Philosophica 60 (1997, 2) pp. 13-43

# BUILT FOR SPEED, NOT FOR COMFORT. DARWINIAN THEORY AND HUMAN CULTURE

*Peter J. Richerson & Robert Boyd*

## 1. *Darwin's Problems With Humans*

### 1.1. 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[.]" 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.

### 1.2. Who Would Do Man?

Darwin knew his theory was considered dangerously radical by the vast

majority 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 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 explosively controversial, species. Lyell (1863), Huxley (1863), and Wallace (1864, 1869) all produced books and papers on the subject. But none of the work was close to satisfactory. Huxley was too busy and inexperienced in ethnology and sociology to consider anything but anatomy, although this work was most effective in showing that human bodies were derived from ape-like progenitors. Lyell, still a sceptic 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. He had succumbed to the Spiritualism fad sweeping England, and the austere materialism of selection no longer satisfied him as an explanation for human origins.

Darwin eventually took on the task of writing the *Descent*, but had little success in convincing any significant body of his contemporaries that natural and sexual selection played fundamental roles in the origin of the human mind. No 20th Century social science derives any significant influence from the *Descent*, and to this day influential 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. 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?

Why did even devoted Darwinians balk at applying their ideas to humans? 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 historian Burrow (1966), a significant segment of Victorian opinion was sceptical of conventional religion, and was willing to grant that evolution occurred. 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 natural laws. If God's Law was to be dismissed by the scientific minded as superstition, it was all that much more important to find a substitute in natural laws that scientists were discovering.

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 an advanced rank for their own societies.[1]

## 1.3. Darwin's Argument

Darwin's project in the *Descent of Man* was different. His theory was one of adaptation to local ecological conditions, not one that led to a theory of progress. As he put it in the N Notebook in 1838, "In my theory there

is no absolute tendency to progression, excepting from favorable circumstances" (Barrett, 1974: 339). The naturalistic ethics so beloved of his secular contemporaries could find no legitimate root in the soil tilled by natural selection. The *Edinburgh Review* was quite right that Darwin wanted human evolution to be subject to the same evolutionary processes as affected other animals. The *Descent*'s chapter on the evolution of the intellectual and moral facilities gives a large role to natural selection, for example.

In the years after he developed the theory of natural selection but before its publication, Darwin adopted a curious rhetorical style to soften this views for Victorian sensibilities. For example, he used 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: 242-7). But, noting the much more "advanced" status of closely related peoples in the nearby benign regions of the Pampas of Argentina, the brief, plainspoken conclusion was that evolution had merely fitted the Fuegans "to the climate and productions of this miserable country," the cold, damp mountainous lands on the Straits of Magellan. "Here," he would have said if he cared to drive the point home, "would go Englishmen, but for the luck of favorable geography."

Darwin was keen to minimize qualitative differences between humans and other animals. He did not want his theory to 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, he imagined that animals had much the same capacity to modify their behavior by imitating others 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), Tomasello (1996), and other modern students of animal imitation have demonstrated some such effects in some vertebrates, but nothing approaching human capabilities.

Darwin (1871, 1868) built his whole theory of inheritance around the idea of the inheritance of acquired variation, of which the role of imitation in behavioral traits was an important example. He imagined that the traits of organisms could be arrayed along a continuum, from those weakly affected in any one generation by the effects of the environment to those much more strongly affected. The more conservative traits included most anatomical features. Thus mutilations, like severing the tails of mice, had no perceptible effect on their offspring's tail length. Behavioral traits, Darwin thought, were much more labile. Habits acquired during one's life could be transmitted to offspring, permitting relatively rapid behavioral adaptation to different circumstances. Under favorable conditions human civilization could "advance" at a pretty impressive pace, or "regress" just as quickly to equip the Fuegans with the rough skills and brutal attitudes necessary to survive under subarctic conditions. He even essayed an elaborate theory involving "gemmules" carried from various parts of the body, including the brain, to the gonads for incorporation into sex cells and transmission to the next generation. In this scheme, humans differed from other animals mainly in having a greater range of relatively labile behavioral traits.

Looking back in light of modern discoveries, the theoretical edifice constructed in the *Descent* is at once very modern and very strange. It was consistent with much biology, anthropology and sociology as known in the 19th Century, and Darwin's notions of the widespread importance of imitation and other forms of the inheritance of acquired variation did provide continuity between humans and other animals. His theory allowed him to account for the essential similarity of all living humans, while accounting for the vast diversity in human behavior, by attributing the underlying similarities to conservative traits and by attributing variation between human groups mostly to labile traits strongly influenced by inherited habits. Darwin's distinction between more conservative and more labile traits did the same work for him that the modern gene-culture distinction does for us.

The main problem is that, for all of its considerable elegance, Darwin's theory of inheritance is mistaken. The conservative traits (read genetic) do not actually exhibit the property of inheritance of acquired variation. Human culture does operate as a system for the inheritance of acquired characteristics, but it is rudimentary or lacking in other animals. The gap was greater than Darwin imagined [2].

Darwin's errors are of more than antiquarian interest. His failure to successfully account for the relation of humans to other animals, or motivate others to do so, left a major gap in evolutionary theory that contemporary workers, beginning with Campbell's (1960, 1965, 1975) path-breaking "blind-variation and selective retention" papers, are only now beginning to fill.

## 2. *The Twentieth Century*

### 2.1. 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 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, the intellectual leaders of the newly emerging social sciences almost entirely ignored the ideas in the *Descent* (Ingold, 1986). 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. 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*. 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).

Dobzhansky and Montagu's (1947) influential paper 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), Carniero (1967), and Lenski and Lenski (1982), remained wedded to progressive evolutionary theories, often in the mistaken belief that Darwinian evolution was also progressive.

## 2.2. 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 1871. 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. Second, in the 1965 chapter, he provided a clear argument for why Darwinian theory ought to applicable to any system of inheritance, including culture. Third, in his 1975 article, he carefully distinguished between Darwinian and Progressivist 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.

Perhaps the most important idea was the concept of vicarious selectors. How could it be that animals could acquire adaptive variations that anticipate what natural selection would favor? Darwin certainly believed that humans and animals could acquire adaptive variations, but he gave

no clue as to how this neat trick could itself evolve. Campbell noted that if variations are acquired other than randomly, it must be because organisms have the capacity to use some sort of rules to modify behaviors or structures. Indeed, plants and animals have many such capacities, the most familiar of which is ordinary trial and error learning, itself an example of blind variation and selective retention in Campbell's view. Natural selection has arranged sensation of reward and punishment so that learning normally favors behaviors that are useful to survive and reproduce. Campbell termed such processes "vicarious selection"; the rules of learning select behaviors on behalf of natural selection. All forms of vicarious selection are derived ultimately from the action of natural selection. Where else could they come from?

This bit of conceptual clarification accounts for the major difference between the cultural and genetic systems of inheritance, and gives a general hypothesis for how they interact. 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, and natural selection, making unvarnished organic evolution a purely random variation and selective retention process[3]. Cultural evolution must be subject to the analogs of these three 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 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).

The idea that genes and culture form a complex, coevolving system in humans, linked by vicarious selection and the operation of natural

selection on the jointly generated phenotype, was well developed in Campbell's work culminating in the 1975 paper. Subsequently, two rather distinctive schools of thought have developed on the nature of gene-culture coevolution, the human sociobiology championed by Wilson and Lumsden (1981), Alexander (1979), and their followers, and the population genetical approach pioneered by Cavalli-Sforza and Feldman (1981).

## 2.3. 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)?

They 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, on the basis of 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 on the senses will favor making them seem 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 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 them justice. Nevertheless, the point of the sociobiologists should be well taken 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 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 Polynesian 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).

## 3. *Evolutionary Theory of Culture*

### 3.1. Population Thinking Applied to Culture

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. Oddly enough, 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, well articulated by Campbell (1965; 9175), 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 is typically subtly different from the previous one. As many generations pass, changes accumulate and evolution occurs. This deep similarity 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 ought to be 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 a neglected thread, the evolution of systems with inheritance of ac-

quired variation and other non-mendelian properties.

### 3.2. Basic Processes of Gene-Culture Coevolution

The task implied by 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; 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 both viruses and bad habits!

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 75 years after it was pioneered by R. A. Fisher (1918).

## 3.3. 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. Why do humans make such *massive use of culture* compared to other animals? Why does our culture include so much *symbolic variation*, for example such a diversity of languages? Why do humans live in such *large, cooperative groups* with an extensive division of labor, again compared to most other animals? There are some interesting tentative answers to these questions emerging from this work.

### 3.3.1. 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: 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, 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 still 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. Theory suggests that culture has a suite of costs and benefits. Understanding what these are is essential to understanding under what circumstances a species might even be a candidate to negotiate any intrinsic barriers to the evolution of complex culture.

Simple population genetics style models that link a capacity for individual learning with a capacity imitation create a basic model of the inheritance acquired variation. They illustrate how culture can have real advantages in some environments, but not 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 systems. The largest advantage to culture comes in environments that are changing a lot on the time scale of tens 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.

Some scholars, especially those influenced by the rational choice model of economists, are prone to view learning costs as low and ac-

curacy as high. This cannot be true in general. It is implausible that people could learn more than a small fraction of their complex skills by themselves. Imagine reinventing calculus, or the germ theory of disease, or how to build computers for yourself, much less all three. Or imagine your life depended upon reinventing San (Bushman) arrow poison. Even with the hint that it is derived from beetles and a significant research budget, it would take a long time to discover a workable recipe, whereas a San hunter acquires the technique with minimum effort by tradition.

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. There is some empirical support for this result. The origin human culture, and further in the past 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). 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. 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. Humans were perhaps the most successful mammalian lineages by the end of the Pleistocene, achieving a global distribution and respectable population densities.

However, there is clearly something 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 common systems for simple social learning.

### 3.3.2. 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, it is an advantage to be able to seek a better mentor. It may also be useful to use the commonness of a trait as a 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 they say. 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). These "mind viruses" defeat the vicarious-selector analogs of the immune system that usually allows us to reject harmful traits by being intensely pleasurable instead of painful. They prey upon the fact that people depend upon non-parental transmission to acquire many useful traits. Natural section acting on parentally transmitted culture and on genes could reduce the chances

of acquiring such traits by making decision-making more sophisticated, but only by foregoing the benefits of being able to imitate superior non-parents.

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 anthropomorphically, 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 sociobiologist's predictions?

Modern societies have greatly expanded non-parental routes of transmission. 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 that 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 countryside. 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 aspiring modern professionals have discovered by experience. The odd rural communities that developed low fertility, by contrast, simply slowly wasted away. Coale (1986) has collected a number of examples from rural 19th Century Europe where norms resulting in below-replacement fertility and population decline in local districts. Isolated peasant communities lack the prestige and communications channels to recruit imitators for their life styles from afar, and their low fertility was unsustainable.

### 3.3.3. 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, and was a close student of ethnicity itself, probably the most ancient and durable form of symbolically marked group (Levine and Campbell, 1972).

To address this problem, we have constructed theoretical models in which individuals use marker traits to assess whom to imitate. 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) 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.

The first appearance of stone tools with unmistakable stylistic variation and the first preserved art so far discovered come from the Aurignacian of Europe beginning 35,000 years ago. 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 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 divide. The ethnic markers model is a candidate explanation for why. 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 florishing 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.

### 3.3.4. 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 in based on kinship, in accordance with Hamilton's 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 generally maintain relatively peaceable relations with each other, and routinely cooperate in subsistence, defense, and other activities. 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 which range up to many millions of people.

Compared to many agriculturally based societies of the last 10,000 years ago, 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. Interband affairs were probably regulated by *ad hoc* negotiations dominated but not controlled by the headmen.[4].

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) have shown how cooperation among pairs of individuals can arise if there are a large enough 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, 1991). 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 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 sceptical that selection between groups is effective. The problems with group selection are relatively 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 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 the 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 there are only a few influential teachers 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). 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. 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") 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 reduced 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, in press).

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 slow, halting evolution of more complex and more powerful polities over the 10,000 years since crop cultivation made complex societies ecologically feasible.

## 4. *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. 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 co-evolutionary 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: 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 vise 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.

University of California-Davis
University of California-Los Angeles

*Acknowledgments*. We dedicate this paper to Don Campbell, whose leadership of the project to apply evolutionary theory in the social sciences meant so much to us personally as well as intellectually. Ramon Margalef inspired its writing and the publication of an earlier version in Catalan. We acknowledge the support of the Alfred P. Sloan Foundation for support of some of the research described in this article. The Zentrum für Interdisziplinare Forschung, Universität Bielefeld, and the head of its project on the Biological Foundations of Culture, Prof. Peter Weingart, gave us the leisure and stimulus to develop some of the new ideas described here.

## NOTES

1. Such ideas are still very popular. Bronowski (1973) wrote a book and produced a popular BBC TV series titled *The Ascent of Man* with a distinctively progressivist flavor in quite recent years. Even paleoanthropologist David Pilbeam's (1972) more sober account carried the same title.
2. Darwin is frequently portrayed as a primitive genetic determinist, biologizing humans (Alland, 1985). Ironically, the truth is the opposite. Darwin humanized biology by projecting a system of inheritance and a set of mental capabilities on all organisms that only humans seem to have in a well

developed form. His theory was in many respects a better starting point for the social sciences than for biology! It is also true that the genetic system does have some inheritance of acquired variation (Jablonka and Lamb, 1989).

3. Vicarious forces can also play a role in organic evolution, as in mate choice sexual selection or in the process Odling Smee et al. (1996) call "niche construction."

4. Price and Brown (1985) argue that analogies with modern hunters and gatherers, who have been evicted from all but the poorest of the world's environments by agriculturalists, somewhat underestimate the social complexity achieved by many earlier societies, so that some Upper Paleolithic societies may have had a formal hierarchy of formal office-holding chiefs, something like the famous American Plains tribes of historic times. In any case, bonds of sentiment were more important than formal leadership in maintaining the coherence of these groups. Bands and individual families almost certainly had very considerable autonomy. The larger scale bonds of sentiment likely led to periodic assemblies of bands for ritual occasions, sharing of resources in hard times, cooperation in hunts if ecological circumstances favoured this, and cooperation in warfare with unrelated or more distantly related peoples Relations among bands were undoubtedly not entirely peaceful. Lacking really effective systems of justice, disputes ultimately had to be settled by self-help violence. Often, feuding is prevalent in simple societies. However, it typically seems that many semiformal mechanisms exist to minimize violence among coethnics. Headmen attempt to mediate disputes, a traditional scale of payments for crimes such as murder often exists, pathologically violent individuals may be killed by their own relatives or handed up to a mob without much complaint, and the most lethal weapons are often proscribed in intra-ethnic fighting. By contrast, violence between ethnically unrelated peoples is typically much less restrained. Often, among hunters and simple agriculturalists, ethnic groups are permanently hostile, with suspicious, armed truce the most peaceable relations feasible (this has a distressingly modern ring; ugly conflicts between ethnic units are common).

## REFERENCES

Alexander R.D. (1979), *Darwinism and Human Affairs*. Seattle: University of Washington Press.

Alexander R.D. (1987), *The Biology of Moral Systems*. New York: Aldine De

Gruyter.
Alland A., jr. (1985), *Human Nature: Darwin's View*. New York: Columbia University Press.
Anonymous. (1871) Review of the Descent of Man and Selection in Relation to Sex by Charles Darwin. *The Quarterly Review* **131** (216), pp. 47-90.
Anonymous. (1871), Review of The Descent of Man and Selection in Relation to Sex by Charles Darwin, Contributions to the Theory of Natural Selection by A.R. Wallace, and On the Genesis of Species by St. George Mivart. *The Edinburgh Review or Critical Journal*, July, pp. 195-235.
Axelrod R., and W.D. Hamilton (1981), The evolution of cooperation. *Science* **211**, pp. 1390-6.
Barkow J.H., L. Cosmides, and J. Tooby (1992), *The Adapted Mind: Evolutionary Psychology and The Generation of Culture*. New York: Oxford Univ. Press.
Barrett P.H. (1974), Darwin's Early and Unpublished Notebooks. In H. E. Gruber, *Darwin on Man*. New York: Dutton, pp. 259-426.
Bettinger R. (1991), *Archaeological and Evolutionary Approaches to Hunter-Gathers*. New York: Plenum.
Borgerhoff Mulder M. (1987), On cultural and reproductive success: Kipsigis evidence. *Amer. Anthrop* **89**, pp. 617-634.
Boyd R. and P.J. Richerson (1985), *Culture and the Evolutionary Process*. Chicago: Chicago University Press.
Boyd R. and P.J. Richerson (1987), The evolution of ethnic markers. *Cultural Anthropology* **2**, pp. 65-79.
Boyd R. and P.J. Richerson (1991), Culture and cooperation. In R.A. Hinde and J Groebel (eds.) *Cooperation and Prosocial Behavior*. Cambridge: Cambridge University Press.
Boyd R. and P.J. Richerson (1996), Why culture is common but cultural evolution is rare. *Proceedings of the British Academy* **88**, pp. 77-93.
Bronowski J. (1973), *The Ascent of Man*. Boston: Little, Brown.
Burrow J.W. (1966), *Evolution and Society: A Study in Victorian Social Theory*. Cambridge: Cambridge University Press.
Campbell D.T. (1960), Blind variation and selective retention in creative thought as in other knowledge processes. *Psychological Review* **67**, pp. 380-400.
Campbell D.T. (1965), Variation and selective retention in sociocultural evolution. In H.R. Barringer, G.I. Blanksten, and R.W. Mack (eds.) *Social Change in Developing Areas: A Reinterpretation of Evolutionary Theory*. Cambridge, Mass.: Schenkman.
Campbell D.T. (1969), Ethnocentrism of disciplines and the fish-scale model of omnicience. In M. Sherif and C.W. Sherif (Eds.) *Interdisciplinary Relationships in the Social Sciences*. Chicago: Aldine.

Campbell D.T. (1975), On the conflicts between biological and social evolution and between psychology and moral tradition. *American Psychologist* **30**, pp. 1103-1126.

Campbell D.T. (1983), Two distinct routes beyond kin selection to ultrasociality: implications for the social sciences and humanities. In: D. Bridgeman (Ed.) *The Nature of Prosocial Development*. New York: Academic Press.

Carniero R.L. (1967), *Editor's introduction to The Evolution of Society* (Selections from H. Spencer's The Principles of Sociology). Chicago: University of Chicago Press.

Cavalli-Sforza L.L. and M.W. Feldman (1981), *Cultural Transmission and Evolution: A Quantitative Approach*. Princeton: Princeton University Press.

Coale A.J. (1986), The decline of fertility in Europe since the Eighteenth Century as a chapter in human demographic history. In A.J. Coale and S.C. Watkins (eds.) *The Decline in Fertility in Europe*. Princeton: Princeton University Press. pp. 1-30.

Coale A.J. and R. Treadway (1986), A summary of the changing distribution of overall fertility, marital fertility, and the proportion married in the provinces of Europe. In A.J. Coale and S.C. Watkins (eds.) *The Decline in Fertility in Europe*. Princeton: Princeton University Press. pp. 31-79.

Daly M., and M. Wilson (1988), *Homicide*. New York: Aldine De Gruyter.

Cravens H. (1978), *The Triumph of Evolution: American Scientists and the Heredity-Environment Controversy, 1900-1941*. Philadelphia: University of Pennsylvania Press.

Darwin C. (1845), *Journal of Researches into the natural History and Geology of the Countries Visited During the Voyage of H.M.S. Beagle Round the World, Under the Command of Capt. Fitz-Roy, R.N.* London: Colonial and Home Library.

Darwin C. (1871), *The Descent of Man and Selection in Relation to Sex*. London: John Murray.

Darwin C. (1868), *The Variation of Plants and Animals Under Domestication*. London: John Murray.

deMenocal P.B. (1995), Plio-Pleistocene African Climate. *Science* **270**, pp. 53-59.

Dobzhansky, T. (1962), *Mankind Evolving*. New Haven: Yale University Press.

Dobzhansky, T. and M.F.A. Montagu (1947), Natural selection and the mental capacities of mankind. *Science* **106**, pp. 587-590.

Fisher, R.A. (1918), The correlation between relatives on the supposition of mendelian inheritance. *Trans. R. Soc. Edinburgh* **52**, pp. 399-433.

Foley, R. (1987), *Another Unique Species: Patterns of Human Evolutionary Ecology*. Essex: Longman.

Galef, B.G., Jr. (1988), Imitation in animals: history, definition, and interpreta-

tion of data from the psychology laboratory. In T.R. Zentall and B.G. Galef, Jr. (eds.), *Social Learning: Psychological and Biological Perspectives*. Hillsdale, New Jersey: Lawrence Erlbaum.

Gruber, H. E. (1974), *Darwin on Man: A Psychological Study of Human Creativity*. New York: Dutton.

Goodenough, O. and R. Dawkins (1995), The St. Jude Mind Virus. *Nature* **371**, pp. 23-24.

Hamilton, W.D. (1964), The genetical theory of social behavior, I, II. *J. Theoret. Biol.* **7**, pp. 1-52.

Hunt, L.G. and C.D. Chambers (1976), *The Heroin Epidemics: A Study of Heroin Use in the United States, 1965-1975*. New York: Spectrum.

Huxley, T.H. 1863 [1984]. *Man's Place in Nature and Other Essays*. London: Macmillan.

Ingold, T. (1986), *Evolution and Social Life*. Cambridge: Cambridge University Press.

Irons, W. (1979), Cultural and biological success. In N. Chagnon and W. Irons (eds.) *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective*. North Scituate, Mass.: Duxbury.

Jablonka, E., and M.J. Lamb (1989), The inheritance of acquired epigenetic variants. *Journal of Theoretical Biology* **139**, pp. 69-84.

Jensen, A.S. (1969), How much can we boost IQ and scholastic achievement? Harvard Educ. *Rev.* **39**, pp. 1-123.

Jerison, H.J. (1963), *Evolution of Brain and Intelligence*. New York: Academic Press.

Knauft, B.M. (1987), Divergence between cultural and reproductive success in preindustrial cities. *Cultural Anthropology* **1**, pp. 94-114.

Landau, M. (1984), Human evolution as narrative. *American Scientist* **72**, pp. 262-68.

Lenski, G. and J. Lenski (1982), *Human Societies: An Introduction to Macrosociology*. New York: McGraw-Hill.

LeVine, R.A. and D.T Campbell (1972), *Ethnocentrism: Theories of Conflict, Ethnic Attitudes, and Group Behavior*. New York: Wiley.

Lorenz, K. (1966), *On Aggression*. London: Methuen.

Lumsden. C.J. and E.O. Wilson (1981), *Genes, Mind, and Culture: The Coevolutionary Process*. Cambridge, Mass.: Harvard University Press.

Lyell, C. (1863), *Geological Evidences of the Antiquity of Man*. Philadelphia: G.W. Childs.

F.J. Odling-Smee (1996), Niche construction, genetic evolution and cultural change. *Behavioral Processes* **35**, pp. 195-205.

Pilbeam, D. (1972), *The Ascent of Man: An Introduction to Human Evolution*. New York: Macmillan. ).

Potts, R. (1996), Evolution and Climate Variability. *Science* **273**, pp. 922-923.

Price, T.D. and J.A. Brown (1985), *Prehistoric Hunter-Gatherers: The Emergence of Cultural Complexity*. Orlando: Academic Press.

Provine, W. B. (1971), *The Origins of Theoretical Population Genetics*. Chicago: University of Chicago Press.

Pulliam, H.R., and C. Dunford (1980), *Programmed to Learn: An Essay on the Evolution of Culture*. New York: Columbia University Press.

Rappaport, R.A. (1979), *Ecology, Meaning, and Religion*. Richmond, Calif.: North Atlantic Books.

Richerson, P.J. and R. Boyd. In press. The evolution of human ultra-sociality. In: I. Eibl-Eibisfeldt and F. Salter (Eds.) *Ideology, Warfare, and Indoctrinability*. Berghahn Books.

Rogers, A.R. (1989), Does biology constrain culture? *Amer. Anthrop.* **90**, pp. 819-31.

Sahlins, M. (1976), *The Use and Abuse of Biology*. Ann Arbor: University of Michigan Press.

Silk, J. (1980), Adoption and Kinship in Oceania. *Amer. Anthrop.* **82**, pp. 799-820.

Simoons, F.J. (1978), Traditional use and avoidance of foods of animal origin. *BioScience* **28**, pp. 178-184.

Smith, E.A. and B. Winterhalder, eds. (1992), *Evolutionary Ecology and Human Behavior*. New York: Aldine De Gruyter.

Soltis, J., R. Boyd, and P.J. Richerson (1995), Can group-functional behaviors evolve by cultural group selection: An empirical test. *Current Anthropology* **16**, pp. 473-494.

Tarde, G. (1903) [1962], *The Laws of Imitation*. Gloucester Mass.: Peter Smith.

Tomasello, M. (1996), Do apes ape? In C.M. Heyes and B.G. Galef, Jr. *Social Learning in animals*. San Diego: Academic Press. pp. 319-346.

Vrba, E.S., G.H. Denton, T.C. Partridge, and L.H. Burckle (1995), *Paleoclimate and Evolution*. New Haven: Yale University Press.

Wallace, A.R. (1864), The origin of human races and the antiquity of man deduced from the theory of "natural selection." *Anthrop. Rev.* **2**, pp. 158-187.

Wallace, A.R. (1869), Geological climates and the origin of species. *Quart. Rev.* **126**, pp. 359-399.

White, L. (1959), *The Evolution of Culture*. New York: McGraw-Hill.

Wilson, E.O. (1975), *Sociobiology: The New Synthesis*. Cambridge, Mass.: Harvard University Press.