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### **What the Biological Sciences Can and Cannot Contribute to Ethics**

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I fully subscribe to the judgment of those writers who maintain that of all the differences between man and the lower animals the moral sense or conscience is by far the most important.

– Charles Darwin, *The Descent of Man* (1871)

The question whether ethical behavior is biologically determined may refer either to the *capacity* for ethics (i.e., the proclivity to judge human actions as either right or wrong), or to the moral *norms* accepted by human beings for guiding their actions. I herein propose: (1) that the capacity for ethics is a necessary attribute of human nature; and (2) that moral norms are products of cultural evolution, not of biological evolution. Humans exhibit ethical behavior by nature because their biological makeup determines the presence of three necessary conditions for ethical behavior: (i) the ability to anticipate the consequences of one's own actions; (ii) the ability to make value judgments; and (iii) the ability to choose between alternative courses of action. Ethical behavior came about in evolution not because it is adaptive in itself, but as a necessary consequence of man's eminent intellectual abilities, which are an attribute directly promoted by natural selection. That is, morally evolved as an exaptation, not as an adaptation. Since Darwin's time there have been evolutionists proposing that the norms of morality are derived from biological evolution. Sociobiologists represent the most recent and most subtle version of that proposal. The sociobiologists' argument is that human ethical norms are sociocultural correlates of behaviors fostered by biological evolution. I argue that such proposals are misguided and do not escape the naturalistic fallacy. The isomorphism between the behaviors promoted by natural selection and those sanctioned by moral norms exist only with respect to the consequences of the behaviors; the underlying causations are completely disparate.

## 1. Introduction

I will define moral behavior for the present purposes as the actions of a person who takes into account in a sympathetic way the impact the actions have on others.<sup>1</sup> Altruism may be defined in a similar way as, for example, “unselfish regard for or devotion to the welfare of others” (*Webster’s New Collegiate Dictionary*, 10th ed.). Altruism, however, is usually taken to imply some cost to the altruist for the benefit of others,<sup>2</sup> and this is the sense in which “altruism” will be used here. I will use the term “ethical behavior” as a synonym of “moral behavior,” and “morality” and “ethics” as synonyms of each other, except when explicitly noted or contextually obvious that they are used with a somewhat different meaning. Some authors use “morality” or “virtue ethics” in a broader sense that would include good feelings in regard to others and exclude inappropriate thoughts or desires, such as entertaining sexual desires for somebody else’s wife or wishes that something harmful would happen to others. So long as these thoughts or desires are not transformed into actions, they will not be included in my use of “morality.” Actions that may be thought to be evil or sinful in some moral systems, such as masturbation, will not be included either in my use of “morality,” so long as the actions have no consequences for others.

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<sup>1</sup> This is similar to the definition of David Copp (2006): “[W]e can take a person’s moral beliefs to be the beliefs she has about how to live her life when she takes into account in a sympathetic way the impact of her life and decisions on others” (p. 4).

<sup>2</sup> *Merriam Webster’s Collegiate Dictionary*, 10th edition, gives a second definition of altruism as “behavior by an animal that is not beneficial to or may be harmful to itself but that benefits others of its species.”

## **2. Theories of Morality**

People have moral values; that is, they accept standards according to which their conduct is judged either right or wrong, good or evil. The particular norms by which moral actions are judged vary to some extent from individual to individual, and from culture to culture (although some norms, like not to kill, not to steal, and to honor one's parents are widespread and perhaps universal), but value judgments concerning human behavior are passed in all cultures. This universality raises the questions whether the moral sense is part of human nature, one more dimension of our biological make-up; and whether ethical values may be the product of biological evolution, rather than being given by religious and cultural traditions.

There are many theories concerned with the rational grounds for morality, such as deductive theories that seek to discover the axioms or fundamental principles that determine what is morally correct on the basis of direct moral intuition; or theories like logical positivism or existentialism that negate rational foundations of morality, reducing moral principles to emotional decisions or to other irrational grounds. After the publication of Darwin's theory of evolution by natural selection, several philosophers as well as biologists attempted to find in the evolutionary process the justification for moral behavior.

Aristotle and other philosophers of classical Greece and Rome, as well as many other philosophers throughout the centuries, held that humans hold moral

values by nature. A human is not only *Homo sapiens*, but also *Homo moralis*. But biological evolution brings about two important issues: timing and causation. We do not attribute ethical behavior to animals (surely, not to all animals and not to the same extent as to humans, in any case). Therefore, evolution raises distinctive questions about the origins and tenets of moral behavior. When did ethical behavior come about in human evolution? Did modern humans have an ethical sense from the beginning? Did Neandertals hold moral values? What about *H. erectus* and *H. habilis*? And how did the moral sense evolve? Was it directly promoted by natural selection? Or did it come about as a by-product of some other attribute (such as rationality, for example) that was the direct target of selection? Alternatively, is the moral sense an outcome of cultural evolution rather than of biological evolution?

### **3. Darwin and the Moral Sense**

Two years after returning from his trip in the *HMS Beagle* (1826-1831), Darwin gathered contemporaneous literature on human moral behavior, including such works as William Paley's *The Principles of Moral and Political Philosophy* (1785), which he had encountered earlier while a student at the University of Cambridge, and the multivolume *Illustrations of Political Economy* by Harriet Martineau, published more recently, in 1832–1834. These two authors, like other philosophers of the time, maintained that morality was a conventional attribute of

humankind, rather than a naturally determined human attribute, using an argument often exploited in our days: the diversity of moral codes.

The proliferation of ethnographic voyages had brought to light the great variety of moral customs and rules. This is something Darwin had observed in South American Indians. But this apparent dispersion had not distracted him. He would eventually develop a more complex and subtle theory of the moral sense than those contemporaneous authors; a theory that, implicitly at least, recognized moral behavior as a biologically-determined human universal but with culturally-evolved differences. For Darwin, the ethnographic diversity of moral customs and rules came about as an adaptive response to the environmental and historical conditions, unique in every different place, without necessarily implying that morality was an acquired, rather than natural, human trait.

A variable adaptive response could very well derive from some fundamental capacity, a common substrate, unique for the whole human race, but capable of becoming expressed in diverse directions. Darwin did not attribute the universality of morality to supernatural origin, but rather saw it as a product of evolution by natural selection. The presence of a universal and common foundation, endowing humans with an ethical capacity, was for Darwin compatible with different cultures manifesting different stages of moral evolution and with different sets of moral norms.

In *The Descent of Man* (chapter III), Darwin writes:

Brehm encountered in Abyssinia a great troop of baboons who were crossing a valley: some had ascended the opposite mountain, and some were still on the valley: the latter were attacked by the dogs, but the old males immediately hurried down from the rocks, and with mouths widely opened, roared so fearfully, that the dogs precipitately retreated. They were again encouraged to the attack; but by this time all the baboons had reascended the heights, excepting a young one, about six months old, who, loudly calling for aid, climbed on a block of rock and was surrounded. Now one of the largest males, a true hero, came down again from the mountain, slowly went to the young one, coaxed him, and triumphantly led him away—the dogs being too much astonished to make an attack. (p. 124)

This is just one of the many examples given by Darwin of animals that help a distressed group member. However, in this particular case, Darwin uses a word that deserves attention: the baboon that comes down from the mountain is called “a true hero.” Heroism is an ethical concept. Is Darwin using it in this sense or only metaphorically?

Darwin belongs to an intellectual tradition, originating in the Scottish Enlightenment of the eighteenth and nineteenth centuries, which uses the moral sense as a behavior that, based on sympathy, leads human ethical choice. In his

account of the evolution of cooperative behavior, Darwin states that an animal, with well-defined social instincts—like parental and filial affections—“would inevitably acquire a moral sense or conscience, as soon as its intellectual powers had become as well developed, or nearly as well developed, as in man.” (Darwin, 1871, Chapter III, pp. 68-69). This is a hypothetical issue, because no other animal has ever reached the level of human mental faculties, language included. But this is an important statement, because Darwin is affirming that the moral sense, or conscience, is a necessary consequence of high intellectual powers, such as exist in modern humans. Therefore, if our intelligence is an outcome of natural selection, so it would be the moral sense. Darwin’s statement further implies that the moral sense is not by itself directly conscripted by natural selection, but only indirectly as a consequence of high intellectual powers.

#### **4. Moral Behavior vs. Moral Norms**

Darwin also states that even if some animal could achieve a human-equivalent degree of development of its intellectual faculties, we cannot conclude that it would also acquire exactly the same moral sense as ours. “I do not wish to maintain that any strictly social animal, if its intellectual faculties were to become as active and as highly developed as in man, would acquire the same moral sense as ours. . . . [T]hey might have a sense of right and wrong, though led by it to follow widely different lines of conduct” (Darwin, 1871, Chapter III, p. 70).

These statements imply that, according to Darwin, having a moral sense does not

by itself determine what the moral norms would be: which sorts of actions might be sanctioned by the norms and which ones would be condemned.

This distinction is important. Indeed, it is a distinction central to my thesis herein. Much of the historical controversy, particularly between scientists and philosophers, as to whether the moral sense is or not biologically determined has arisen owing to a failure to make the distinction. Scientists often affirm that morality is a human biological attribute because they are thinking of the predisposition to pass moral judgment: that is, to judge some actions as good and others as evil. Some philosophers argue that morality is not biologically determined, but rather comes from cultural traditions or from religious beliefs, because they are thinking about moral codes, the sets of norms that determine which actions are judged to be good and which are evil. They point out that moral codes vary from culture to culture and, therefore, are not biologically predetermined.

I consider this distinction fundamental. Thus, I'll argue that the question of whether ethical behavior is biologically determined may refer to either one of the following two issues. First, is the capacity for ethics—the proclivity to judge human actions as either right or wrong—determined by the biological nature of human beings? Second, are the systems or codes of ethical norms accepted by human beings biologically determined? A similar distinction can be made with respect to language. The question whether the capacity for symbolic creative



language is determined by our biological nature is different from the question whether the particular language we speak—English, Spanish, Chinese, etc.—is biologically determined, which in the case of language obviously it is not.

The distinction between the *inclination* to judge certain sorts of actions as either morally good or evil and the *norms* according to which we determine which actions are good and which actions are evil, has affinity with the distinction made by moral philosophers between *metaethics* and *normative ethics*. The subject of metaethics is why we ought to do what we ought to do, while normative ethics tells us what we ought to do. I will propose that the moral evaluation of actions emerges from human rationality or, in Darwin's terms, from our highly developed intellectual powers. Our high intelligence allows us to anticipate the consequences of our actions with respect to other people and, thus, to judge them as good or evil in terms of their consequences for others. But I will propose that the norms according to which we decide which actions are good and which actions are evil are largely culturally determined, although conditioned by biological predispositions.

### **5. Darwinian Aftermath**

Herbert Spencer (1820-1903) was among the first philosophers seeking to find the grounds of morality in biological evolution. In *The Principles of Ethics* (1893), Spencer seeks to discover values that have a natural foundation. Spencer argues that the theory of organic evolution implies certain ethical principles. Human

conduct must be evaluated, like any biological activity whatsoever, according to whether it conforms to the life process; therefore, any acceptable moral code must be based on natural selection, the law of struggle for existence. According to Spencer, the most exalted form of conduct is that which leads to a greater duration, extension, and perfection of life; the morality of all human actions must be measured by that standard. Spencer proposes that, although exceptions exist, the general rule is that pleasure goes with that which is biologically useful, whereas pain marks what is biologically harmful. This is an outcome of natural selection: thus, while doing what brings them pleasure and avoiding what is painful, organisms improve their chances for survival. With respect to human behavior, we see that we derive pleasure from virtuous behavior and pain from evil actions, associations which indicate that the morality of human actions is also founded on biological nature.

Spencer proposes as the general rule of human behavior that anyone should be free to do anything that they want, so long as it does not interfere with the similar freedom to which others are entitled. The justification of this rule is found in organic evolution: the success of an individual, plant or animal, depends on its ability to obtain that which it needs. Consequently, Spencer reduces the role of the state to protecting the collective freedom of individuals so that they can do as they please. This *laissez faire* form of government may seem ruthless, because individuals would seek their own welfare without any consideration for

others' (except for respecting their freedom), but Spencer believes that it is consistent with traditional Christian values. It may be added that, although Spencer sets the grounds of morality on biological nature and on nothing else, he admits that certain moral norms go beyond that which is biologically determined; these are rules formulated by society and accepted by tradition.

Social Darwinism, in Spencer's version or in some variant form, was fashionable in European and American circles during the latter part of the nineteenth century and the early years of the twentieth century, but it has few or no distinguished intellectual followers at present. Spencer's critics include the evolutionists J.S. Huxley and C.H. Waddington who, nevertheless, maintain that organic evolution provides grounds for a rational justification of ethical codes. For Huxley (1953; Huxley and Huxley, 1947), the standard of morality is the contribution that actions make to evolutionary progress, which goes from less to more "advanced" organisms. For Waddington (1960), the morality of actions must be evaluated by their contribution to human evolution.

Huxley and Waddington's views are based on value judgments about what is or is not progressive in evolution. But, contrary to Huxley's claim, there is nothing objective in the evolutionary process itself (i.e. outside human considerations; see Ayala, 1982, 1987) that makes the success of bacteria, which have persisted as such for more than 2 billion years and which consist of a huge diversity of species and astronomic numbers of individuals, less desirable than

that of the vertebrates, even though the latter are more complex. The same objection can be raised against Waddington's human evolution standard of biological progress. Are the insects, of which more than one million species exist, less desirable or less successful from a purely biological perspective than humans or any other mammal species? Waddington fails to demonstrate why the promotion of human biological evolution by itself should be the standard to measure what is morally good.

More recently, numerous philosophers as well as scientists have sought to give accounts of moral behavior as an evolutionary outcome (e.g., Blackmore, 1999; Hauser, 2005; Maienschein & Ruse, 1999; Ruse, 1995; Sober & Wilson, 1998). Particularly notable are the contributions of Edward O. Wilson (1975, 1978, 1998), founder of sociobiology as an independent discipline engaged in discovering the biological foundations of all social behavior. Wilson and other sociobiologists, as well as the derivative subdisciplines of evolutionary psychology (e.g., Barkow et al., 1992) and memetics (Blackmore, 1999), have sought to solve the naturalistic fallacy by turning it on its head. They assert that moral behavior does not exist as something distinct from biological, or biologically determined, behavior. As Ruse and Wilson (1985) have asserted, "Ethics is an *illusion* put in place by natural selection to make us good cooperators" (emphasis added). I shall return later to these sociobiological and related proposals.

## 6. Moral Behavior as Rational Behavior

The first proposition I will defend here is that humans, because of their high intellectual powers, are necessarily inclined to make moral judgments and to accept ethical values; that is, to evaluate certain kinds of actions as either right or wrong. The claim I make is that moral behavior is a necessary outcome of the biological make-up of humans, a product of their evolution. This view would fall within the metaethical theories known as deontological or rational. It is the exalted degree of rationality that we humans have achieved that makes us moral beings. Humans are *Homo moralis* because they are *Homo rationalis*.

This thesis does not imply that the norms of morality are also biologically determined or that they are unambiguous consequences of our rationality. Independent of whether or not humans have a biologically determined moral sense, it remains to be ascertained whether particular moral prescriptions are in fact determined by the biological nature of humans, or whether they are products of cultural evolution, whether chosen by society or established by religious beliefs, or even selected according to individual preferences. Even if we were to conclude that people cannot avoid having moral standards of conduct, it might be that the choice of the particular standards used for judgment would be arbitrary or a product of cultural evolution. The need for having moral values does not necessarily tell us what the moral values should be, like the capacity for language does not determine which language we shall speak.

I will first argue that humans are ethical beings by their biological nature; that humans evaluate their behavior as either right or wrong, moral or immoral, as a consequence of their eminent intellectual capacities, which include self-awareness and abstract thinking. These intellectual capacities are products of the evolutionary process, but they are distinctively human. Thus, I will assert that ethical behavior is not causally related to the social behavior of animals, including kin selection and the so-called reciprocal altruism.

A second argument that I will put forward is that the moral norms according to which we evaluate particular actions as either morally good or morally bad (as well as the grounds that may be used to justify the moral norms) are products of cultural evolution, not of biological evolution. The norms of morality belong, in this respect, to the same category of phenomena as political and religious institutions, or the arts, sciences, and technology, as well as the particular languages we speak. The moral codes, like these other products of human culture, are often consistent with the biological predispositions of the human species, and of other animals. But many moral norms are formulated independently of biological necessity or predisposition, simply because they don't have necessary biological consequences. Biological welfare (survival and reproduction) is not determinant of all ethical norms in any given society or culture.

Moral codes, like any other cultural system, depend on the existence of human biological nature and must be consistent with it in the sense that they could not counteract it without promoting their own demise. Moreover, the acceptance and persistence of moral norms is facilitated whenever they are consistent with biologically conditioned human behaviors. But the moral norms are independent of such behaviors in the sense that some norms may not favor, and may hinder, the survival and reproduction of the individual and its genes, which survival and reproduction are the targets of biological evolution. Discrepancies between accepted moral rules and biological survival are, however, necessarily limited in scope or would otherwise lead to the extinction of the groups accepting such discrepant rules.

### **7. Biology to Ethics**

I will now refer to the moral sense in its strict meaning as the evaluation of some actions as virtuous, or morally good, and others as evil, or morally bad. Morality in this sense is the urge or predisposition to judge human actions as either right or wrong in terms of their consequences for other human beings. In this sense, humans are moral beings by nature because their biological constitution determines the presence in them of the three necessary conditions for ethical behavior. These conditions are: (i) the ability to anticipate the consequences of one's own actions; (ii) the ability to make value judgments; and (iii) the ability to

choose between alternative courses of action. These abilities exist as a consequence of the eminent intellectual capacity of human beings.<sup>3</sup>

The ability to anticipate the consequences of one's own actions is the most fundamental of the three conditions required for ethical behavior. Only if I can anticipate that pulling the trigger will shoot the bullet, which in turn will strike and kill my enemy, can the action of pulling the trigger be evaluated as nefarious. Pulling a trigger is not in itself a moral action; it becomes so by virtue of its relevant consequences. My action has an ethical dimension only if I do anticipate these consequences.

The ability to anticipate the consequences of one's actions is closely related to the ability to establish the connection between means and ends; that is, of seeing a means precisely as a means, as something that serves a particular end or purpose. This ability to establish the connection between means and their ends requires the ability to anticipate the future and to form mental images of realities not present or not yet in existence.

The ability to establish the connection between means and ends happens to be the fundamental intellectual capacity that has made possible the development of human culture and technology. An evolutionary scenario, seemingly the best hypothesis available, proposes that the remote evolutionary roots of this capacity

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<sup>3</sup> Notice that, as I will state later, I am not taking the position known as "utilitarianism," because I am not claiming that maximizing the benefits to others, and to as many others as possible, is the ultimate standard by which the morality of actions should be determined.



to connect means with ends may be found in the evolution of bipedalism, which transformed the anterior limbs of our ancestors from organs of locomotion into organs of manipulation. The hands thereby gradually became organs adept for the construction and use of objects for hunting and other activities that improved survival and reproduction; that is, which increased the reproductive fitness of their carriers. The construction of tools depends not only on manual dexterity, but on perceiving them precisely as tools, as objects that help to perform certain actions; that is, as means that serve certain ends or purposes: a knife for cutting, an arrow for hunting, an animal skin for protecting the body from the cold. According to this evolutionary scenario, natural selection promoted the intellectual capacity of our bipedal ancestors because increased intelligence facilitated the perception of tools as tools, and therefore their construction and use, with the ensuing amelioration of biological survival and reproduction.

The development of the intellectual abilities of our ancestors took place over several million years, gradually increasing the ability to connect means with their ends and, hence, the possibility of making ever-more complex tools serving more remote purposes. According to the hypothesis I am proposing, the ability to anticipate the future, essential for ethical behavior, is therefore closely associated with the development of the ability to construct tools, an ability that has produced the advanced technologies of modern societies and that is largely responsible for the success of humans as a biological species.

The second condition for the existence of ethical behavior is the ability to make value judgments, to perceive certain objects or deeds as more desirable than others. Only if I can see the death of my enemy as preferable to his survival (or vice versa) can the action leading to his demise be thought of as moral. If the consequences of alternative actions are neutral with respect to value, an action cannot be characterized as ethical. Values are of many sorts: not only ethical, but also aesthetic, economic, gastronomic, political, and so on. But in all cases, the ability to make value judgments depends on the capacity for abstraction; that is, on the capacity to perceive actions or objects as members of general classes. This makes it possible to compare objects or actions with one another and to perceive some as more desirable than others. The capacity for abstraction requires an advanced intelligence such as it exists in humans and apparently in them alone.

I will note at this point that the model that I am advancing here does not necessarily imply the ethical theory known as utilitarianism (or, more generally, consequentialism). According to the so-called “act consequentialism” the rightness of an action is determined by the value of its consequences, so that the morally best action in a particular situation is the one, the consequences of which would have the most benefit to others. I am proposing that the morality of an action depends on our ability (1) to anticipate the consequences of our actions, and (2) to pass value judgments. But I am not asserting that the morality of

actions is exclusively measured in terms of how beneficial their consequences will be to others.

The third condition necessary for ethical behavior is the ability to choose between alternative courses of actions. Pulling the trigger can be a moral action only if you have the option not to pull it. A necessary action beyond conscious control is not a moral action: the circulation of the blood or the process of food digestion are not moral actions. Whether there is free will is a question much discussed by philosophers and the arguments are long and involved.<sup>4</sup> Here, I will advance two considerations that are common-sense evidence of the existence of free will. One is personal experience, which indicates that the possibility to choose between alternatives is genuine rather than only apparent. The second consideration is that when we confront a given situation that requires action on our part, we are able mentally to explore alternative courses of action, thereby extending the field within which we can exercise our free will. In any case, if there were no free will, there would be no ethical behavior; morality would only be an illusion. A point to be made, however, is that free will is dependent on the existence of a well-developed intelligence, which makes it possible to explore alternative courses of action and to choose one or another in view of the anticipated consequences.

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<sup>4</sup> For a brief but insightful discussion of free will in the context of evolution, see Ruse, 2006, chapter 12.

## **8. Adaptation *versus* Exaptation**

I will now consider explicitly two issues that are largely implicit in the previous section. I have proposed that the moral sense emerges as a necessary implication of our high intellectual powers, which allow us to anticipate the consequences of our actions and evaluate such consequences. But is it the case that the moral sense may have been promoted by natural selection in itself and not only indirectly as a necessary consequence of our exalted intelligence? The question in evolutionary terms is whether the moral sense is an adaptation or, rather, an exaptation. Evolutionary biologists define exaptations as features of organisms that evolved because they served some function, but are later co-opted to serve a different function, which was not originally the target of natural selection. The new function may replace the older function or coexist together with it. Feathers seem to have evolved first for conserving temperature, but were later co-opted in birds for flying. The beating of the human heart is an exaptation used by doctors to diagnose the state of health, although this is not why it evolved in our ancestors. The issue at hand is whether moral behavior was directly promoted by natural selection or rather it is a consequence of our exalted intelligence, which was the target of natural selection, because it made possible the construction of better tools. Art, literature, religion and many other human cultural activities might also be seen as exaptations that came about as consequences of high intelligence and tool making.

The second issue is whether some animals, apes or, other nonhuman primates, for example, may have a moral sense, however incipient, either as directly promoted by natural selection or as a consequence of their own intelligence.

The position that I'll argue here is that the human moral sense is an exaptation, not an adaptation. The moral sense consists of *judging* certain actions as either right or wrong; not of choosing and carrying out some actions rather than others, or evaluating them with respect to their practical consequences. It seems unlikely that making moral judgments would promote the reproductive fitness of those judging an action as good or evil. Nor does it seem likely that there might be some form of "incipient" ethical behavior that would then be further promoted by natural selection. The three necessary conditions for there being ethical behavior are manifestations of advanced intellectual abilities.

It, indeed, rather seems that the target of natural selection was the development of the advanced intellectual capacities. This was favored by natural selection because the construction and use of tools improved the strategic position of our biped ancestors. In the account I am advancing here, once bipedalism evolved and after tool-using and tool-making became practical, those individuals more effective in these functions had a greater probability of biological success. The biological advantage provided by the design and use of tools persisted long

enough so that intellectual abilities continued to increase, eventually yielding the eminent development of intelligence that is characteristic of *Homo sapiens*.

A related question is whether morality would benefit a social group within which it is practiced, and, indirectly, individuals as members of the group. This seems likely to be the case, if indeed moral judgment would influence individuals to behave in ways that increase cooperation, or benefit the welfare of the social group in some way; for example, by reducing crime or protecting private property. This brings about the issue of whether there is in humans “group selection,” and the related issues of kin selection and inclusive fitness, which I will discuss below.

Group selection based on altruistic behavior is generally not an evolutionary stable strategy (ESS). This is because mutations that favor selfish over altruistic behavior will be favored by natural selection within a given population, so that selfish alleles will drive out altruistic alleles. Of course, it may be the case that populations with a preponderance of altruistic alleles will survive and spread better than populations consisting of selfish alleles. This would be group selection. But typically there are many more individual organisms than there are populations; and individuals are born, procreate, and die at rates much higher than populations. Thus, the rate of multiplication of selfish individuals over altruists is likely to be much higher than the rate at which altruistic populations multiply relative to predominantly selfish populations.

There is, however, an important difference between animals and humans that is relevant in this respect. Namely, the fitness advantage of selfish over altruistic behavior does not apply to humans, because humans can *understand* the benefits of altruistic behavior (to the group and indirectly to them) and thus adopt altruism and protect it, by laws or otherwise, against selfish behavior that harms the social group. As Darwin wrote in *The Descent of Man* (1871, chapter V, p. 159): “It must not be forgotten that, although a high standard of morality gives but a slight or no advantage to each individual man and his children over the other men of the same tribe, yet that an advancement in the standard of morality and an increase in the number of well-endowed men will certainly give an immense advantage to one tribe over another.”

The theory of sociobiology advances a ready answer to the second question raised above, whether morality occurs in other animals, even if only as a rudiment. The theory of kin selection, they argue, explains altruistic behavior, to the extent that it exists in other animals as well as in humans. I will propose, however, moral behavior properly so does not exist, even incipiently, in nonhuman animals. The reason is that the three conditions required for ethical behavior depend on an advanced intelligence—which includes the capacities for free will, abstract thought, and anticipation of the future—such as it exists in *H. sapiens* and not in any other living species. It is the case that certain animals exhibit behaviors analogous with those resulting from ethical actions in humans,

such as the loyalty of dogs or the appearance of compunction when they are punished. But such behaviors are either genetically determined or elicited by training (conditioned responses). Genetic determination and not moral evaluation is also what is involved in the altruistic behavior of social insects and other animals. I will argue below that biological altruism ( $\text{altruism}_b$ ) and moral altruism ( $\text{altruism}_m$ ) have disparate causes: kin selection in  $\text{altruism}_b$ , regard for others in  $\text{altruism}_m$ .

The capacity for ethics is an outcome of gradual evolution, but it is an attribute that only exists when the underlying attributes (i.e. the intellectual capacities) reach an advanced degree. The necessary conditions for ethical behavior only come about after the crossing of an evolutionary threshold. The approach is gradual, but the conditions only appear when a degree of intelligence is reached such that the formation of abstract concepts and the anticipation of the future are possible, even though we may not be able to determine when the threshold was crossed. Thresholds occur in other evolutionary developments—for example, in the origins of life, multicellularity, and sexual reproduction—as well as in the evolution of abstract thinking and self awareness. Thresholds also occur in the physical world; for example, water heats gradually, but at 100°C boiling begins and the transition from liquid to gas starts suddenly. Surely, human intellectual capacities came about by gradual evolution. But when looking at the world of life as it exists today, it would seem that there is a radical breach



between human intelligence and that of other animals. The rudimentary cultures that exist in chimpanzees (Whiten et al., 1999, 2005) do not imply advanced intelligence as it is required for moral behavior.

The question remains, when did morality emerge in the human lineage? Did *Homo habilis* or *Homo erectus* have morality? What about the Neandertals, *Homo neanderthalensis*? When in hominid evolution morality emerged is difficult to determine. It may very well be that the advanced degree of rationality required for moral behavior may only have been reached at the time when creative language came about, and perhaps in dependence with the development of creative language. When creative language may have come about in human evolution is a question that transcends the scope of this essay.<sup>5</sup>

### **9. Whence Moral Codes?**

I have distinguished between moral behavior—judging some actions as good, others as evil—and moral codes—the precepts or norms according to which actions are judged. Moral behavior, I have proposed, is a biological attribute of *H. sapiens*, because it is a necessary consequence of our biological make-up, namely our high intelligence. But moral codes, I argue, are not products of biological evolution, but of cultural evolution.

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<sup>5</sup> For the evolutionary model of the evolution of language that I favor, see Cela-Conde and Ayala (2007), ch. 10.3, pp. 339-353.

It must, first, be stated that moral codes, like any other cultural systems, cannot survive for long if they run in outright contrast to our biology. The norms of morality must be consistent with biological nature, because ethics can only exist in human individuals and in human societies. One might therefore also expect, and it is the case, that accepted norms of morality will promote behaviors that increase the biological fitness of those who behave according to them, such as child care. But the correlation between moral norms and biological fitness is neither necessary nor indeed always the case: some moral precepts common in human societies have little or nothing to do with biological fitness and some moral precepts are contrary to fitness interest.

Before going any further, it seems worthwhile to consider briefly the proposition that the justification of the codes of morality derives from religious convictions and only from them. There is no necessary, or *logical*, connection between religious faith and moral principles, although there usually is a motivational or psychological connection. Religious beliefs do explain why people accept particular ethical norms, because they are motivated to do so by their religious convictions. But in following the moral dictates of one's religion, an individual is not rationally justifying the moral norms that one accepts. It may, of course, be possible to develop such rational justification; for example, when a set of religious beliefs contains propositions about human nature and the world, from which a variety of ethical norms can be logically derived. Indeed, religious

authors, including, for example, Christian theologians, do often propose to justify their ethics on rational foundations concerning human nature. But in this case, the logical justification of the ethical norms does not come from religious faith as such, but from a particular conception of the world; it is the result of philosophical analysis grounded on certain premises.

It may well be that the motivational connection between religious beliefs and ethical norms is the decisive one for the religious believer. But this is true in general: most people, religious or not, accept a particular moral code for social reasons, without trying to justify it rationally by means of a theory from which the moral norms can be logically derived. They accept the moral codes that prevail in their societies, because they have learned such norms from parents, school, or other authorities. The question therefore remains, how do moral codes come about?

The short answer is, as already stated, that moral codes are products of cultural evolution, a distinctive human mode of evolution that has surpassed the biological mode, because it is a more effective form of adaptation; it is faster than biological evolution and it can be directed. Cultural evolution is based on cultural heredity, which is Lamarckian, rather than Mendelian, so that acquired characteristics are transmitted. Most important, cultural heredity does not depend on biological inheritance, from parents to children, but is transmitted also horizontally and without biological bounds. A cultural mutation, an invention

(think of the laptop computer, the cell phone, or rock music) can be extended to millions and millions of individuals in less than one generation.

Darwin's chapter V of *The Descent of Man* is entitled, "On the Development of the Intellectual and Moral Faculties during Primeval and Civilized Times." There, he writes:

There can be no doubt that a tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to give aid to each other and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection. At all times throughout the world tribes have supplanted other tribes; and as morality is one element in their success, the standard of morality and the number of well-endowed men will thus everywhere tend to rise and increase. (pp. 159-160)

Darwin is making two important assertions. First, that morality may contribute to the success of some tribes over others, which is natural selection in the form of group selection. Second, that the standards of morality will tend to improve over human history, because the higher the standards of a tribe, the more likely the success of the tribe. This assertion depends on which standards are thought to be "higher" than others. If the higher standards are defined by their contribution to the success of the tribe, then the assertion is circular. But Darwin

asserts that there are some particular standards that, in his view, would contribute to tribal success: patriotism, fidelity, obedience, courage, and sympathy.

### **10. Sociobiology's Account of Moral Behavior**

Darwin was puzzled by the social organization and behavior of hymenopterans: bees, wasps, ants, and termites. Consider Meliponinae bees, with hundreds of species across the tropics. These stingless bees have typically single-queen colonies with hundreds to thousands of workers. The queen generally mates only once. The worker bees toil, building the hive and feeding and caring for the eggs and larvae, even though they themselves are sterile and only the queen produces progeny. Assume that in some ancestral hive, a gene arises that prompts worker bees to behave as they now do. It would seem that such a gene would not be passed on to the following generation because such worker bees do not reproduce. But such inference would be erroneous.

Meliponinae bees, like other hymenopterans, have a haplo-diploid system of reproduction. Queen bees produce two kinds of eggs: some are unfertilized and develop into males (which are therefore haploid; i.e. they carry only one set of genes); others are fertilized (hence, are diploid, carry two sets of genes) and develop into worker bees and occasionally into a queen. W.D. Hamilton (1964) demonstrated that with such a reproductive system the queen's daughters share in three-quarters of their genes among them, whereas the queen's daughters and their mother share in only one-half of their genes. Hence, the worker-bee genes are

more effectively propagated by workers caring for their sisters than if they would produce and care for their own daughters. Natural selection can thus explain the existence in social insects of sterile castes, which exhibit a most extreme form of apparently altruistic behavior by dedicating their life to care for the progeny of another individual, the queen.

Hamilton's discovery solved the mystery that had puzzled Darwin and had continued puzzling specialists in hymenopteran biology and other evolutionists for somewhat more than a century. In 1975, the notable Harvard ant specialist Edward O. Wilson published *Sociobiology, the New Synthesis*, a treatise appropriately considered the founding document of the new discipline of sociobiology. The last chapter of *Sociobiology* was concerned with the social organization of human societies, with the telling title "Man: From Sociobiology to Sociology," and with sections dedicated to "Culture, Ritual, and Religion" and "Ethics." The first sentence of the "Ethics" section startled many readers: "Scientists and humanists should consider together the possibility that the time has come for ethics to be removed temporarily from the hands of the philosophers and biologicized" (p. 562). Wilson (1975, 1978, 1998), like other sociobiologists (Barash, 1977; Alexander, 1979; see also Kitcher, 1985; Sober & Wilson, 1998; Ruse, 2000, 2006), sees that sociobiology may provide the key for finding a naturalistic basis for ethics.

According to Wilson: “The requirement for an evolutionary approach to ethics is self-evident. It should also be clear, for example, that no single set of moral standards can be applied to all human populations, let alone all sex-age classes within each population. To impose a uniform code is therefore to create complex, intractable moral dilemmas” (p. 564). Moral pluralism is, for Wilson, “innate.” It seems, therefore, that, according to Wilson, biology helps us at the very least to decide that certain moral codes (e.g. all those pretending to be universally applicable) are incompatible with human nature and therefore unacceptable.

However, Wilson (1978) goes further when he writes: “Human behavior—like the deepest capacities for emotional response which drive and guide it—is the circuitous technique by which human genetic material has been and will be kept intact. *Morality has no other demonstratable ultimate function*” (p. 167, my italics). How is one to interpret this statement? It is possible that Wilson is simply giving the reason why ethical behavior exists at all; his proposition would be that humans are prompted to evaluate morally their actions as a means to preserve their genes, their biological nature. But this proposition is, in my view, erroneous. Human beings are by nature ethical beings in the sense I have expounded: they judge morally their actions because of their innate ability for anticipating the consequences of their actions, for formulating value judgments, and for free choice. Human beings exhibit ethical behavior by nature

and necessity, rather than because such behavior would help to preserve their genes or serve any other purpose.

Wilson's statement may alternatively be read as a justification of human moral codes: the function of these would be to preserve human genes. But this would entail the naturalistic fallacy<sup>6</sup> and, worse yet, would seem to justify a morality that most people detest. If the preservation of human genes (be those of the individual or of the species) is the purpose that moral norms serve, Spencer's Social Darwinism would seem right; racism or even genocide could be justified as morally correct, if they were perceived as the means to preserve those genes thought to be good or desirable and to eliminate those thought to be bad or

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<sup>6</sup> The "naturalistic fallacy" (Moore, 1903) consists in identifying what "is" with what "ought to be." This error was pointed out already by Hume (1740; 1978, p. 469): "In every system of morality which I have hitherto met with I have always remarked that the author proceeds for some time in the ordinary way of reasoning ... when of a sudden I am surprised to find, that instead of the usual copulations of propositions, *is* and *is not*, I meet with no proposition that is not connected with an *ought* or *ought not*. This change is imperceptible; but is, however, of the last consequence. For as this *ought* or *ought not* express some new relation or affirmation, it is necessary that it should be observed and explained; and at the same time a reason should be given, for what seems altogether inconceivable, how this new relation can be a deduction from others, which are entirely different from it." The naturalistic fallacy occurs whenever inferences using the terms "ought" or "ought not" are derived from premises that do not include such terms but are rather formulated using the connections "is" or "is not." An argument cannot be logically valid unless the conclusions only contain terms that are also present in the premises. In order to proceed logically from that which "is" to what "ought to be," it is necessary to include a premise that justifies the transition between the two expressions. But this transition is what is at stake, and one would need a previous premise to justify the validity of the one making the transition, and so on in a regression *ad infinitum*. In other words, from the fact that something is the case, it does not follow that it *ought to be so* in the ethical sense; *is* and *ought* belong to disparate logical categories. Because evolution has proceeded in a particular way, it does not follow that that course is morally right or desirable. The justification of ethical norms on biological evolution, or on any other natural process, can only be achieved by introducing value judgments, human choices that prefer one rather than other object or process. Biological nature is in itself morally neutral.



undesirable. Surely, however, Wilson is not intending to justify racism or genocide.

I believe that what Wilson and other sociobiologists are saying is something else, something of great philosophical import that has been stated, with characteristic verve and clarity by Michael Ruse in the companion chapter, as well as elsewhere (1985): “To be blunt, my Darwinian says that substantive morality is a kind of *illusion*, put in place by our genes, in order to make us good social cooperators” (p. 37, my italics). Ruse (in the companion chapter) proceeds to explain why the illusion of ethics is a powerful adaptation:

I would add that the reason why the illusion is such a successful adaptation is that not only do we believe in substantive morality, but we also believe that substantive morality does have an objective foundation. An important part of the phenomenological experience of substantive ethics is, not just that we feel that we ought to do the right and proper thing, but that we feel that we ought to do the right and proper thing because it truly is the right and proper thing. (p. x)

The deceit achieved on us by our genes is complete: “There are in fact no foundations, but we believe that there are in some sense foundations” (p. x).

How come that “selfish genes” move us to act altruistically and otherwise behave in ways that seem morally right? The answer comes, according to

sociobiologists, from the theory of kin selection that explains the altruism of haplo-diploid insects and much more, as well as from other related theoretical constructs such as inclusive fitness and reciprocal altruism. The sociobiologist's argument concerning normative ethics is not that the norms of morality can be grounded in biological evolution, but rather that evolution predisposes us to accept certain moral norms, namely those that are consistent with the "objectives" of natural selection. It is because of this predisposition that human moral codes sanction patterns of behavior similar to those encountered in the social behavior of animals. According to sociobiologists, the commandment to honor one's parents, the incest taboo, the greater blame usually attributed to the wife's adultery than to the husband's, and the banning or restriction of divorce, are among the numerous ethical precepts and practices that endorse behaviors that are promoted by natural selection. The sociobiologists reiterate their conviction that science and ethics belong to separate logical realms; that one may not infer what is morally right or wrong from a determination of how things are or are not in nature. The sociobiologists avoid the naturalistic fallacy by the drastic move of denying that ethical behavior exists as an activity with different causation than any other activities or traits simply determined by our genes. Ethical behavior is simply an expression of our genes and a direct consequence of natural selection as it adapts humans, as well as other organisms, to their environments.

Evolutionists had for years struggled to find an explanation for the apparently altruistic behavior of animals. When a predator attacks a herd of zebras, adult males attempt to protect the young in the herd, even if they are not their progeny, rather than fleeing. When a prairie dog sights a coyote, it will warn other members of the colony with an alarm call, even though by drawing attention to itself this increases its own risk. Darwin tells the story of adult baboons protecting the young. Examples of altruistic behaviors of this kind can be multiplied. But to speak of animal altruism is not to claim that explicit feelings of devotion or regard are present in them, but rather that animals act for the welfare of others at their own risk just as humans are expected to do when behaving altruistically.

The problem is precisely how to justify such behaviors in terms of natural selection. Assume, for illustration, that in a certain species there are two alternative forms of a gene (two alleles), of which one but not the other promotes altruistic behavior. Individuals possessing the altruistic allele will risk their life for the benefit of others, whereas those possessing the non-altruistic allele will benefit from altruistic behavior without risking themselves. Possessors of the altruistic allele will be more likely to die or fail to reproduce, and the allele for altruism will therefore be eliminated more often than the non-altruistic allele. Eventually, after some generations, the altruistic allele will be completely replaced by the non-altruistic one. But then, how is it that altruistic behaviors are

common in animals without the benefit of ethical motivation? The explanation comes from the theory of kin selection.

To ascertain the consequences of natural selection it is necessary to take into account a gene's effects not only on a particular individual but also on all individuals possessing that gene, as in the explanation of the social organization of bees and other hymenopterans. When considering altruistic behavior, one must take into account not only the risks for the altruistic individual, but also the benefits for other possessors of the same allele. Zebras live in herds where individuals are blood relatives. This is also the case for baboon troops. A gene prompting adults to protect the defenseless young would be favored by natural selection if the benefit (in terms of saved individuals that are carriers of that gene) is greater than the cost (due to the increased risk of the protectors). An individual that lacks the altruistic gene and carries instead a non-altruistic one, will not risk its life, but the non-altruistic gene is partially eradicated with the death of each defenseless relative.

It follows from this line of reasoning that the more closely related the members of a herd, troop, or animal group are, the more altruistic behavior should be present. This seems to be generally the case. Consider parental care. Parental care is most obvious in the genetic benefits it entails. Parents feed and protect their young because each child has half the genes of each parent: the genes are

protecting themselves, as it were, when they prompt a parent to care for its young. That is why parental care is widespread among animals.

Sociobiologists point out that many of the moral norms commonly accepted in human societies sanction behaviors also promoted by natural selection, such as the commandment to honor one's parents and the incest taboo, as pointed out above. Once again, the sociobiologists' argument is that human ethical norms are sociocultural correlates of behaviors fostered by biological evolution. Ethical norms protect such evolution-determined behaviors as well as being specified by them.

I, however, believe that the sociobiologists' arguments to that effect are misguided. Consider altruism as an example. Altruism in the biological sense (altruism<sub>b</sub>) is defined in terms of the population genetic consequences of a certain behavior. Altruism<sub>b</sub> is explained by the fact that genes prompting such behavior are actually favored by natural selection (when inclusive fitness is taken into account), even though the fitness of the behaving individual is decreased. But altruism in the moral sense (altruism<sub>m</sub>) is explained in terms of motivations: a person chooses to risk his/her own life (or incur some kind of cost) for the benefit of somebody else. The similarity between altruism<sub>b</sub> and altruism<sub>m</sub> is only with respect to the consequences: an individual's chances are improved by the behavior of another individual who incurs a risk or cost. The underlying causations are completely disparate: the ensuing genetic benefits in altruism<sub>b</sub>;

regard for others in altruism<sub>m</sub>. As Darwin put it, the behavior of a baboon and a human are similar in that they both save an infant (from the dogs or from drowning), but they differ in that humans carry out an assessment, which baboons do not. As I have argued above humans make moral judgments as a necessary consequence of their eminent intellectual abilities. Their judgments, as well as the moral norms on which they are based, are not always accompanied by biological gain.

Parental care is a behavior generally favored by natural selection, which may also be present in virtually all codes of morality, from primitive to more advanced societies. There are other human behaviors sanctioned by moral norms that have biological correlates favored by natural selection. One example is monogamy, which occurs in some animal species but not in many others. It is also sanctioned in many human cultures, but surely not in all. Polygamy is sanctioned in some current human cultures and surely was more so in the past. Food sharing outside the mother–offspring unit rarely occurs in primates, with the exception of chimpanzees and capuchin monkeys, although even in chimpanzees food sharing is highly selective and often associated with reciprocity. A more common form of mutual aid among primates is coalition formation; alliances are formed in fighting other conspecifics, although these alliances are labile, with partners readily changing partners.

One interesting behavior, associated with a sense of justice, or equal pay for equal work, has been described by Sarah Brosnan and Frans de Waal (2003; see also de Waal, 1996) in the brown capuchin monkey, *Cebus paella*. Monkeys responded negatively to unequal rewards in exchanges with a human experimenter. Monkeys refused to participate in an exchange when they witnessed that a conspecific had obtained a more attractive reward for equal effort.

Is the capuchin behavior phylogenetically related to the human virtue of justice? This seems unlikely, since similar behavioral patterns have not been observed in other primates, including apes, phylogenetically closer to humans. Cannibalism is practiced by chimps, as well as by human cultures of the past. Do we have a phylogenetically acquired predisposition to cannibalism as a morally acceptable behavior? This seems unlikely. Moral codes arise in human societies by cultural evolution. Those moral codes tend to be widespread that lead to successful societies.

Since time immemorial, human societies have experimented with moral systems. Some have succeeded and spread widely through humankind, like the Ten Commandments, although other moral systems persist in different human societies. Many moral systems of the past have surely become extinct because they were replaced or because the societies that held them became extinct. The moral systems that currently exist in humankind are those that were favored by

cultural evolution. They were propagated within particular societies for reasons that might be difficult to fathom, but that surely must have included the perception by individuals that a particular moral system was beneficial for them, at least to the extent that it was beneficial for their society by promoting social stability and success. Acceptance of some precepts in many societies is reinforced by civil authority (e.g., those who kill or commit adultery will be punished) and by religious beliefs (God is watching and you'll go to hell if you misbehave). Legal and political systems, as well as belief systems, are themselves outcomes of cultural evolution.

**Postscript: Counterpoint**

According to E.O. Wilson (1992), progress “is a property of the evolution of life as a whole by almost any conceivable intuitive standard, including the acquisition of goals and intentions in the behavior of animals” (p. 187).

Herbert Spencer (1851) was perhaps the first philosopher seeking to find the grounds of morality in biology. Spencer argued that the theory of evolution implies certain ethical principles: any acceptable moral code must be based on natural selection, the law of struggle for existence. The morality of human actions must be measured by their contribution to the greater duration, extension, and perfection of life; that is, as they conform to the progress of life, because this is the goal of evolution as promoted by natural selection. Julian Huxley (1927, 1953) did not quite endorse Spencer's view of evolution as progressive on the



whole, but there are privileged lines of evolutionary progress as it occurs, for example, in the evolution towards higher levels of organization [more complex organisms], from amoeba to animals and from fish to mammals and, ultimately, humans.

I join Ruse (1995, 2009) in his unambiguous rejection of any efforts to justify ethical values on the supposedly progressive character of the evolutionary process. “It is far from obvious,” he writes “that natural selection promotes progress or that progress actually occurs in any clear definable and quantifiable way” (Ruse, p. xx). I would add that this is the case because the concept of progress contains two elements: one descriptive—that directional change has occurred; the other axiological—that the change represents an improvement or betterment. The notion of progress requires that a value judgment be made of what is better and what is worse, or what is higher and what is lower, according to some axiological standard (Ayala, 1974).

Ruse’s next move amounts, however, to throwing the baby out with the bathwater: morality does not exist in objective reality, except as a mirage placed in our genes by natural selection so that we may become good cooperators (Ruse and Wilson, 1985, 1986). This Ruse had stated before, but he now goes farther. On top of the illusion that there is right and wrong, is the additional mirage, “put in place by biology,” that morality has an objective foundation. It is “not just that we

feel we ought to do the right and proper thing, but that we feel that ... it truly is the right and proper thing” (companion manuscript, p. 30).

I rather see it that morality exists in objective reality because our exalted intelligence allows us to anticipate the consequence of our action sin regards to others and to evaluate the actions in terms of these consequences. Such are the biological foundations of moral behavior. Morality is an adaptation that contributes to the biological success of our species, but it is an exaptation, rather than an adaptation, because it was not directly promoted by natural selection. The target of natural selection was rather exalted intelligence, because tool making improved the fitness of our Pleistocene ancestors. Human societies have experimented over millennia with different moral systems. Those that persist in modern mankind are those that proved successful within the societies in which they exist. Moral codes are products of cultural evolution, not direct outcomes of natural selection.

## **References**

- Alexander, R. D. (1979). *Darwinism and human affairs*. Seattle: University of Washington Press.
- Ayala, F. J. (1974). The concept of biological progress. In: F. J. Ayala & Th. Dobzhansky (Eds.), *Studies in the Philosophy of Biology* (pp. 339-355). London: Macmillan and Berkeley: University of California Press.

- Ayala, F. J. (1982). The evolutionary concept of progress. In G. Almond, M. Chodorow, & R. Pearce (Eds.), *Progress and its discontents* (pp. 106-124). Berkeley: University of California Press.
- Ayala, F. J. (1987). The biological roots of morality. *Biology and Philosophy*, 2, 235-252.
- Barash, D. (1977). *Sociobiology and behavior*. New York: Elsevier.
- Barkow, J., Cosmides, L., & Tooby, J. (Eds.). (1992). *The adapted mind: Evolutionary psychology and the generation of culture*. Oxford: Oxford University Press.
- Blackmore, S. (1999). *The meme machine*. Oxford: Oxford University Press.
- Brosnan, S., & de Waal, F. (2003). Monkeys reject unequal pay. *Nature*, 425, 297-299.
- Cela-Conde, C., & Ayala, F. J. (2007). *Human evolution: Trails from the past*. Oxford: Oxford University Press.
- Copp, D. (2006). *The Oxford handbook of ethical theory*. Oxford: Oxford University Press.
- Darwin, C. R. (1871). *The descent of man, and selection in relation to sex*. London: John Murray. (Also: New York: Appleton and Company, 1971).
- de Waal, F. (1996). *Good natured: The origins of right and wrong in humans and other animals*. Cambridge, MA: Harvard University Press.

- Hamilton, W. (1964). The genetical evolution of social behavior. *Journal of Theoretical Biology*, 7, 1-51.
- Hauser, M. (2006). *Moral minds: How nature designed our universal sense of right and wrong*. New York: HarperCollins.
- Hume, D. (1978). *Treatise of human nature*. Oxford: Oxford University Press.  
(Original work published in 1740).
- Huxley, J. S. (1927). *Religion without Revelation*. London: Ernest Benn.
- Huxley, J. S. (1953). *Evolution in action*. New York: Harper.
- Huxley, T. H., & Huxley, J. S. (1947). *Touchstone for ethics*. New York: Harper.
- Kitcher, P. (1985). *Vaulting ambition: Sociobiology and the quest for human nature*. Cambridge, MA: MIT Press.
- Maienschein, J., & Ruse, M. (Eds.). (1999). *Biology and the foundations of ethics*. Cambridge: Cambridge University Press.
- Moore, G. E. (1903). *Principia ethica*. Cambridge: Cambridge University Press.
- Ruse, M. (1995). *Evolutionary naturalism*. London: Routledge.
- Ruse, M. (2000). *The evolution wars: A guide to the controversies*. Santa Barbara, CA: ABC-CLIO.
- Ruse, M. (2006). *Darwinism and its discontents*. Cambridge: Cambridge University Press.

- Ruse, M. (2009[?]). The Biological Sciences Can Act as a Ground for Ethics. In Ayala, Francisco and Arp, Robert, *Contemporary Debates in Philosophy of Biology*. Oxford: Wiley-Blackwell.
- Ruse, M., & Wilson, E. O. (1985). The evolution of ethics. *New Scientist*, 108, 50-52.
- Ruse, M., & Wilson, E. O. (1986). Moral philosophy as applied science. *Philosophy*, 61, 173-192.
- Sober, E., & Wilson, D. S. (1998). *Unto others: The evolution and psychology of unselfish behavior*. Cambridge, MA: Harvard University Press.
- Spencer, H. (1851). *Social status or the conditions essential to human happiness specified and the first of them developed*. London: J. Chapman.
- Spencer, H. (1893). *The principles of ethics*. London: Williams and Norgate.
- Waddington, C. H. (1960). *The ethical animal*. London: Allen and Unwin.
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, E. G., Wrangham, R. W., & Boesch, C. (1999). Cultures in chimpanzees. *Nature*, 399, 682-685.
- Whiten, A., Horner, V., & de Waal, F. (2005). Conformity to cultural norms of tool use in chimpanzees. *Nature*, 437, 737-740.
- Wilson, E. O. (1975). *Sociobiology, the new synthesis*. Cambridge: Belknap Press.
- Wilson, E. O. (1978). *On human nature*. Cambridge, MA: Harvard University Press.

Wilson, E. O. (1992). *The Diversity of Life*. Cambridge, MA: Harvard University Press.

Wilson, E. O. (1998). *Consilience: The unity of knowledge*. New York: Knopf.