Draft 2.3: March 20, 2016

The Use and Non-use of the Human Nature Concept by Evolutionary Biologists

Peter J. Richerson

Environmental Science and Policy

University of California—Davis

pjricherson@ucdavis.edu

Intended for *Why We Disagree About Human Nature*, Elizabeth Hanlon and Tim Lewens, Editors, Oxford University Press

What does evolution teach us about human nature? It tells us that human nature is a superstition.

Michael Ghiselin (1997: 1)

Introduction

"Human nature" seems on the face of it to be an essentialist concept with no place in a proper Darwinian analysis of human behavior. David Hull (1986) wrote a powerful critique along these lines. Tim Lewens (Lewens, 2012) endorses and extends Hull's analysis but points out that a very weak version of human nature is tenable, one in which it just refers to the ensemble of genetic differences between ourselves and other species. Lewens argues that any strong conception of human nature in which the term does real work—his examples are evolutionary psychology and the morality of altering our supposed nature—cannot be sustained. Nevertheless, the term "human nature" figures heavily in the writings of many of the most important scholars over the last 40 years who want to use evolutionary theory to explain human behavior.

The aim of this paper is to examine a sample of the most prominent papers and books using the term human nature in what seems to be a strong way and contrasting them with evolutionary scholars who do not use the term at all or at least not in a strong way. Several of the human nature pieces I will examine were written by eminent evolutionary biologists who have taken an interest in human evolution. The others are evolutionary psychologists whose knowledge of evolution is better than adequate. They would not defend a simplistic typological notion of human nature, though some arguments could almost be construed as such. They use the term in titles of books and papers, suggesting that it does do real work in their thinking. What work does it do? Does it do this work successfully? How do the recent users of human nature fit into the larger picture of evolution literate accounts of human behavior? Do users and non-users of the term have significantly different ideas about the processes active in human evolution? I will proceed in an historical fashion, starting with Darwin, whose ideas about human evolution in the *Descent of Man* were rather detailed and sophisticated.

The main issue turns out to be how strongly authors are committed to the tenets Modern Synthesis. The authors who use the term "human nature" in a strong form are committed to natural selection acting on genes being the "ultimate" explanation for human evolution. Ernst Mayr's (1961) famous paper "Cause and Effect in Biology" argued that causes in biology could be divided into ultimate causes, like those resulting from natural selection on genes, and proximate causes, those resulting from physiology and mechanisms of phenotypic flexibility like individual learning. He held that ultimate causes explain how proximate causes evolve but that proximate causes play no role in explaining how ultimate causes like selection operate. If human culture is just a mechanism of phenotypic flexibility, then it cannot be a part of the ultimate explanation of human behavior. The human nature theorists reviewed here want to collect all the results of selection acting on genes under the term human nature, providing the ultimate answer to why humans are the creatures they are.

Those of us who use "human nature" in Lewens' weak way, if at all, doubt that non-genetic inheritance systems like human culture can be treated as proximate causes that have no effect on human genetic evolution (Mesoudi et al., 2013; P. J. Richerson & Boyd, 2005). First, human culture can be subject to natural selection just as genes can, so culture is part of the ultimate causal process. Second, we have examples of culture acting as a selective force on genes (Laland, Odling-Smee, & Myles, 2010; Ross & Richerson, 2014). More broadly, culture may well have shaped many innate aspects of human psychology, physiology and anatomy by gene-culture coevolution (Richerson et al., 2016). Cultural evolution is affected by forces considered unimportant in the Modern Synthesis such as Lamarckian inheritance of acquired variation. If cultures can act as selective forces on genes, then the toolkit of the Modern Synthesis is inadequate to provide a complete account for human evolution. The broader version of this critique based on other non-genetic inheritance systems and applying to many species is called the Extended Evolutionary Synthesis (Laland, Sterelny, Odling-Smee, Hoppitt, & Uller, 2011). For models that illustrate the basic dynamic differences between the Modern Synthesis and the gene-culture coevolutionary treatments of culture see (Morgan, In press).

Darwin

It is interesting to consider contemporary writings on human nature in light of Darwin's ideas. In the *Descent of Man and Selection in Relation to Sex* Darwin (1874) spent 430 pages laying out his ideas about human evolution. In the preface to the second edition he writes that "great weight must be attributed to the inherited effects of use and disuse, with respect both to the body and the mind." He protests that he entertains the importance of many evolutionary processes besides natural selection.

Two important themes are relevant to the 20th and 21st century writing on human nature.

First, in Chapter V, he considers "The Improvement of the Intellectual and Moral Faculties During Primeval and Civilized Times." He distinguishes between the processes important in primeval and civilized times. During primeval times natural selection would have been the primary force advancing the intellectual and moral faculties. He also remarks that "as soon as the progenitors of man became social (and this probably occurred at a very early period) the principle of imitation, and reason, and experience would have increased, and much modified the intellectual powers in a way of which we see only traces in lower animals." [174] Even during the primeval period he imagines that what we would summarize today as intellectual and cultural factors were already important:

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

As regards civilized times the role of what we now call cultural factors was even more important:

> With highly civilized nations, continued progress depends in a subordinate degree on natural selection. . . . The more efficient causes of progress seem to consist of a good education during youth while the brain is impressible, and of a high standard of excellence, inculcated by the

> ablest and best men, embodied in the laws, customs, and traditions of the nation, and enforced by public opinion (Darwin 1874: 192).

Second, in Chapter 7 "On the Races of Man" argued in favor of the psychic unity of humans and against the idea that the races could be considered separate species (a major plank in the racist ideology of his day):

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

The term "human nature" is absent from the detailed index of the *Descent of Man*. Clearly, Darwin saw inherited variation everywhere and if he had used the phrase it would likely have been in Lewens' permissible but powerless vein. Darwin's own ideas on human evolution were influential in the late 19th century but had little influence on the emerging social science disciplines as they crystalized at the turn of the 20th Century (Hodgson, 2004; Richards, 1987). Nor do most evolutionary biologists or Evolutionary Psychologists[1] writing about human evolution cite the *Descent of Man* in any detail. From the viewpoint of evolutionists writing after the mid-20th century Modern Synthesis, Darwin's subscribing to the inheritance of acquired variation was perhaps his greatest error according to the Modern Synthesis (Huxley, 1942). Thus evolutionary biologists came to the problem of human evolution with a worldview strongly influenced by genes as the dominant if not exclusive means of inheritance. Social scientists were aware that culture could be viewed as a Lamarckian sort of inheritance system (Kroeber, 1948), but until the late 20th Century they did not develop this idea in anything like the theoretical and empirical intensity that evolutionary biologists pursued the gene-based view of organic evolution.

Theodosius Dobzhansky

Dobzhansky (1937) was the architect of the Modern Synthesis who took the most interest in human evolution. His (Dobzhansky, 1962) prizewinning book *Mankind Evolving: The Evolution of the Human Species* had gone through 17 printings by 1975 when it suddenly fell in the shadow of important developments in the evolution of social behavior that E.O. Wilson summarized in *Sociobiology: The New Synthesis*. Dobzhansky used the term human nature in Lewens innocent sense, but it does not appear in the index. *Mankind Evolving* is notable for its attempt to reconcile the then dominant view of genetic

[1] The capitalized "Evolutionary Psychologists" refers to the influential school of evolutionary psychology established by John Tooby and Leda Cosmides. Steven Pinker is a well know adherent. But many evolution-minded psychologists are not Evolutionary Psychologists in this sense.

inheritance as fundamental to the organic evolution of all species including humans with the then well-established view of most social scientists that the dominant source of variation in humans was cultural. He introduces his view thusly:

> The thesis to be set forth in the present book is that man has both a nature and a "history." Human evolution has two components, the biological or organic, and the cultural or superorganismic. These components are neither mutually exclusive nor independent but interrelated and interdependent. Human evolution cannot be understood as a purely biological process, nor can it be adequately described as a history of culture. It is the interaction of biology and culture. There exists a feedback between biological and cultural processes [p. 18].

He goes on to critique biologists who disparage the importance of culture and social scientists who want biological evolution to have merely evolved a vehicle for cultural evolution. He introduces some science fiction examples of how cultural evolution of the science of human biology might eventually produce human populations without the need for sexual reproduction; culture could be that powerful.

Other passages in his introduction reinforce these thoughts:

> In producing the genetic basis for culture, biological evolution has transcended itself—it has produced the superorganic. Yet the superorganic has not annulled the organic [p. 20].

> The fact which must be stressed, because it has been frequently missed or misrepresented, is that biological and cultural evolution are parts of the same natural process [p. 22].

Dobzhansky's thesis sounds a lot like Darwin's (1874) in the *Descent* with the now strongly established genetic inheritance theory substituted for Darwin's ideas of inheritance, which were, by his own admission, unsatisfactory speculations. Interestingly, the *Descent of Man* is not formally cited in *Mankind Evolving*, although at one point he remarks

> In his books Darwin confined himself to biological matters, even in the *Descent of Man* and *The Expression of Emotion in Man and Animals* (1872) [p. 7].

As we have seen, this is quite incorrect, suggesting that Dobzhansky had never read the *Descent* carefully or, if he did, politely passed over those of Darwin's ideas that were incompatible with the Modern Synthesis.

Mankind Evolving is full of interesting discussions on a great variety of topics. Its treatment of human organic evolution and genetics is detailed and authoritative for its day, as one might expect from a great evolutionist. It engages well with the social sciences of its day, for example discussing Freudian psychotherapy, the role of genes and culture in race, caste in India, the nature-nurture controversy, the feedback between genes and culture among many others. He sympathetically cites social scientists, historians and humanistic writers. He does insist that evolution of genes was and continues to be important even if genetic evolution has transcended itself to produce the superorganic, but he gives cultural evolution a large role to play.

The difficulty is that the discussions of cultural evolution never climb down from the lofty generalities evident in the passages cited above. Just how did the transcendence happen? What exactly is involved in the superorganic? What is the natural process that biological and cultural evolution are both part of? Part of the problem was the fact noted above that social scientists had not followed up on Darwin's program for the study of cultural evolution after 1900. There was simply no large body of literature, like that in evolutionary genetics, to use to build its cultural partner. Furthermore, Dobzhansky's political beliefs and personal style probably led him to have a distaste for challenging social scientists on such issues. He coauthored a paper in *Science* with Ashley Montague (Dobzhansky & Montagu, 1947), an activist anti-racist with whom he worked on the UNESCO statement *The Race Question* following WWII. Montagu was not inclined to view genetic differences between groups as important at all, but Dobzhansky and other biologists reviewing the draft statement were more cautious (Brattain, 2007). They could see that some genetic differences between human groups were real, although few of them were well understood at the time. Although Dobzhansky and the other UNESCO biologists wanted to forestall invidious distinctions based on biological differences, they also wanted to make sure that human biologists were not to be condemned as racists just because they were investigating biological differences between human groups. I interpret the result as a sort of political compromise between biologists and social scientists. As Dobzhansky and Montagu put it in their *Science* paper:

> The effect of natural selection in man has probably been to render genotypic differences in personality traits, as between individuals and particularly as between races, relatively unimportant compared to phenotypic plasticity. Instead of having his responses genetically fixed as in other animal species, man is a species that invents its own responses, and it is out of this unique ability to invent, to improvise, his responses that his culture is born.

This formulation gives human biologists plenty of room to work while granting that the study of human culture by social scientists and humanists was also an entirely legitimate enterprise. Everyone could do their customary work without stepping on toes. When the next generation of scholars tried to build concrete models of transcendence, the superorganic, and a common natural basis of cultural and genetic evolution, the Dobzhansky/Montagu compromise immediately led to serious intellectual conflicts, some of them highly politicized, for example Jensen's (1969) argument that racial differences in IQ in the US are largely genetic.

The immediate cause of the rise in the use of the term human nature was seminal advances in the theory of behavioral evolution. These included W.D. Hamilton's (1964) model of inclusive fitness, George Williams (1966) casting doubt on group selection as an explanation of helping behavior, Robert Trivers (1971) paper on reciprocal altruism, Richard Alexander's (1974) synthetic review, and John Maynard Smith's (1976) application of game theory to evolutionary questions. Now evolutionists had real tools to apply to the study of behavior. The last chapter of Edward O. Wilson's (1975) magisterial *Sociobiology* showed how these tools could be applied to explaining human behavior from an evolutionary perspective. The negative reaction to this chapter on the part of certain left-wing biologists and social scientists is a famous episode that has colored relations between the natural and social sciences to this day (Segerstrale, 2000). Dobzhansky and Montague's peace treaty, if that is the right conception, broke down almost completely.

Edward O. Wilson

Wilson's (1978) *On Human Nature* enlarges upon his last chapter of *Sociobiology*. No biologist as sophisticated as Wilson would have an essentialist view of humans but by using the term as his title he must have thought it could do work for him. In the 2004 preface to the reprint of the book, he summarizes his position in 1978 thusly:

> [The naturalistic view] held that the brain and mind are entirely biological in origin and have been highly structured through evolution by natural selection. Human nature exists, composed of the complex biases of passion and learning propensities often loosely referred to as instincts. The instincts were created over millions of years, when human beings were Paleolithic hunter-gatherers. As a consequence, they still bear the archaic imprint of our species' biological heritage. Human nature can thus be ultimately understood only with the aid of the scientific method. Culture evolves in response to environmental and historical contingencies, as common sense suggests, but its trajectories are powerfully guided by the inborn biases of human nature [p. ix-x].

In his first chapter, he emphasizes that the brain is a purely biological implement that includes direct adaptations to past environments and innate censors and motivators that control culture. He speaks of reductionism, yet also of emergent phenomena. Human behavior must conform to the laws of biology but also might transcend them. This chapter is little different from Dobzhansky's (1962) position except for the invoking of the human nature term. In the rest of the book he explains that he means something rather stronger than Dobzhansky's position.

The second chapter of *On Human Nature* discusses both human universals and genetic variation for important traits much as Dobzhansky (1962) had. Wilson is sympathetic to the innatist cognitive science picture of the mind and doubts the behaviorist picture of behavior substantially shaped by general purpose learning mechanisms, arguing against the *tabula rasa* view of the mind. It is a little difficult to know how to take these passages arguing against the blank slate idea. It is quite hard for anyone with any commitment to evolutionary biology to believe that genes play no role in the properties of the mind. Behaviorists, often falsely associated with the idea of a blank slate, who want to talk about the environmental control of behavior know well that different species and even different individuals are reinforced by different stimuli; the wolf and the moose may live in the same environment, but the wolf is not reinforced by browsing on plants and the moose is not reinforced by eating wolves. Furthermore, behaviorists are perfectly comfortable with innate reflexes and fixed action patterns (Baum, 2005: Chapter 4). Rejecting the *tabula rasa* is to reject a near straw argument held in pure form only perhaps by few social scientists ignorant of modern biology. But rejecting a straw argument is no support at all for a strongly innatist one. Cultural evolutionists, like behaviorists, are quite well aware that genes and genetic evolution have a large role to play in explaining human behavior, simply hold that cultural evolution and a history of reinforcement are important as well.

A remark Wilson makes in Chapter 2 of *On Human Nature* is interesting in the light of later developments I discuss in the penultimate section of this chapter.

> Let me now rephrase the central proposition in a somewhat stronger and more interesting form: if the genetic components of human nature did not originate by natural selection, fundamental evolutionary theory is in trouble. At the very least the theory of evolution would have to be altered to account for new and as yet unimagined form of genetic change in populations. Consequently, an auxiliary goal of human sociobiology is to learn whether the evolution of human nature conforms to conventional evolutionary theory. The possibility that the effort will fail conveys to more adventurous biologists the not unpleasant whiff of grapeshot, a crackle of thin ice [p. 33-4].

It is not clear if Wilson considers himself to be an adventurous biologist in this context, but he is fairly clear that if anyone imagines that culture could somehow play a selective role in human genetic evolution that would represent a revolutionary challenge to evolutionary theory. If culture evolves in a partly Lamarckian way, or if culture exerts selection on genes via social selection, or if natural selection operates via culturally constructed environments, then the Modern Synthesis toolkit is incomplete, at least in the human case. The evolutionary biologists had struggled in the 1930s to disprove the idea of the inheritance of acquired variation and correct Darwin's greatest error. They did not follow Darwin's lead in giving cultural processes a fundamental role in human evolution. In so doing they "hardened the Synthesis" in the eyes of some (Burian, 1988; Gould, 1982). What the cultural evolutionists threaten, it seems, is not merely a minor amendment to the Modern Synthesis appropriate for one peculiar species (which is how I viewed it at the time).

Wilson invokes the theme that we already saw in Dobzhansky, a temporal subdivision of human evolution into a long period when natural selection was dominant and a short, recent period when culture became important:

> We can be fairly certain that most of the genetic evolution of human social behavior occurred over the five million years prior to civilization, when the species consisted of sparse, relatively immobile populations of hunter-gatherers. On the other hand, by far the greater part of cultural evolution has occurred since the origin of agriculture and cities approximately 10,000 years ago. Although genetic evolution of some kind continued during this latter, historical sprint, it cannot have fashioned more than a tiny fraction of the traits of human nature [p. 34].

Contrast this with Darwin's picture that imitation, reason and experience began to modify the human intellect early in human evolution.

In chapter 3 on development Wilson articulates a strongly innatist picture of development.

> The newborn infant ['s brain] is now seen to be wired with awesome precision [p. 54].
>
> This marvelous robot [the infant] is launched into the world under the care of its parents. Its rapidly accumulating experience will soon transform it into an independently thinking and feeling individual. Then the essential components of social behavior will be added—language, pair bonding, rage at ego injury, love, tribalism, and all the remainder of the human-specific

> repertory. But to what extent does the wiring of the neurons, so undeniably encoded in the genes, preordain the directions that social development will follow? [p. 54-5]

Wilson has a complex answer to this question. Human behavior is certainly not composed entirely of reflexes and fixed action patterns the way insects seem to be. "Human genes prescribe the capacity to develop a certain array of traits [p. 56]." The degree and kind of prescription is variable depending upon the trait, and pathological conditions that affect prescriptions frequently has a strong heritable component, such as schizophrenia. Some traits such as the expression of emotions are practically invariant. He rejects the alleged behaviorist idea that human learning gives rise to unlimited flexibility in response to environmental contingencies saying "The learning potential of each species appears to be fully programmed by the structure of the brain, the sequence of release of its hormones, and, ultimately, its genes [p. 65]." He comments favorably on the leading child development researcher of the time, Jean Piaget's, theory of development:

> "Piaget, who was originally trained as a biologist, views intellectual development as the interaction of an inherited genetic program with the environment. It is no coincidence that he calls this conception 'genetic epistemology,' in effect the study of the hereditary unfolding of understanding [p. 66-67]."

Wilson offers many examples of human universals in support of these ideas. Recent work on brains tends to emphasize the flexibility and responsiveness of brain development to environmental factors (e.g. Krubitzer & Seelke, 2012). Recent work on child development tends to emphasize that children are adept social learners and that development is highly structured by their cultures (e.g. Carey, 2009).

In Chapter 4, of *On Human Nature* entitled Emergence, Wilson gives culture what he thinks is its due. He says

> When societies are viewed strictly as populations, the relationship between culture and heredity can be defined more precisely. Human evolution proceeds along a dual track of inheritance: cultural and biological. Cultural evolution is Lamarckian and very fast, whereas biological evolution is Darwinian and usually very slow [p. 78].

By "Darwinian" here Wilson means the Modern Synthesis not Darwin's own ideas as expressed in the *Descent of Man*. He remarks that "Lamarckism has been entirely discounted as the basis of biological evolution, but it is precisely what happens in the case of cultural evolution [p. 79]" showing again his conventional commitment to the Modern Synthesis. A key passage follows:

> Because it is far slower than Lamarckian evolution, biological evolution is always quickly outrun by cultural change. Yet the divergence cannot become too great, because ultimately the social environment created by cultural evolution will be tracked by biological natural selection [p. p.79].

This theme is much elaborated by Lumsden and Wilson (1981: Ch. 6) in *Genes, Mind, and Culture: The Coevolutionary Process*. There they develop a mathematical model of what they consider to be the

"complete coevolutionary circuit" which they try to capture by their famous leash metaphor of the genetic master controlling the cultural dog.

In some passages Wilson does seem to invoke cultural evolution as a creative process in human evolution:

> [T]he earliest men or man-apes started to walk erect when they came to spend most or all of their time on the ground. Their hands were freed, the manufacture and handling of artifacts was made easier, and intelligence grew as the tool-using habit improved. With mental capacity and the tendency to use artifacts increasing through mutual reinforcement, the entire materials-based culture expanded. Now the species moved onto the dual track of evolution: genetic evolution by natural selection enlarged the capacity for culture and culture enhanced the genetic fitness of those who made maximum use of it. Cooperation during hunting was perfected and provided a new impetus for the evolution of intelligence, and so on through repeated cycles of causation [p. 85].

Here, cultural evolution is doing all the work that gene-culture coevolutionists would attribute to it, but they would additionally argue that the Lamarckian properties of culture and other processes outside the Modern Synthesis have to be introduced into models of the evolutionary processes. To be plausible, the human nature account needs cultural evolution to be like Darwin imagined it, but the human nature view derived from the Modern Synthesis forbids that. Wilson's human nature position is on the horns of a dilemma. If culture lacks key evolutionary properties not part of the Modern Synthesis it can't do what the above passage requires, but if it does then how can natural selection on genes be guaranteed to track cultural evolution and keep it tame at the end of a genetic leash? Will not fast cultural evolution by social selection and niche construction impose the results of its own evolution on genes? The main remaining question is whether any of the later authors who have espoused the human nature concept are free of this dilemma.

Most of the rest of *On Human Nature* takes up major thematic issues, aggression, sex, altruism, and religion. These chapters point out that these categories of behavior have roots in pre-human behavior and quite plausibly have important genetic influences. They also invoke cultural factors, such as group selection at the level of whole cultural groups and rational thought in the chapter on aggression.

> Although the evidence suggests that the biological nature of humankind launched the evolution of organized aggression and roughly directed its early history across many societies, the eventual outcome of evolution will be determined by cultural processes brought under the control of rational thought [p. 116].

This is not too different from the *Descent of Man*'s [p. 185-6] proposal that factors like reason played a role in moral progress. Cultural evolutionists also see reason playing a role in human behavior with their suggestion that humans often carefully consider which cultural variants to adopt and sometimes their thinking leads them to create new variations by modifying an existing variant to developing a new one. Trouble arises with Wilson's human nature idea when we consider the question of when it is in human evolution that reason begins to play a role in directing human behavior. If the influence of reason comes

early enough it introduces the process of culture driven gene-culture coevolution deep into human evolution. Given that our great ape ancestors were already rather big brained animals and that progressive brain size increase characterizes our genus throughout the Pleistocene, much as the p. 85 quote above suggests, reason and culture could quite plausibly have generated cultural social selection and niche construction effects on human genes for much or potentially all of the history of *Homo*. Humans have artificially selected the genes of domesticates following purposive procedures for ten millennia. Half-reasonable and moderately cultural early *Homo* might have used purposive procedures to select mates and hunting partners, and sanction enemies, that would act as a selective force on any genetic variation for cooperative abilities. Humans in effect might have domesticated themselves via social selection (Boehm, 2008).

Social selection is the effect of social actors rewarding or punishing other actors on their partners' genetic fitness. Social selection is perhaps a mechanism by which culturally transmitted norms might strongly select for genes leading to the easier conformity of behavior to norms. Human populations have relatively low frequencies of psychopathy, arguably because we have been living for much of our evolution in norm bound groups that have rewarded cooperation and punished those who could not follow norms (Chudek & Henrich, 2011).

Wilson is comfortable with group selection, perhaps even culture-based group selection, playing a role in the evolution of human aggression:

> The evolution of warfare was an autocatalytic reaction that could not be halted by any people, because to attempt to reverse the process unilaterally was to fall victim. A new mode of natural selection was operating at the level of entire societies [p. 116].
>
> [A]s societies become more centralized and complex, they develop more sophisticated military organizations and techniques of battle, and the greater their military sophistication, the more likely they are to expand their territories and to displace competing cultures [p. 117].

But there is no reason not to think that this process is restricted to relatively modern societies. In the *Descent* [p. 175], Darwin supposed that conflict between ancient tribes would have favored courage, sympathy, faithfulness and mutual aid because tribes more endowed with such virtues would outcompete those less endowed. We know from patterns of languages, artifacts, and violence in the archaeological record that humans moved, expanded, and contracted long before they became centralized and complex (e.g. Jorgensen, 1980; Schwitalla, Jones, Pilloud, Codding, & Wiberg, 2014; Tostevin, 2013).

The final 9th chapter of *On Human Nature* is entitled Hope. A human nature evolved for hunting and gathering in the Pleistocene might not seem likely to offer much ground for hope. We may try earnestly to promote peace via reason and culture but isn't our behavior ultimately governed by a human nature that is innately aggressive? Wilson states the issue as a circularity with a solution:

> [W]e are forced to choose among the elements of human nature by reference to the value systems which these same elements created in an evolutionary age now long vanished.

> Fortunately, this circularity of the human predicament is not so tight that it cannot be broken through an exercise of will. The principle task of human biology is to identify and to measure the constraints that influence the decisions of ethical philosophers and everyone else, and to infer their significance through neurophysiological and phylogenetic reconstructions of the mind. This enterprise is a necessary complement to the continued study of cultural evolution. It will alter the foundation of the social sciences but in no way diminish their richness and importance. In the process it will fashion a biology of ethics, which will make possible the selection of a more deeply understood and enduring code of moral values. [p. 196]

Once again, if an exercise of will can break the circularity nowadays, then why not also for an evolutionarily relevant span of the past? The famously fierce Comanche were also adept peace-makers and alliance builders when it suited their interests (Hämäläinen, 2008).

To summarize, *On Human Nature* defends a concept of human nature that boils down to these:

1. Natural selection for most of human evolution shaped human genes with little influence from cultural processes.
2. Naturally selected genes powerfully influence human development irrespective of cultural differences.
3. Cultural evolution and the effects of such forces as reason are recent in human evolution.
4. The scientific study of human nature will permit us to work around its limitations.

Wilson's concept of human nature is not essentialist; it is fully based on Modern Synthesis evolutionary biology as applied to social behavior so it is not objectionable on the grounds that Hull (1986) articulated. Indeed, it privileges Modern Synthesis evolutionary processes to the point of denying any fundamental contribution of cultural evolutionary processes in the evolution of human nature. In this sense, the outline of the argument is very similar to Dobzhansky's, although less tolerant of the social sciences' general disinterest in genes and evolution. Like Dobzhansky, it does give great weight to cultural processes in recent periods, under the control of reason, and especially when guided by science. In his tools and brains scenario Wilson does introduce an element of gene-culture coevolution apparently not thinking this is a problem for a Modern Synthesis account. These concessions to cultural processes are necessary to explain the emergence of complex cultural adaptations and to offer a path to improving the human condition. In Lumsden and Wilson's (1981) "complete coevolutionary circuit" genetic evolution can adapt to cultural changes and force them to be consistent with selection acting on genes, but cultural processes following their imperatives cannot impose themselves on genes. The trouble is that this picture doesn't offer a principled reason to restrict the operation of cultural processes to a very late phase of human evolution when it is fairly clear that culture driven gene-culture coevolutionary processes operated fairly deep in the history of *Homo* if not throughout the whole history of the genus, as the cultural evolutionists are prone to think (Ross & Richerson, 2014). Indeed, his scenario of tool evolution driving the growth of the intellect does imagine that a form of cultural evolution drove biological evolution. If so then the Modern Synthesis, as extended to behavioral phenomena by Hamilton, Trivers, and Maynard Smith, did not furnish all the evolutionary tools needed

explain the evolution of the human genome any more than the human genome gives us all the tools to understand culture (Morgan, In press).

Wilson was the first sophisticated evolutionary biologist to expound at book length on human nature. The next question is how the usages of human nature, and reactions to it, have evolved in the last nearly four decades.

Richard D. Alexander

Alexander (1974) wrote an interesting review paper on the evolution of social behavior which he followed up by two book-length contributions (Alexander, 1979, 1987). Alexander's 1974 paper is a strong polemic for the then-recent advances in the evolutionary theory of social biology:

> For several years the study of social behavior has been undergoing a revolution with far-reaching consequences for the social and biological sciences. Partly responsible are three recent changes in the attitudes of evolutionary biologists. First was growing acceptance of the evidence that the potency of natural selection is overwhelmingly concentrated at levels no higher than that of the individual. Second was revival of the comparative method, especially as applied to behavior and life histories. Third was spread of the realization that not only are all aspects of structure and function of organisms to be understood solely as products of selection, but because of their peculiarly direct relationship to the forces of selection, behavior and life history phenomena, long neglected by the evolutionists, may be among the most predictable of all phenotypic attributes.

Mentions of the human case in his broad comparative discussion are frequent under such headings as individual versus group selection, kin selection and nepotism, the evolutionary forces favoring group living, parental investment and manipulation of progeny, and social interactions in different kinds of social groups. Since the theory for interpreting all the cases is based on the work of Hamilton, Trivers, and like-minded authors, the hewing to the amended Modern Synthesis orthodoxy is conspicuous. So it is rather remarkable that in the end he entertains the possibility of group selection in the human case:

> I began with a denial of any great significance for the phenomenon of group selection. It is appropriate, perhaps, to finish with a caveat. For two reasons human social groups represent an almost ideal model for potent selection at the group level. First, the human species is (and possibly always has been) composed of competing and essentially hostile groups that frequently have not only behaved toward one another in the manner of different species, but also have been able quickly to develop enormous differences in reproductive and competitive ability because of cultural innovation and its cumulative effects. Second, human groups are uniquely able to plan and act as units, to look ahead and purposely carry out actions designed to sustain the group and improve its competitive position. These features may actually represent an exhaustive list of the precise attributes of a species that would maximize its likelihood of significant group selection, or evolution by differential extinction of groups. Thus group selection involves the paradox that competing populations must be sufficiently isolated to

> become different in ways that may lead to their differential extinction yet close enough together that they can replace one another. This condition is obviously fulfilled with sympatric competing species, which are intrinsically isolated. So, to some extent, are hostile neighboring populations of humans.
>
> It is an important result of the above considerations that in seeking to define the adaptiveness of culture, to analyze directions of cultural change, and to identify sources of cultural rules, we cannot ignore or downplay effects significant at the group level.

Alexander here appears to be talking about genes responding to group selection. In his first book on humans, *Darwinism and Human Affairs*, he (Alexander, 1979) devotes a chapter to culture. Like Wilson, Alexander is reluctant to give any fundamental evolutionary role to culture and cultural evolution:

> Cultural novelties do not replicate or spread themselves, even indirectly. They are replicated as a consequence of the behavior of the vehicles [individuals] of gene replication. Only if decisions or tendencies of such vehicles of gene replication (individuals) to use or not use a cultural novelty are independent of the interests of the genetic replicators can it be said that cultural change is independent of the differential reproduction of genes [p. 80].

The writing of the early cultural evolutionists may not have been entirely clear at this early date, but our thinking was not that culture was independent of genes but that genes and culture were locked together in a coevolutionary dance with strong reciprocal interactions.

Much of *Darwinism and Human Affairs* applies evolutionary theories of behavior to anthropological issues such as kinship. For example, in matrilineal societies men are expected to care for their sister's offspring rather than their own. But if paternity certainty is sufficiently low, men will tend to more closely related to their sister's offspring than to their own (putative) offspring. This direct address of anthropological problems on Alexander's (1971) part, going back some years, was an important inspiration for the first generation of human behavioral ecologists (Chagnon & Irons, 1979). In spite of his general explanatory strategy being similar to Wilson's he is not a fan of the human nature concept. In a short epilogue to *Darwinism and Human Affairs* entitled "On the Limits of Human Nature" Alexander writes that the three reviewers of his manuscript "were disappointed that I had not more explicitly attacked the problem of human nature, identifying its limits and explaining the consequences." He explains why:

> As it concerns human social behavior, human nature would seem to be represented by our learning capabilities and tendencies in different situations. The limits of human nature, then, could be identified by discovering those things that we cannot learn. But there is a paradox in this, for to understand human nature would then be to know how to change it—how to create situations that would enable or cause learning that could not previously occur. To whatever extent this is so, the limits of human nature become will'-o'-the-wisps that inevitably retreat ahead of our discoveries about them. [p. 279].

As we have seen in the case of Wilson, perhaps one of the three reviewers of *Darwinism and Human Affairs*, a purist account of human evolution based on the Modern Synthesis would lead to an account that cannot do justice to human culture. It would also lead to an account that would offer no room for improving the human condition. But any concession at all to culture or reason, while still trying to rest exclusively on the Modern Synthesis for theory, leads to paradoxes, as Alexander notes.

John Tooby and Leda Cosmides

Tooby and Cosmides (1990) wrote an evolutionarily-theory-heavy paper entitled "On the universality of human nature and the uniqueness of the individual: The role of genetics and adaptation." The paper includes a rather thorough rehearsal of Modern Synthesis evolutionary theory as it applies to human evolution.

They do stress two principles that are foundational for their later thinking. First they emphasize what they call "universal functional design." By this principle, most adaptations are tightly integrated function complexes that do not vary within a species. Functional complexity is simply intolerant of variation. Most variation that does exist is in the form of trivial neutral differences. If this principle is true, evolution is a slow process, and adaptation to the Pleistocene would have equipped humans with a complex of adaptations that would have equipped human nature for the regularities of that environment. If human cognitive adaptations are adaptations to Pleistocene life then their nature can be deduced by what would have been adaptive in that environment. Their subsequent quarter century long research program rests heavily on this principle. It comes from R.A. Fisher's (1958) picture of adaptation. Interestingly, evolutionary biology in the ensuing years has found reasons to be quite skeptical of Fisher's ideas in this regard (Thompson, 2013). Selection seems often to favor adaptations to features of the environment that are quite local in time and space, as in the famous case of the evolution of the beaks of Galapagos finches in response to a succession of drought and rain (Grant & Grant, 2002). It is also interesting that "the" Pleistocene turns out to have been characterized by an enormous amount of quite noisy variation on the millennial and submillennial time scales. This variation seems to have increased progressively over the last few hundred thousand years. Cultural evolutionary theory suggests that this is just the kind of variation that could favor the evolution of a costly system of culture (Richerson & Boyd, 2013).

Tooby and Cosmides second foundational principle is the idea of "condition-responsive adaptive strategies." Much variation arises because of environmentally sensitive contingent developmental programs, or alternative genetically programmed morphs like the two sexes. Modern developmental biology has amply confirmed the existence of condition responsive regulatory circuits active during development and even in response to environmental contingencies in adulthood (Gilbert & Eppel, 2008). Ironically some of these developmental processes include forms of gene based Lamarckian inheritance as well as more conventional alternative developmental pathways (Jablonka, 2012). Tooby and Cosmides (1992) used this principle for a full-scale assault to the social sciences' dependence on the concept of culture, to the point of dismissing learning and culture as ideas that must die (Tooby, 2015).

In some ways Tooby and Cosmides were thus the most uncompromising human nature theorists, offering no comforting notions of how we might deal with the failure of Pleistocene adaptations in a Holocene world by reason, acts of will, or scientific progress. But, in the end, they embraced the now familiar idea of human reason (Cosmides & Tooby, 2001). In earlier work, they had championed the idea of the mind as massively modular, built up of specialized, informationally encapsulated cognitive subsystems evolved in Pleistocene environments and of limited functionality in the Holocene (never mind that we have been much more successful in the Holocene than in the Pleistocene). Only such systems could possibly evolve. However, in (2001) they took the contrary tack that human minds also have a powerful "improvisational intelligence" that can account for how humans have done so well in the Pleistocene and Holocene. See also Pinker (2010). In other words, after some lapse they made one of the standard moves the Modern Synthesis based theory of human nature must make to rescue it from a patent inability to explain facts of the human condition or offer a way out of the moral and political problems it poses. The cultural evolutionists make their now familiar objections. Developments in technology and social organization in both the Pleistocene and the Holocene have been faster than is easy to explain by genetic evolution, but far slower and with a Darwinian pattern of descent with modification, than can be accounted for by powerful individual improvisational intelligence alone (Boyd, Richerson, & Henrich, 2011; Richerson et al., 2016).

Steven Pinker

Pinker's (2002) *The Blank Slate: The Modern Denial of Human Nature* is a long book that attributes to the pioneers of the social sciences a taste for biology-free, blank slate explanations of human behavior while also exhibiting a tendency to have a noble savage view of human nature. This seems confused at the outset. The noble savage idea that virtue is built into human nature seems to be at odds with a blank slate view. On the Modern Synthesis view, human prosociality is hard to explain. On the noble savage view, human vice is hard to explain. Both are strong human nature positions with obvious problems. For example, experimental games reveal variation in prosocial behavior at the individual, intra-cultural community, and inter-cultural levels (Henrich et al., 2004). A few humans are noble, and a few are psychopaths. Most of us are morally muddled to various degrees.

Pinker thinks that biology needs to be brought into the science of human behavior via evolutionary cognitive psychology, an argument very similar to that of Tooby and Cosmides. He offers Chomsky's ideas of the innate cognitive foundations of language as a successful model [p. 37-8]. (Evolutionary linguists mostly now consider such highly innatist approaches to syntax dubious (Hurford, 2011; Newmeyer, 2004).) Like Wilson, he discusses culture at some length, arguing, for example, that its foundation must be the cognitive architecture that humans evolved during the Pleistocene. He recognizes that life in complex societies is built upon social realities. Of the human nature theorists I discuss in this chapter, it is Pinker that makes the most use of cultural factors and processes in his explanations of human behavior. However, he ignores the claims of cultural evolutionists that cultural evolution might have played some fundamental role in the evolution of genes.

Pinker, in fact, in the *Blank Slate* really only defends a very weak version of human nature in the same vein as Wilson (1978). He rehearses the human universals argument of Brown (1991). One can make a

very long list of human traits that are universal or near-universal in human societies. Some of these plausibly have biological components, such as childhood fear of strangers. But such emotions are not restricted to humans (Panksepp & Biven, 2012). Other "universals" like marriage and kinship are culturally quite variable. The proper universal with regard to marriage is physiological in the first instance, not cognitive. The very large brain, helplessness, and slow growth of human infants means that, unlike other apes, mothers cannot raise them unaided (Burkart, Hrdy, & Van Schaik, 2009; Hrdy, 2009). Humans use a great variety of marriage and kinship systems to organize the assistance that mothers need to raise their children. As we have seen, arguments of this type just point to the fact that biological factors and biological evolution are important in humans no matter how important culture and cultural evolution might also be. It is hard to believe any educated person would believe differently. Blank slaters are not an important part of ongoing debates. Gene-culture coevolutionists do argue that the evolution of our big brain was driven by the advantages of having the complex culture that large brains make possible.

The Gene-Culture Coevolution Alternative to Human Nature

As some evolutionary biologists and evolutionary social scientists were beginning to develop ideas about human nature, other social scientists and evolutionary biologists began again to work on the problem of cultural evolution in much the same vein as Darwin outlined. These efforts would eventually lead to a theory, much of it built on formal population genetics style models, that pictured in some detail the way genes and culture might interact in a unified evolutionary system. Currently a fair number of researchers work on various empirical projects inspired by the modeling work or independent of it (Richerson & Christiansen, 2013). The view of these scholars came to be that the theory of human nature developed by Wilson and his Modern Synthesis inspired successors misrepresents the relationship between genetic and cultural evolution. Theory and some evidence suggests that for at least the last few tens of thousands of years, if not for far longer, human organic evolution was substantially driven, not by natural selection acting on genes but by culturally mandated social selection directly on human genes and indirectly by natural selection in human constructed environments.

This work began early but was a long time in reaching maturity. Gerard, Kluckhohn and Rapaport (1956) wrote a prescient programmatic essay outlining how cultural evolution could be studied with concepts and methods similar to those used by evolutionary biologists. Donald Campbell (1965) wrote a similar essay that was more widely read. Cavalli-Sforza and Feldman (1973a, 1973b) showed how population genetic models could be modified to make models of cultural transmission and evolution. A brief mention in Richard Dawkins' (1976) *The Selfish Gene* invited readers to consider that cultural elements (memes) could evolve much like genes. Richerson and Boyd (1978) modelled the idea that even under the assumption that the human culture capacity is at a genetic fitness optimum, individual cultural traits could deviate from their genetic fitness optimizing value if genetic mechanisms could only optimize the genetic fitness optimum of the culture capacity as a whole, not cultural trait by cultural trait. In essence, humans might be the analog of a two-species mutualism in which the interests of the two partners are fairly closely but not perfectly aligned.

In the first instance, the difference of opinion between the cultural evolutionists and the proponents of human nature turned on different intuitions derived from formal models. The assumptions of the models constructed by Lumsden and Wilson (2006 [1981]) differed in critical details from the population genetics style models Cavalli-Sforza and Feldman (1973) pioneered. The former considered that culture consists of an inventory of knowledge items that everyone knows ("culturgens"). What varies is the usage of the items and this is guided by "epigenetic rules," genetically coded rules that are either indifferent to usage rates (*tabula rasa* genotype) or genotypes that bias usage in favor of one culturgen or another. Lumsden and Wilson allow for cultural variation by incorporating "trend watching," a tendency to use the same culturgen as others (in the simplest case). In models in the Cavalli-Sforza and Feldman tradition, cultural variation is assumed to represent different people having different knowledge; cultural variation is analogous different genetic loci. These structure differences are less important than the simplifying assumptions used in their analysis. In key parts of their analysis Lumsden and Wilson simplify away innovation and make trend watching extremely weak. Thus, the only things that can evolve in their analysis are the gene-based epigenetic rules. This leads to what they call the "thousand year rule." A more-fit epigenetic rule will undergo a selective sweep from low to high frequency in roughly 40 human generations. As humans adapt to environments that vary in time and space, including cultural components, epigenetic rules will evolve to adapt people to them.

In the population genetic style models of cultural evolution innovation, migration and errors of learning will create patterns of culturally heritable variation. If individual decision-making is a very strong effect, the heritability effect will be slight and models collapse back to something like Lumsden and Wilson's analysis or to the picture given by Tooby and Cosmides (Boyd & Richerson, 1985). However, many cultural traditions are complex and difficult for individuals to evaluate. People will mostly have to acquire such cultural variants by learning from others. At the same time, we have general purpose learning biases that can exert at least weak selective effects on cultural variants (Henrich, 2016). Foods that are high in energy and protein are more reinforcing than ones low in the nutrients humans need. Such biases have shaped a huge variety of cuisines around the world, usually starting with ingredients that are inedible without sophisticated extraction and processing (Hill, Barton, & Hurtado, 2009). To the extent that culture acts as an inheritance system, natural selection can also act directly on cultural variation. Furthermore, culture creates environments that can select genetic variants, including social systems that exert social selection by rewarding those who conform to cultural rules or punishing those who don't. By the early 1980s the cultural evolution position was well articulated (Boyd & Richerson, 1983; Campbell, 1975; Pulliam & Dunford, 1980; Richerson & Boyd, 1978) and Wilson (1978; see note pg. 235-6) associated the term human nature with his position in the debate.

The issues between these two approaches thus became, in the final analysis, whether the evolution of genes as extended to behavior by Hamilton, Trivers, and Maynard Smith is to be the main theoretical toolkit to explain human behavior or whether the evolution of culture makes a fundamental difference to the process of evolution in our species. My argument in this chapter is that "human nature" became a common cover term for the position that the Modern Synthesis, as extended to behavior by Hamilton, Trivers, and Maynard Smith, provides all the evolutionary theory needed to explain human behavior and that culture plays no ultimate explanatory role. As with Lewens' (2012) critique of Neo-Aristotelian

ethics, I also argue that in fact this version of the human nature account can't do the work it is intended to do, as evidenced by most such authors giving culture and reason strong roles to play without conceding a theoretically important role for culture in human evolution, at least until recent, contemporary, or future phases of our evolution.

If stone tools and larger brains are a valid index, the species at the inception of our genus some 2.6 million years ago show more signs of culture than do other ape species. Brain size and stone tool complexity grow more or less in tandem throughout the Pleistocene (Richerson & Boyd, 2013), as if brain enlargement was for the purpose of acquiring and managing an increasingly larger cultural repertoire. Some paleoanthropologists suggest that many of the elements of modern human behavior appear progressively over the last 250,000 years (Marean, 2010; McBrearty & Brooks, 2000), although equally competent authorities see a more punctuated pattern associated with the Upper Paleolithic Transition in Europe 50,000-40,000 years ago (Klein & Edgar, 2002). Even this foreshortened time scale leaves a 4-5 times longer period than Wilson allowed in 1978 over which cultural evolutionary processes might affect genetic evolution. Good evidence suggests that the best documented case of culture-driven gene culture coevolution, the evolution of adult lactase persistence following the evolution of dairying, resulted from culture driven selection acting on the time scale of a millennium (Itan, Powell, Beaumont, Burger, & Thomas, 2009), recalling Lumsden and Wilson's (1981) 1000 year rule. Many other genetic changes in human populations appear to have been driven by cultural changes (Laland et al., 2010; Richerson, Boyd, & Henrich, 2010). Cultural evolutionists thus argue that the basic Pleistocene hunting and gathering adaptation evolved under the influence of cultural evolution, including willful processes like selective imitation of more successful groups by less successful ones and selective migration from poorly performing to better performing groups (Richerson et al., 2016). While we know very little about the exact trajectory of gene-culture coevolution, we know that stone tools were present at the beginning of the genus *Homo*, and that living and Late/Upper Paleolithic hunter-gatherers seem essential modern as regards genetic factors (Hill et al., 2009).

Conclusion

Lewens' (2012) analysis of the human nature concept and the uses to which people have tried to put it, receives support from this review of its use by sophisticated evolutionary biologists and psychologists. A weak version of human nature that points out that genes and their evolution ought to have an important part in the explanation of human behavior should be uncontroversial. Some social scientists and humanists might have and may still resist even this version of human nature, but on what persuasive grounds is hard to imagine.

But the several users of the human nature term reviewed here at least seem to want to have a stronger version of human nature that does real work. The strong claim is that natural selection acting on genes is the master force in human evolution and that culture is a proximate system that has only an indirect role in evolutionary analysis (Dickins & Rahman, 2012). In Wilson's original formulation, echoed in several subsequent authors' work, is that selection on genes was first in time and that genes are first in development. Therefore, culture and learning, coming late in evolutionary time and late in development play only a proximal role in explaining human behavior. The cultural evolutionists argue that culture and

intelligence were probably already present in simple forms in our ape ancestors (de Waal, 2000; Whiten et al., 1999). For more than two million years human brains and human culture evolved together (Klein, 2009). Similarly, in development, one of the earliest skills to mature in infants is the capacity for social learning (Carey, 2009). Thus, the strong claim is undermined by the fact that genes and culture coevolve and codevelop in our species. Cultural evolution is part of the ultimate explanation for human behavior and perhaps proximate factors have a role in evolution, contra Mayr (1961). It is further undermined by the need of human nature theorists to appeal to culture and reason in various ways to repair or supplement their accounts.

How do we account for the resistance of the authors reviewed here to providing theoretical room for cultural evolution and other processes in their accounts? As I say, in the early days I regarded cultural evolutionary theory to be a minor amendment to the orthodox Modern Synthesis in the case of one species. Some objections to cultural evolution theory have been quite passionate even while showing no sign of actually understanding the cultural evolutionists' arguments (West, El Mouden, & Gardner, 2011). One strong thread that ties Dobzhansky to all the subsequent sophisticated biologists defending the human nature concept is a strong commitment to the Modern Synthesis with its rejection of a fundamental role for cultural evolutionary processes in human evolution. This is often coupled with a commitment to a strong version of Ernst Mayr's (1961) proximate-ultimate distinction that culture is a proximate mechanism that evolutionary explanations rooted in genes furnish the only legitimate ultimate explanation. Processes like gene-culture coevolution, transgenerational epigenetic inheritance, and niche construction suggest that the Modern Synthesis needs to be replaced by an Expanded Evolutionary Synthesis (Laland et al., 2011). The espousal of a strong concept of human nature, or the denial that such is possible, is part of a deep debate in modern evolutionary biology. A whiff of grapeshot and a crackle of thin ice, indeed!

Acknowledgements

Thanks to Thomas Morgan and Lesley Newson for their suggestions. Most of the ideas here were developed in my long collaboration with Robert Boyd from which this essay owes much. Of course, any errors are mine.

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