolution based mainly on natural and sexual selection. However, 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*, and to this day eminent social scientists are quite hostile to Darwinism. Wilson's (1975) call in his book *Sociobiology, a New Synthesis* for incorporating humans into modern Darwinian theory provoked an outburst of heated reaction quite reminiscent of the Victorian reaction to Darwin himself (Segerstråle 2000). 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?

Although these questions have an admittedly whig-history flavor, we believe that as practicing scientists not historians we have license to pursue our particular roots amid the welter of competing theories in the past (Bowler, 1993: 4). The work that we and others embarked upon in the last quarter of the 20th Century applied basic Darwinian concepts to the study of cultural evolution. We were happily surprised to find that social scientists had not done basic things that occur immediately to a Darwinian confronted with a system of inheritance with many analogs to genes. Darwin himself was confused about the mechanism of inheritance, and, by always imagining that organic inheritance included the feature of the inheritance of acquired variation and by liberally using the concept of inherited habits, devised a theory that was more applicable to culture than to genes. In the early part of the 20th Century, biologists developed a practical agenda

for evolutionary biology that involved quantitative theory and quantitative field studies of evolutionary processes, based upon Darwin's and his successors verbal theory (Provine 1971). In our view, no fundamental impediment existed in the first quarter of the 20th Century to the highly analogous problems of cultural evolution based on imitation. Nevertheless, the program was not actually taken up until about 1970. In this essay we seek to know why students of culture left such a promising field of investigation untilled for two generations and why it still generates much resistance.

II. Darwin's Problems With Humans

A. The Early Notebooks

Darwin's early M and N notebooks on Man, Mind and Materialism make clear the important place that the human species played in the formation of his ideas on evolution (Barrett 1974). In 1838 Darwin wrote "Origin of man now proved.--Metaphysics must flourish.--He who understand baboon would do more toward metaphysics than Locke" (Barrett 1974: 281). These words were written in the heat of Darwin's most creative period, a few weeks *before* his first clear statement of the principle of natural selection was recorded in his notebook on *The Transmutation of Species*. The passage is an expression of hopeful enthusiasm rather than triumph. He was actively pursuing a purely materialistic theory of organic evolution, and was already committed to the idea that humans would belong under the theory. Given the scope of the theory, it could hardly be otherwise. Right down to the present, the promise and perils of understanding the origins of humans and human behavior have been an unavoidable part of the Darwinian agenda. On the one hand, evolutionary theory, if correct, should provide powerful tools to understand human behavior. On the other, if humans are not understandable in Darwinian terms, perhaps there are deep, general, problems with the theory.

B. Who Would Do Man?

Darwin knew his theory was considered dangerously radical by the vast majority of his contemporaries, and he long delayed publication of even the biological part of it (Gruber 1974). Eventually stimulated to action by the arrival in 1858 of Wallace's paper describing natural selection, Darwin published *Origin of Species*, to the end of which he added the famous teaser "light would be thrown on the origin of man and his history." Darwin delayed a further dozen years making good on his promise to discuss humans. In the Introduction to the *Descent of Man and Selection in Relation to Sex* (1871), he wrote of his fear that publication of his views on the subject would inflame prejudices against his theory. This fear was not unfounded. As the *Quarterly Review*'s commentator, 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 1871).

Darwin hoped that someone else would carry the burden of applying Darwinism to the origin of that most interesting, most controversial, species. Lyell (1863), Huxley (1863), and Wallace (1864, 1869) all produced books and papers on the subject. However, none of their work was close to satisfactory. Huxley was too busy and too inexperienced in ethnology and sociology to consider anything but anatomy, although this emphasis was most effective in showing that human bodies were derived from ape-like progenitors. Lyell, still a skeptic about the role of natural selection, certainly did not accord it a central role in human evolution. Darwin held out much hope for Wallace, whose essay in 1864 he judged a good start, and offered to transmit to him his accumulated notes by way of aid. But then Wallace became an apostate on the role of natural selection in human evolution, arguing that it could not account for the moral and higher intellectual qualities of humans. The austere materialism of selection no longer satisfied him as an explanation for human origins.

Darwin thus eventually took on the task of writing the *Descent*. It was as rich and sophisticated treatment even by contemporary standards, as we shall try to show. Yet, even during his life, Darwin's treatment of evolution generally and humans specifically had many competitors (Bowler 1988). For example, Herbert Spencer and Darwin debated in a rather modern way over the relative importance of natural selection and the inheritance of acquired variation in shaping the evolution of minds (Richards 1987). Both admitted that both processes were important in evolution, but Darwin thought selection and Spencer acquired variation the dominant process. Further, Spencer's stress on acquired variation was linked to his belief that the fundamental principle of evolution was the "never-ceasing transformation of the homogeneous to the heterogeneous" (Richards, 1987: 271). He believed that the creation of celestial structure, the increasing complexity of organisms, the increasing division of labor in human societies, and the moral perfection of these societies were all a product of this same progressive principle. The linkage of a progressive principle during individual development to longer-term change provided the main motor that drove populations along the trajectory to greater differentiation of parts.

Natural selection's subtractive rather than creative property makes it a less plausible force for progress. As Darwin confided to his N notebook in 1838 (Barrett 1974: 339)

> 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!))

We believe that Darwin's skepticism about evolutionary progress and his failure to make it a central theme of even his theory of human evolution were major reasons why his theory was not popular among his contemporaries (Bowler 1986: 41). Even Huxley was prone to Spencer's account in critical respects (Bowler 1993:15). We admit that in other quotes Darwin speaks more

favorably of progress (Richards 1988). An ambivalence about the theoretical status of progress has afflicted evolutionary biologists down to the present day (Nitecki 1988). Certainly progress is not the basic evolutionary motor of Darwin's theory as it is Spencer's, as the N notebook quote shows.

Why were Darwin's contemporaries so keen on progressive theories of evolution? The original nub of the matter was that almost all Victorians understood and feared the direction that a thoroughly Darwinian theory of human origins would lead. As the *Edinburgh Review's* anonymous (1871) commentator on the *Descent* 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....

According to Burrow (1966), a significant segment of Victorian opinion was skeptical about conventional religion and was often enthusiastic about evolution. Even the idea that humans were descended from apes did not bother these secular intellectuals. However, they did believe that human morality required the support of natural laws. If God's Law were to be dismissed by the scientific minded as superstition, then all that much more important to find a substitute in natural laws that scientists were elucidating. Spencer's law of progress included the moral sphere and Spencer was not shy in drawing moral norms from his theory (Richards 1987: 203-213). His theory fit the bill, Darwin's didn't.

Further, Burrow argues, Victorians had become acutely aware of the tremendous diversity in human behavior displayed by past and present human societies. The scientific minded secularists were not ready to condemn "barbarian" practices as evil out of hand if for no other reason than they were intensely curious about them. On the other hand, Victorians were not ready to be moral relativists and give other ways of life equal moral standing with their own. The solution was to imagine that foreign lifeways were not so much evil as primitive, representative of a stage that

European societies had transcended. Spencer and like-minded evolutionists developed theories of progressive evolution that seemed to give authoritative scientific support to moral philosophy and to award an advanced moral and intellectual rank for their own societies. Some, like the Catholic convert St. George Mivart and in his later years even Wallace, saw the Designer's hand rather than a natural law as the ultimate engine driving progressive evolution, giving religious believers a comfortable way to accommodate human diversity in an evolutionary scheme (Richards 1987: 179-184, 353-357).

C. Darwin's Argument

Darwin's theory in the *Descent* is in many respects one more typical of the last half of the 20th Century that of the Victorian 19th. Because he did not make progress the centerpiece of his story, he did not he did not rank humans, as regards their minds or their moral intuitions, on a primitive-advanced progressive scale. The extent to which Darwin subscribed to what we now call the doctrine of psychic unity is widely misunderstood. Even otherwise knowledgeable scholars believe that Darwin shared the widespread Victorian belief that the living races could be ranked on a primitive-advanced scale (e.g. Ingold 1986: 53). 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." Alexander Alland (1985: 4-5) approving quotes Stephen Jay Gould to the point that Darwin shared the typical Victorian idea that the dark races are lower in the progressive evolutionary sense. Such a reading of Darwin is quite wrong!

Darwin's first publish views on humans in the *Journal of Researches (Voyage of the Beagle* were made several years after formulating his early ideas on natural selection, but more than a decade before their publication and 25 years before the *Descent.* His descriptions of the Fuegans in the *Journal* are often quoted to demonstrate that his views of the hierarchy of races were stereotypically Victorian. He did use the most purple Victorian prose to describe the wretched and

lowly state of the Fuegans, whom he had observed first-hand on the *Beagle* voyage (Darwin 1845, pp. 242-7):

> 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 (243).

He goes on at some length in this fashion, but this is the bait not the hook of the argument. The passage on the Fuegans begins with a description of the rigors of the environment of Tierra del Fuego and ends by attributing the low nature of the people to the poor quality of the environment rather than as representing inherently primitive people:

> 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° (242).

> 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 (246-247).

The argument is quite in keeping with his idea that progress under his theory could only come from favorable circumstances. In effect he is saying that any humans forced to live under such

conditions with such limited technology would rapidly come to behave similarly. Note the reference to hereditary habits; this concept figures large in his mature ideas on human evolution.

Darwin routinely condemns White Christians' morals, as when discussing slavery and the genocidal Argentinean war against the natives of Patagonia in the *Journal* (Darwin, 1845: 36-37; 121-125; 561-563). For example, he ends the recounting of a story of an Indian's daring escape from a genocidal attack by Christian Argentineans with his small son:

> 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 on a white horse, thus leaving far behind him the host of his pursuers! (124)

His paean against slavery begins (561-563):

> 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.

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 the slaves in all her colonies in 1838.]

Gruber (1974: 65-68) notes that Darwin's deep antipathy to slavery was shared with his extended family circle, though not nearly so widely shared by his contemporaries, leading for example, to a furious argument with Captain Fitzroy on the *Beagle* voyage. Darwin certainly thought that moral

progress was possible, and no doubt thought that Europeans had achieved some notable advances relative to savages. Things like the rule of law and the having of just laws supported by enlightened public opinion, such has had ended slavery in the British Empire, he counted as progress. Most of us would agree. This sort of progress is far from setting up a hierarchy of races justifying the extermination or enslavement of the lower races by the higher! We find it quite odd that contemporary social scientists, operating in a liberal to radical political milieu, fail to recognize that Darwin's politics, while not often worn on his sleeve to the extent that came out in his views on slavery, were far to the left for his day, and not so different from those of the modern non-doctrinaire academic left (Sulloway 1996:Chapter 10; Desmond 1989: Afterword; Richards 1987: 597).[1] One must except his attitudes toward women's mental characteristics (Darwin 1874: 725-728), which allowed for a marked sexual division of labor and attendant mental and physical traits. He did speculate that appropriate early education of women would erase these differences via the effects of inherited habit, though he was skeptical that this would be desirable. Darwin was certainly not a misogynist. His care of his sick young daughter Annie during her illness and his grief upon her death are part of the Darwin legend.

Of course it is in his mature work *The Descent of Man and Selection in Relation to Sex* that we should find Darwin's (1874) best effort to account for human evolution and the diversity of human behavior (all page numbers below refer to the edition in the literature cited). In Chapters 3 and 4 "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 lowest man and the highest animal is immense" (170). In these chapters he struggles with the challenge the great gap between humans and other animals poses for his theory of the gradual, step by small step, emergence of humans from their ape ancestors. How much easier his task would have been if he seen fit to people the gap with the living human races, as so many of his contemporaries did! As it is, he has to project hypothetical continuities across the gap (as in the *Expression of Emotion in Man and*

Animals) rather than peopling it with living savages and barbarians. In general, when discussing the vices and virtues of different groups, Darwin is as even-handed in the *Descent* as in the *Journal*. For example he uses the aristocratic European *Law of Honor* giving special weight to the opinion of class peers rather than countrymen more generally, usually involving trifling matters of etiquette, as an example of maladaptive customs along side Hindu beliefs about uncleanliness (164).

In Chapter 5 of the *Descent* "On the Development of the Intellectual and Moral Faculties During Primeval and Civilized Time," Darwin's argument is quite clear. Unlike Wallace, who came to believe that natural selection was not sufficient to explain the mental powers of humans, Darwin certainly believed that natural selection operated in *primeval* times to produce human mental and social capacities (172-180). In particular, he posits that human moral sentiments arose by group selection in primeval times:

> 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 (178-179).

He pointedly credits "savages" with a loyalty to their tribes sufficient to motivate self-sacrifice to the point of death and with the "instinct" of sympathy, with the objective of making sure that the reader understands that these moral sentiments are of primeval age, shared by the living savage and the civilized alike. The large role that sympathy plays in his evolutionary ethics is noteworthy,

as is the active role it played in his detestation of slavery. For further advances, he puts great weight on customs acquired by imitation (174). He spends several pages reviewing the tendency of advancing civilization, if anything, to weaken natural selection, and the evidence the retrogressions are common (180-193). 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 (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 (192).

Note that the list of processes of advance applying in his mind to the lower races is virtually identical to those applying to the highest. *Primeval* evolution endowed living savages with the same social instincts as civilized men, and hence susceptible to the same improvement from "good education" and the rest. The lower races have the same moral instincts as the higher; the higher have just had the advantage of a favorable environment to push moral progress a little further. Whatever progress has occurred does not obscure the fact that "civilized" men often behave atrociously (and should know better) and "savages" often with the admirable moral courage (even lacking a civilized education).

The climax of Darwin's argument in the *Descent* is Chapter 7 "On the Races of Man." He considers two hypotheses, that the races are sufficiently distinct to count as different species, and

the hypothesis that they are alike in all important organic respects. He first spends several pages outlining all the evidence in favor of the different species hypothesis (Darwin, 1874: 224-231). Darwin's dispassionate tone in these pages makes it easy for careless readers to believe that this is the alternative Darwin favors. However, he then goes immediately on to demolish the separate species argument in favor of the trivial differences alternative (231-240).

> 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 Fuegians 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 (237).

The contrast between Darwin and others like Ernst Haeckel who really did think that "natural men are closer to the higher vertebrates than to highly civilized Europeans" could hardly be more stark (Richards 1987: 596). Darwin concludes:

> We have thus far been baffled in all our attempts to account for the differences between the races of man; but there remains one important agency, namely Sexual Selection, which appears to have acted powerfully on man, as on many other animals (262-263).

Thus, the pairing of Darwin's main thoughts on humans with his main thoughts on sexual selection is not at all accidental. He proposes to account for all the conspicuous differences

between the races, such head shape, color, and hair, as the result of superficial fads and fashions in good looks! Using conventional racial characters to classify races into the higher and lower is exactly what he rejects. He even rejects an adaptive explanation for skin color differences in terms of exposure to sunlight (255-256); adaptive explanations for skin color are today commonly accepted (e.g. Jablonski and Chaplin 2000).

Since people from different places do differ substantially in behavior, Darwin does, of course, need an account of human diversity. In Chapter 7 of the *Descent* he makes something like the modern distinction between organic differences and customs:

> 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 (238).

Darwin's favorable citations of Tylor, the founder of cultural anthropology and one of the important 19th Century defenders of the Enlightenment doctrine of the psychic unity of all humans, is surely significant and quite in keeping with his sympathy for savages and slaves. Tylor's (1958 [1871]: 7) postulate of organic similarity but customary difference 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.

Darwin sometimes uses the exactly same distinction:

> 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 . . . . (239)

Darwin here suggests that the main explanation for differences between races is customs, not organic differences. The story is complicated for us to understand because of Darwin's frequent

use of the concept of inherited habits, as in the quote about the Fuegians above. In the preface to the second edition of the Descent, 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 (3-4).

One of the most important forms of the inherited effects of use and disuse in Darwin's mind is "inherited habits." Custom, good education, imitation, example of the best men, and his other versions of culture would tend to become hereditary in Darwin's scheme. Lacking the 20th Century concept of a gene isolated from direct environmental modification, a rigid distinction between inheritance by imitation and inheritance by organic structures was foreign to his thinking. He does seem to divide traits into more and less conservative poles. On the conservative side are basic anatomy and basic features of the mind, little influenced by the inheritance of acquired variation but mainly by selection over long spans of time. More labile traits are much more sensitive to environmental and cultural influences, though also coming to be inherited, but susceptible to being rapidly remodeled again by inherited habit if the environment changes. In this feature of his theory was erroneous and archaic, but the conservative-labile distinction does the same work for Darwin that the innate-acquired one does for us. Indeed, some cultural traits are pretty conservative (e.g. Nisbett and Cohen 1996) and gloss pretty well as the inherited habits in Darwin's theory. The genetics revolution was more conceptual than practical in the 20th Century, as its intractable quarrels over nature-nurture issues illustrate. Only contemporary advances in genomics promise the tools solve the difficult riddle of the interactions between inheritance and development.

Darwin was much more modern in his commitment to the essential similarity of all races and the explanation of the differences in terms of either non-functional differences (sexual selection), functional differences due to rapid responses to favorable and unfavorable environments via custom/inherited habit (as with the Fuegians). He did hold that some residuum of real progress existed in the differences between savage and civilized societies, driven by the prosocial instincts acquired long ago by our primeval common ancestor under group selection, at least when environments were favorable. Certain archaic features of his views notwithstanding, Darwin's moral judgments would put him on the left side of the political spectrum even today.

Another problem interpreting Darwin is the he was keen to minimize qualitative differences between humans and other animals lest his theory face unbridgeable gaps that would imply unique processes applying only to human evolution, and inevitably problems for his general account. The *Descent* reports many observations of animal behavior in which near-human moral and intellectual faculties are credited to animals. Modern behavioral data show that Darwin exaggerated the capacities of animal minds.

Most important for our story here, Darwin imagined that animals had much the same capacity to modify their behavior by imitating other individuals as do humans. One of Darwin's own observations used to make this point involved bees imitating each other. Early one morning he observed bumble bees cutting holes in the sides of difficult-to-enter bean flowers to steal nectar. Later in the morning honeybees began using the same technique. Darwin imagined that the honeybees observed the bumble bees using flowers in this way and simply imitated them using mental apparatus analogous to ours (Galef 1988, pp. 4-6). Galef and other modern students of animal imitation have demonstrated some such effects in many vertebrates (Heyes and Galef 1996), but nothing approaching human capabilities. Even young children are considerably better imitators than adult hand reared chimpanzees that have a long history of being rewarded for

human-like acts of imitation (Tomasello 1996, Whiten and Custance 1996). Accurate imitation revolutionizes social learning (Boyd and Richerson 1996). Rapid, accurate, imitation increases the number and sophistication of behaviors that are acquired by imitation. Individual learning is comparatively slow and costly, and can support behaviors that are only as sophisticated as one animal can learn. Given accurate imitation, cultural sophistication can increase as a succession of innovators each adds a new wrinkle to a gradually improving behavior. Even technology as simple as a stone-tipped spear contains a considerable number of design components susceptible to cumulative improvement (type of wood, length, distribution of weight along the shaft, type of stone used for tip, shape and weight of tip, technology for hafting the point). Thus, sophistication of imitation is, in fact, part of the "great gulf" Darwin admitted separate humans from their ape relatives. In other words, to bridge the great gulf Darwin had a tendency 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.

III. The Twentieth Century

A. Darwin's Evolutionary Theory Used in Biology, Neglected in the Social Sciences

The rediscovery of Mendel's Laws of inheritance at the turn of the 20th century set in motion a 35-year-long process of excising erroneous ideas on inheritance and reconciling the new genetic system with natural selection and other mechanisms of evolution (Provine 1971). In this period, biologists had to struggle against rear-guard defenders of notion of the inheritance of acquired variation and were not predisposed to examine the special cases of animal social learning and human culture. In the meantime, most of the intellectual leaders of the newly emerging social sciences almost entirely ignored the ideas in the *Descent* (Ingold 1986, Richards 1987: 507-519). 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*. 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 did 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 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 (294).

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).

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 over-ride pleasure and pain, but these 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 Fairfield Osborn (Richards 1987: 483-495).

As we shall see, all of Baldwin's ideas have found echo in late 20th Century theories of cultural evolution. However, they had no immediate issue. The reasons are similar to the reasons other evolutionary influences on the rapidly evolving social sciences winked out around the same. The individuals espousing a truly Darwinian perspective were few. Aside from Baldwin, the sociologist Albert G. Keller taught a version of social evolution rather 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 developed in subsequent work. 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 that direction while his younger colleagues turned sharply in the opposite (Richards 1987: 501-503). In anthropology, Franz Boas reacted negatively to all forms of theorizing, wanting field workers to have minimal preconceptions when collecting ethnography (Harris 1979: 308-9). Collecting unbiased ethnography while time still existed to interview people who had lived in societies with little or no contact with the modern West was an important mission that attracted many students.

Part of the problem was that Darwin's own view of evolution reached its lowest ebb of influence 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: Chapter 5). In the meantime, economics, in some ways the most ambitious of the social sciences, abandoned biology and adopted physics as its model natural science (Hodgson 1993).

James Griesemer (personal communication) once pointed out to us that the populations of scientists are always small, particularly considering that a few leading scientists typically exert much more influence than the rank-and-file. In the early 20th Century, the actual headcount of scientists was very small. Today the headcount is much larger, but specialization is much greater, so the number influential in any one field is still small. In such a system, the accidental effects of the cultural analog of genetic drift will be very high (Cavalli-Sforza and Feldman 1981: 192-204). The influential proponents of a Darwinian program in the social sciences were always few and could have winked out by chance. Scandal played a large role in Baldwin's professional demise (Richards 1987: 496-501). Keller's role as Sumner's devoted disciple overshadowed his own

rather more Darwinian ideas (Campbell 1965). These personal foibles limited the influence of the most sophisticated Darwinian social scientists of the early 20th Century.

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 1968). Various attempts were made to heal or at 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 every really specifying how the coevolution works or just what transcendence means in this context. His and Montagu's 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.

B. Donald Campbell's "Vicarious Forces"

By the centennial of the publication of the *Descent* Darwinism was a highly successful research program as regards genetic inheritance and non-human organisms, but its application to systems for the inheritance of acquired variation, most conspicuously human culture, had hardly progressed at all since 1895. The major exception was Donald Campbell, who 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, again exactly as Darwin argued. Second, in the 1965 chapter, he provided a clear argument for why Darwinian theory ought to be applicable 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 an account of the processes of change, given that Spencer's homogeneity-to-heterogeneity mechanism is 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 purely random variation and selective retention process.[2] 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 make 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 of cuisine, like addictive drugs, and others over-ridden 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 in the world's dairying populations during the last few thousand years (Simoons 1978).

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 (as were we until we did the research for this paper).[3] Subsequently, two rather distinctive schools of thought have developed on the nature of gene-culture coevolution, the human sociobiology championed by Lumsden and Wilson (1981), Alexander (1979), and their followers, and the population genetical approach pioneered by Cavalli-Sforza and Feldman (1981).

C. Human Sociobiology

The sociobiologists argue that it is certain that the very fancy human abilities to use culture must have evolved from the rudimentary social learning typical of other animals. As our mental capacities to use culture developed, their evolution would have been under the control of natural selection acting on the genes that expanded our brain, set up our larynx to produce speech, and otherwise made culture possible. Unless the culture that resulted from the use of these organs increased the chance those genes would make for better surviving and reproducing individuals, they would not have evolved. Humans arose by natural selection. Shouldn't we follow the same rules as other organisms? Aren't we just "another unique species" (Foley, 1987)?

Sociobiologists point out that Campbell's vicarious forces provide a mechanism to ensure that cultural evolution does favor the fitness of our genes. If the decisions individuals make about what

culture to invent, and which preexisting variants to acquire and use, are based upon genetically transmitted tastes, senses of pleasure and pain, and the like, cultural evolution will be driven directly by genetically transmitted decision rules and ultimately by natural selection acting on those rules. Food, sex, warm houses, and boon companions are rewarding because they lead to survival and reproduction. If cultural traits tend to arise that favor something else, selection will favor individuals who regard them as painful, distasteful, unthinkable, or otherwise unrewarding. Cultural evolution will be on a genetic leash, in Lumsden's and Wilson's (1981) metaphor. As necessary, selection on genes can always rearrange our minds to adjust the leash on cultural evolution.

The application of sociobiological reasoning to humans has attracted intense controversy, because many people view it as giving far too large a role to genes, thus ignoring the unique features of human culture. This criticism is apt, but misses an important point. Many aspects of human behavior can be explained quite well by sociobiologists. Human nepotism, and the key role that kinship plays in the organization of most societies, are in reasonable conformance with expectations generated by Hamilton's (1964) theory of kin selection. For example, Daly and Wilson (1988) showed that children are much more likely to be abused by a step-parent than a biologically related individual, and that a number of other patterns of homicide are in conformance with kin selection. The contributors to Smith and Winterhalder (1992) use models from evolutionary biology to explain food acquisition, time allocation, spatial organization, social structure, and reproductive decisions. The contributors to Barkow, Cosmides, and Tooby (1992) apply evolutionary theory to the study of human cognition rather than behavior directly. Much as Campbell argued, there is considerable evidence that selection will favor mental adaptations that act as effective vicarious selectors.

In our view, the natural history of humans exhibits more than just normally unique features and standard sociobiological reasoning fails to do them justice. Nevertheless, the sociobiologists should be taken seriously by the social scientists. It will not do to be glib about human uniqueness automatically guaranteeing that evolutionary biology can be ignored. If our particular unique features, like the possession of culture, win us any autonomy from the dictates of natural selection, it is an important task to trace out exactly how this might work. Even when biology-based predictions of human behavior or cognition turn out to be wrong for humans, the sociobiological hypothesis is an important reference point to compare to other explanations. The sociobiologist, by showing us what natural selection can be expected to produce by way of human cognition and behavior, can at least save us from the common error of asserting that humans do things differently, when in fact they don't. For example, Sahlins (1976) used the example of the high frequency of adoption in Polynesia as the bedrock example of his critique of sociobiology. People were often caring for children of others, in defiance, Sahlins said, of sociobiological theory. The trouble is Polynesian adoption does closely follow biological kinship, and results from the inability of the natal family to care for the child, and similar contingencies, in close accord with Hamilton's theory (Silk 1980).

IV. Evolutionary Theory of Culture

A. Darwinian Principles Applied to Cultural Evolution

One way that culture might make us theoretically interesting, as opposed to merely taxonomically unique, is if culture affects the evolutionary process in fundamental ways. Sociobiologists 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 *methods* of Darwinian biology to study cultural evolution, work pioneered by Cavalli-Sforza and Feldman (1981), 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. This analogy between genetic and cultural evolution is undoubtedly what led Darwin to so thoroughly confuse the two. Both are population level, historical processes that frequently result in the adaptive diversification of behavior.

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. Human behavior today is the product of the processes of genetic and cultural evolution operating human populations of the past. To understand these evolutionary processes is to understand human behavior, just as Darwin asserted in his baboon versus Locke remark in his notebook. Given that Darwin's theory of inheritance really resembles culture more than genes, the project begun by Cavalli-Sforza and Feldman is a return to the 19th Century roots of Darwinism to pick up Balwin's neglected thread, the evolution of systems with inheritance of acquired variation and other non-mendelian properties.

B. 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 Richerson 1985 for amplification):

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. Heroin addiction has been studied as a pathological cultural character (Hunt and Chambers 1976). 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!

Third, we acquire and discard items of culture throughout our lives. One is stuck with the genes one inherits at conception. 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 old behaviors. 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 the vicarious selection processes in cultural evolution.

Fourth, variations that we acquire for ourselves can be inherited. 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 task of exploring just the theoretical properties of these differences has only just begun. Some sense for the magnitude of the task can be had by noting that culture is at least as complex a system as genes, and mathematical population genetics remains an exciting discipline 80-some years after it was pioneered by R. A. Fisher (1918).

C. The Evolution of Human Uniqueness

Our own work, and that of a few others including Pulliam and Dunford (1980) and Rogers (1989), has been devoted to trying to use the tools of the population genetic approach to address the kind of basic evolutionary problems posed by the sociobiologists. There are three major differences between humans and even our close primate relatives that are basic for understanding ourselves in the Darwinian framework: i, a fancier capacity for imitation and the associated massive use of culture; ii, much symbolism and stylistic variation (e.g. many languages) in culture of no obvious practical use; and iii, 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.

1. 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 answer is very strongly flavored by non-Darwinian progressivist evolutionary ideas. Almost everyone assumes that human culture is an intrinsically superior method of acquiring and transmitting 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 adaptation. Landau (1984) has shown that all accounts of human origins, *even by professional physical 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 Wilson and Lumsden (1981, p. 330) are led to speak of humankind's "cosmic good fortune of being in the right place at the right time" to overcome the resistance to advanced mental 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 increase when rare, even if having complex traditions is a great adaptive advantage, because when the capacity for learning complex traditions is rare, there will be no complex traditions to imitate!

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 culture 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 specialized niche in an unusual environment leads 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 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, Chap. 4). 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 half animals, but experience indicated that 10% was best (say in some new environment), individuals would end up collecting enough plants to make up 30% of 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 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 tradition. Let us also assume that individual learning is either fairly costly or fairly error prone. (These two variables will tend to be 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 very slowly changing, 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 evolutionary 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 form their children's. In such an environment, each individual does best to depend entirely on experience, since only individual learning has a better than random chance of alighting on 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 a lot on the time scale of tens of generations, but not too rapidly in any one generation. A cultural system of inheritance, by making individual learning cumulative, can track changing environments more rapidly than genes yet economize substantially on the costs and errors associated with individual learning.

Given the assumption that individual learning is costly relative to imitation, the results of the model recovers 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 (deMenocal 1995, Potts 1996, Vrba, et al. 1995, Richerson and Boyd 2000a, 2000b). 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 et al. 1996). 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.

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 1963) and many have simple social learning systems. 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.

2. More Complex Benefits and Costs of a Massive Capacity For Culture

Further clues 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 will frequently be a good guide to whether to acquire it or not; often the most common way of doing things is the locally correct way. When in Rome, do as the Romans do. 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 (Goodenough and Dawkins 1995, 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 biases 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 section 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 and school mass media propaganda are used to 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 thrive during the Pleistocene and spread from its tropical homeland to the Arctic regions and the New World is testimony to this flexibility. 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 Treadway 1986). Today wealthy nations, and the wealthier people within these nations, have extremely low birth rates, often below replacement. Borgerhoff Mulder (1987) and Irons (1979) have argued quite 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 fitness—children. Why do Westerners 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. (Pathological from the perspective of genetic fitness maximization; we do not mean to suggest that the demographic transition is a bad thing from the perspective of protecting the earth's environment or from people's own subjective well-being.) Urbanization brings more people into contact, and specialized non-parental roles have arisen, such as teachers, that 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 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.

Knauft (1987) argues ancient and early modern urban areas had low fertility for similar reasons. Cities and elite classes could persist despite below replacement fertility because their culture dominated the country-side. City and elite life were prestigious, glamorous, and exciting. New recruits were drawn inward and upward from high-fertility rural and lower class communities to maintain the population of cities and elites through immigration. Urban society was demographically parasitic on the countryside. If there is enough opportunity for non-parental transmission of culture, what constitutes cultural success (prestige, a successful career, membership in a governing bureaucracy) may come to conflict with reproductive success, as most modern professionals have discovered by experience. Rural communities that develop low fertility, by contrast, simply slowly waste away. Coale (1986) has collected a number of examples from rural 19th Century Europe where norms resulted in below-replacement fertility and population declined as a result. Isolated peasant communities lack the prestige and communications channels to recruit imitators for their life styles from afar, and their low fertility was unsustainable. Bongaarts and Watkins (1996) argue that the current nearly worldwide acceleration of the demographic transition is caused by increasing diffusion of ideas from the developed to the less developed world, including both specific ideas related to fertility control and the broader knowledge, aspirations, and attitudes that encourage low fertility in the developed countries. Few human communities are any longer isolated from the influence of mass media, and much of the content of the mass media is produced in the developed countries and much locally produced content portrays elite Westernized life styles (e.g. Latin American telenovelas).

3. Symbols: The Origin of Modern Humans

What of the large scale of human societies and our elaborate use of apparently non-functional symbols, such as elaborate costumes, artistic creations, and complex supernatural belief systems? Do models of cultural evolution give any insights into the evolution of these attributes that, along with culture itself, differentiate our species from its ancestors?

These two features are empirically closely associated. Social groups are usually also symbolically marked. 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 symbolic conflicts 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 (Boyd and Richerson 1987, McElreath et al. n.d.) also demonstrate that an adaptively neutral symbolic character like language can serve as an adaptive marker. 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 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. A long, less well investigated, sequence of gradual changes in Africa, stretching back some 280,000 years, leads up

to the Aurignacian level of stylistic sophistication (McBearty and Brooks 2000). 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. Stringer and Gamble (1993) present a strong case for the transition from ancient asymbolic to modern symbol-using humans being a major adaptive change. The ethnic markers model is a candidate explanation for why (Bettinger et al. 1996). Ethnic markers make marked groups pseudo-species that can preserve fine local adaptations in the face of a flow of ideas from other environments. The flourishing of cultural adaptations closely tailored to local environments in turn stimulated a jump in population sizes. The isolation of ethnic groups need not be complete. The suspicion of foreigners can be over-ridden in the case of variants that confer conspicuous success on foreign migrants in their new habitat without damaging the utility of the suspicion to screen out subtler mistaken ideas.

4. 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 the "lower" animals, such as bees, ants, and termites. However, altruism in such cases is based on kinship, in accordance with Hamilton's inclusive fitness rule. The workers in insect colonies are all siblings, and each colony consists of a few reproductives and many non-reproducing workers. The same is the case in African Naked Mole Rats (an animal about as attractive as its name suggests), aside from humans, the mammal with the most complex social organization. Among our close relatives, the apes and monkeys, cooperation appears to be largely restricted to close relatives. Typically one sex or the other transfers from the

troop of their birth to another troop at maturity. Individuals usually transfer alone, so only one sex has close relatives in the same troop. Thus in macaques and baboons, altruism among related females is common, while among chimpanzees, it is the males that remain and that cooperate. The other sex is substantially bereft of any benefits of cooperation. Humans took a route to ultra-sociality different from that of the social insects, one not based on kin altruism (Campbell 1983).

To judge from contemporary simple societies, three overlapping levels of social organization 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 agriculturally based societies of the last 10,000 years, the sophistication of political organization of ancient ethnic groups was slight. 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.

Nothing like the relatively peaceful, cooperative relationship between hunting and gathering bands of common ethnicity is known from any other animal species; the degree of relationship between coethnics is quite low on average, too low to support the degree of altruism observed by

the kinship mechanism. Other animals do conform quite closely to the Hamilton's theory of kin altruism; humans pose a problem.

A number of hypotheses have been proposed to explain human cooperation. For example, Alexander (1987) supposes that human intelligence allows us to greatly extend the range of a mechanism for supporting cooperation known as reciprocal altruism. Axelrod and Hamilton (1981) showed how cooperation among pairs of individuals can arise if there are a large enough number of interactions between the individuals. According to this theory, individuals should be cautious cooperators, playing a strategy like tit-for-tat. Using this strategy, you cooperate with a stranger in the first interaction. If the other person also cooperates, you continue to cooperate; if the other individual fails to cooperate, you do not cooperate on the next interaction. This system is effective at detecting non-cooperators and denying them the benefits of cooperation except on the first interaction. If there are many interactions, pairs of cooperators will do well compared to non-cooperators, who benefit from at most one episode of cooperation. Hence, a propensity to cooperation can increase.

The problem comes in scaling this process up to larger groups. As groups become larger, potentially cooperative individuals' contribution to the common welfare is smaller, as are their effects on non-cooperators when they decide there are too many non-cooperators to continue cooperating. There are many more possible strategies to follow. How many members of your group can be non-cooperators before you decide not to cooperate? None, a few, quite a few? The theoretical models that we have worked on suggest that it is hard to get reciprocity stared in large groups, and easy to loose it (Boyd and Richerson 1988). Among other problems, both kin selection and reciprocity work best in the smallest possible groups. Even if reciprocity arises in large groups, it would be vulnerable to subversion by cabals of close kin or small, tight-knit bands of reciprocators.

Another idea, originally proposed by Wallace in 1864 before his apostasy, is that humans are selected at the level of whole groups. Darwin, as we have seen, favored this theory and Hamilton (1975) has more recently suggested that because of the intense, organized, violent competition between human groups, it might actually apply.

Most evolutionary biologists, including Darwin and Hamilton, are normally skeptical that selection between groups is effective (but see Sober and Wilson 1998). 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 heritably variable entities. In the case of group selection, reproduction of groups must ordinarily be slower that 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 if a few non-cooperators enter the group, they will enjoy the benefits of altruism without paying the costs. Inside the group, non-cooperators will increase rapidly. It is hard to set up conditions where the extinction rate of groups with too many selfish individuals is fast enough to keep up with the "infection" of altruist dominated groups by selfish individuals due to migration between groups, combined with the advantage selfish individuals have in groups dominated by altruists. Empirically, migration across even ethnic boundaries seems to have been fairly large in hunting and gathering societies (as in almost all others), and the rates of group extinction and reproduction relatively low. Warfare is seldom genocidal, and women and children from defeated groups are often incorporated into the societies of the victors, spreading any genes for selfish cowardice that might have contributed to their defeat.

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.

Second, the conformist "When in Rome" imitation rule has a strong tendency to minimize the effects of migration on the variation between groups (Boyd and Richerson 1985, Chap. 7, Henrich and Boyd 1998). Even if migrants are fairly common, so long as they do not approach half the population of a group, resident culture will have an advantage over that of minority migrants; it 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 (Boyd and Richerson 1985, Chap. 8). Ritual, religious belief, and language isolate groups. Symbolic differences can also arise in isolated groups through a kind of runaway process that perhaps explains the extreme exaggeration we observe in fads and fashions, and in the colorful excesses with regard to ordinary utility in many ritual systems. 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 for 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 physical 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 submitted). This form of cultural group selection is potentially very rapid. Much of the spread of European culture in the last 500 years was due to the displacement and/or replacement of indigenous peoples, as in the case of the Indians and White settlers in North America. Currently, however, Europeanization ("modernization," and "globalization") depends much more upon the voluntary adoption of party systems, parliaments, Marxism, factory organization of work, and so forth than it does on displacement or forced conversion.

Thus, human-scale societies may have evolved because the peculiar properties of the cultural inheritance system lend themselves to group selection. Originally, processes like conformity may merely have functioned to reduce the risk of adopting foreign traits that are less likely to be useful than home grown 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 merely 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 "correcting" the situation. The association of altruistic norms with complex, apparently useless or even dangerously erroneous, religious and ritual systems suggests that cultural systems have evolved to hide group-functional behavior from attack by genetically selfish decision rules. As Rappaport (1979: 100) puts it in the context of cultural rules that prevent over-exploitation of the environment, "to drape nature in supernatural veils may be to provide her with some protection

against human folly and extravagance." Conflicts between narrower loyalties to self-interest and kin and larger loyalties to groups often do seem to generate considerable conflict in individuals, as if genetic and culture rules do still struggle for mastery of our behavior (Campbell 1975; Richerson and Boyd 1998, 1999).

We have attempted to measure the rate of group selection in simple societies, using data on local group extinctions in Highland New Guinea in pre-contact time (Soltis et al. 1995). These rates are fairly substantial, and might result in the replacement of more group-favorable traits in a metapopulation in something like 1,000 years. This seems about right to account for the relatively slow, halting evolution of more complex and more powerful polities over the 10,000 years since crop cultivation made complex societies ecologically feasible.

V. Discussion

Many readers may find a fully Darwinian theory of human behavior as disconcerting as did Darwin's Victorian colleagues. It is pleasant to believe that human evolutionary "achievements" give us an exalted place on nature's stage. It is comforting to believe that natural laws underpin the moral order. At least these ideas are deeply entrenched in Western thought. Darwin's view does seem rather austere and a threat to common justifications for ethical beliefs (but see Richards 1987: Appendix 2). It encourages us to look upon human traits as products of ecological circumstances and historical accidents, not of a progressive trajectory. Even in the case of traits where natural selection has clearly played a dominant role, it encourages us to count the cost of adaptations as well as their benefits.

Human culture appears to us to have originated as an adaptation permitting rapid evolution in a noisy environment of the Pleistocene. The costs include the very considerable complexity and clumsiness of a coevolutionary system in which genes and culture are often antagonists, though more often collaborators. 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.

However discomforting Darwinism may be to our conventional views of humans, there is no convincing evidence that it is actually dangerous to ethics. Darwin himself, a devoted father of 9 children, was far indeed from becoming a moral degenerate as a result of entertaining the hypothesis that humans arose due to natural selection. And he spoke of “a certain grandeur” of his view of a living world governed by materialistic laws.

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[1] Marx was an admirer of Darwin; one of the custodians of Down House was pleased to furnish us with a copy of the title page of Das Kapital, a gift from Marx with Marx' respect indicated by the note scribbled at the top.

[2] Vicareous forces can also play a role in organic evolution, as in mate choice sexual selection or in the process Odling Smee (1996) calls “niche construction.”

[3] The historian of ecology Robert McIntosh (1985) notes that in that discipline, “precursors,” people whose ideas are reinvented without any obvious influence the reinventor, are common, probably because so many ideas are implied by other ideas. Campbell, having the basic Darwinian ideas clearly in mind, needed little specific guidance to apply them to culture.