

came wrongly to be called *social Darwinism*, and saddled the theory with an undeserved reputation for beastliness over a century or more.

Alex Rosenberg's chapter from the *Cambridge Companion to Darwin* (chapter 25 in this volume) shows the limits of Darwinian theory's relevance to ethics, and the mistakes made by the repeated attempts since Spencer to harness natural selection to the vindication of any ethical claims whatever.

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Sociobiology: The New Synthesis

Edward O. Wilson

The Morality of the Gene

Camus said that the only serious philosophical question is suicide. That is wrong even in the strict sense intended. The biologist, who is concerned with questions of physiology and evolutionary history, realizes that self-knowledge is constrained and shaped by the emotional control centers in the hypothalamus and limbic system of the brain. These centers flood our consciousness with all the emotions – hate, love, guilt, fear, and others – that are consulted by ethical philosophers who wish to intuit the standards of good and evil. What, we are then compelled to ask, made the hypothalamus and limbic system! They evolved by natural selection. That simple biological statement must be pursued to explain ethics and ethical philosophers, if not epistemology and epistemologists, at all depths. Self-existence, or the suicide that terminates it, is not the central question of philosophy. The hypothalamic-limbic complex automatically denies such logical reduction by countering it with feelings of guilt and altruism. In this one way the philosopher's own emotional control centers are wiser than his solipsist consciousness, "knowing" that in evolutionary time the individual organism counts for almost nothing. In a Darwinist sense the organism does not

live for itself. Its primary function is not even to reproduce other organisms; it reproduces genes, and it serves as their temporary carrier. Each organism generated by sexual reproduction is a unique, accidental subset of all the genes constituting the species. Natural selection is the process whereby certain genes gain representation in the following generations superior to that of other genes located at the same chromosome positions. When new sex cells are manufactured in each generation, the winning genes are pulled apart and reassembled to manufacture new organisms that, on the average, contain a higher proportion of the same genes. But the individual organism is only their vehicle, part of an elaborate device to preserve and spread them with the least possible biochemical perturbation. Samuel Butler's famous aphorism, that the chicken is only an egg's way of making another egg, has been modernized: the organism is only DNA's way of making more DNA. More to the point, the hypothalamus and limbic system are engineered to perpetuate DNA.

In the process of natural selection, then, any device that can insert a higher proportion of certain genes into subsequent generations will come to characterize the species. One class of such devices promotes prolonged individual survival.

Another promotes superior mating performance and care of the resulting offspring. As more complex social behavior by the organism is added to the genes' techniques for replicating themselves, altruism becomes increasingly prevalent and eventually appears in exaggerated forms. This brings us to the central theoretical problem of sociobiology: how can altruism, which by definition reduces personal fitness, possibly evolve by natural selection? The answer is kinship: if the genes causing the altruism are shared by two organisms because of common descent, and if the altruistic act by one organism increases the joint contribution of these genes to the next generation, the propensity to altruism will spread through the gene pool. This occurs even though the altruist makes less of a solitary contribution to the gene pool as the price of its altruistic act.

To his own question, "Does the Absurd dictate death?" Camus replied that the struggle toward the heights is itself enough to fill a man's heart. This arid judgment is probably correct, but it makes little sense except when closely examined in the light of evolutionary theory. The hypothalamic-limbic complex of a highly social species, such as man, "knows," or more precisely it has been programmed to perform as if it knows, that its underlying genes will be proliferated maximally only if it orchestrates behavioral responses that bring into play an efficient mixture of personal survival, reproduction, and altruism. Consequently, the centers of the complex tax the conscious mind with ambivalences whenever the organisms encounter stressful situations. Love joins hate; aggression, fear; expansiveness, withdrawal; and so on; in blends designed not to promote the happiness and survival of the individual, but to favor the maximum transmission of the controlling genes.

The ambivalences stem from counteracting pressures on the units of natural selection. Their genetic consequences will be explored formally later. For the moment suffice it to note that what is good for the individual can be destructive to the family; what preserves the family can be harsh on both the individual and the tribe to which its family belongs; what promotes the tribe can weaken the family and destroy the individual; and so on upward through the permutations of levels of organization. Counter-acting selection on these different units will result in certain genes

being multiplied and fixed, others lost, and combinations of still others held in static proportions. According to the present theory, some of the genes will produce emotional states that reflect the balance of counteracting selection forces at the different levels.

I have raised a problem in ethical philosophy in order to characterize the essence of sociobiology. Sociobiology is defined as the systematic study of the biological basis of all social behavior. For the present it focuses on animal societies, their population structure castes, and communication, together with all of the physiology underlying the social adaptations. But the discipline is also concerned with the social behavior of early man and the adaptive features of organization in the more primitive contemporary human societies. Sociology *sensu stricto*, the study of human societies at all levels of complexity, still stands apart from sociobiology because of its largely structuralist and nongenetic approach. It attempts to explain human behavior primarily by empirical description of the outermost phenotypes and by unaided intuition, without reference to evolutionary explanations in the true genetic sense. It is most successful, in the way descriptive taxonomy and ecology have been most successful, when it provides a detailed description of particular phenomena and demonstrates first-order correlations with features of the environment. Taxonomy and ecology, however, have been reshaped entirely during the past forty years by integration into neo-Darwinist evolutionary theory – the "Modern Synthesis," as it is often called – in which each phenomenon is weighed for its adaptive significance and then related to the basic principles of population genetics. It may not be too much to say that sociology and the other social sciences, as well as the humanities, are the last branches of biology waiting to be included in the Modern Synthesis. One of the functions of sociobiology, then, is to reformulate the foundations of the social sciences in a way that draws these subjects into the Modern Synthesis. Whether the social sciences can be truly biologized in this fashion remains to be seen.

This book makes an attempt to codify sociobiology into a branch of evolutionary biology and particularly of modern population biology. I believe that the subject has an adequate richness of detail and aggregate of self-sufficient concepts

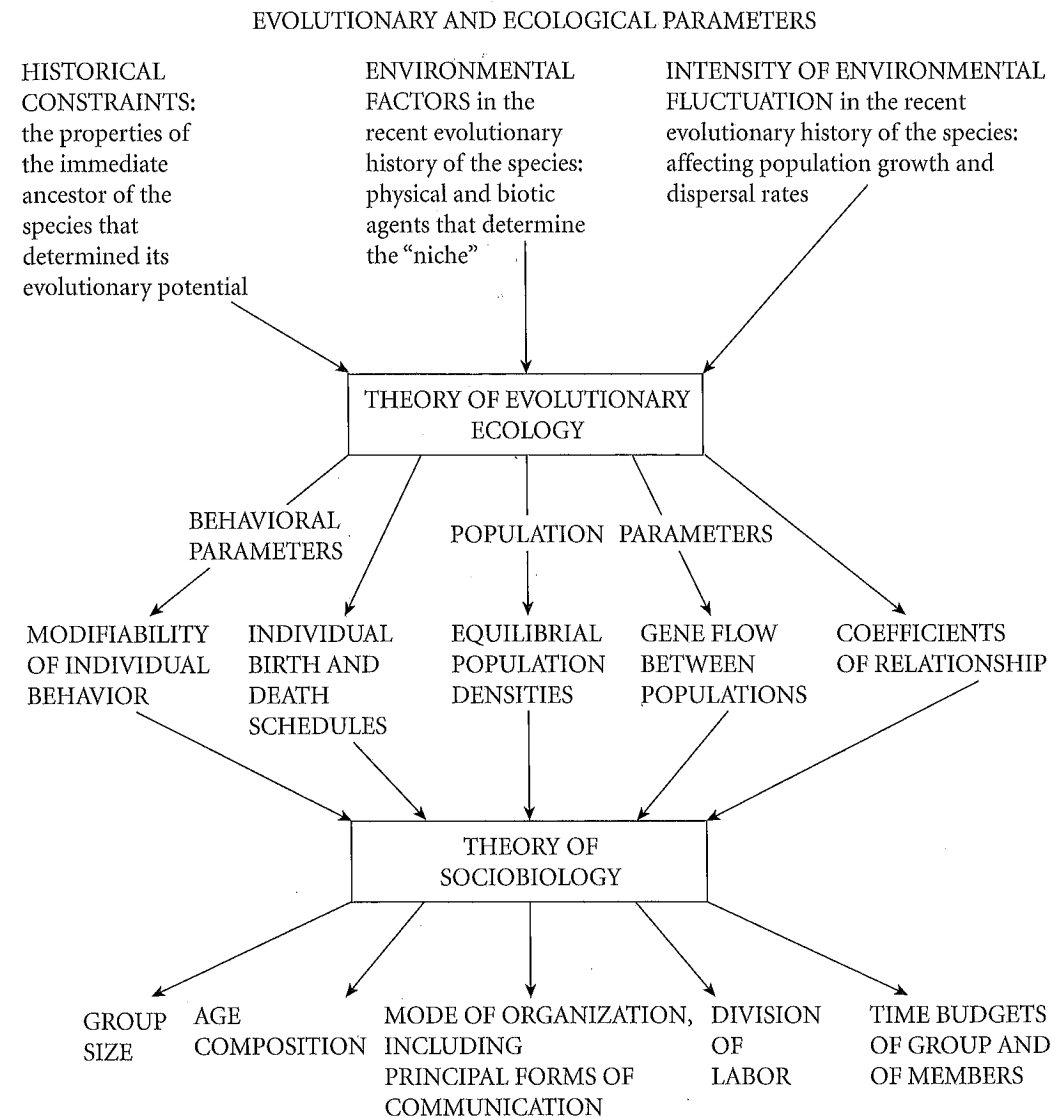


Figure 23.1 The connections that can be made between phylogenetic studies, ecology, and sociobiology.

to be ranked as coordinate with such disciplines as molecular biology and developmental biology. In the past its development has been slowed by too close an identification with ethology and behavioral physiology. In the view presented here, the new sociobiology should be compounded of roughly equal parts of invertebrate zoology, vertebrate zoology, and population biology. Figure 23.1 shows the schema with which I closed *The Insect Societies*, suggesting how the amalgam can be achieved. Biologists have always been intrigued by comparisons between societies of

invertebrates, especially insect societies, and those of vertebrates. They have dreamed of identifying the common properties of such disparate units in a way that would provide insight into all aspects of social evolution, including that of man. The goal can be expressed in modern terms as follows: when the same parameters and quantitative theory are used to analyze both termite colonies and troops of rhesus macaques, we will have a unified science of sociobiology. This may seem an impossibly difficult task. But as my own studies have advanced, I have been increasingly impressed with the

functional similarities between invertebrate and vertebrate societies and less so with the structural differences that seem, at first glance, to constitute such an immense gulf between them. Consider for a moment termites and monkeys. Both are formed into cooperative groups that occupy territories. The group members communicate hunger, alarm, hostility, caste status or rank, and reproductive status among themselves by means of something on the order of 10 to 100 nonsyntactical signals. Individuals are intensely aware of the distinction between groupmates and nonmembers. Kinship plays an important role in group structure and probably served as a chief generative force of sociality in the first place. In both kinds of society there is a well-marked division of labor, although in the insect society there is a much stronger reproductive component. The details of organization have been evolved by an evolutionary optimization process of unknown precision, during which some measure of added fitness was given to individuals with cooperative tendencies – at least toward relatives. The fruits of cooperativeness depend upon the particular conditions of the environment and are available to only a minority of animal species during the course of their evolution.

This comparison may seem facile, but it is out of such deliberate oversimplification that the beginnings of a general theory are made. The formulation of a theory of sociobiology constitutes, in my opinion, one of the great manageable problems of biology for the next twenty or thirty years. The prolegomenon of Figure 23.1 guesses part of its future outline and some of the directions in which it is most likely to lead animal behavior research. Its central precept is that the evolution of social behavior can be fully comprehended only through an understanding, first, of demography, which yields the vital information concerning population growth and age structure, and, second, of the genetic structure of the populations, which tells us what we need to know about effective population size in the genetic sense, the coefficients of relationship within the societies, and the amounts of gene flow between them. The principal goal of a general theory of sociobiology should be an ability to predict features of social organization from a knowledge of these population parameters combined with information on the behavioral constraints imposed by the genetic constitution of the species. It will

be a chief task of evolutionary ecology, in turn, to derive the population parameters from a knowledge of the evolutionary history of the species and of the environment in which the most recent segment of that history unfolded. The most important feature of the prolegomenon, then, is the sequential relation between evolutionary studies, ecology, population biology, and sociobiology.

In stressing the tightness of this sequence, however, I do not wish to underrate the filial relationship that sociobiology has had in the past with the remainder of behavioral biology. Although behavioral biology is traditionally spoken of as if it were a unified subject, it is now emerging as two distinct disciplines centered on neurophysiology and on sociobiology, respectively. The conventional wisdom also speaks of ethology, which is the naturalistic study of whole patterns of animal behavior, and its companion enterprise, comparative psychology, as the central, unifying fields of behavioral biology. They are not, both are destined to be cannibalized by neurophysiology and sensory physiology from one end and sociobiology and behavioral ecology from the other (see Figure 23.2).

I hope not too many scholars in ethology and psychology will be offended by this vision of the future of behavioral biology. It seems to be indicated both by the extrapolation of current events and by consideration of the logical relationship behavioral biology holds with the remainder of science. The future, it seems clear, cannot be with the ad hoc terminology, crude models, and curve fitting that characterize most of contemporary ethology and comparative psychology. Whole patterns of animal behavior will inevitably be explained within the framework, first, of integrative neurophysiology, which classifies neurons and reconstructs their circuitry, and, second, of sensory physiology, which seeks to characterize the cellular transducers at the molecular level. Endocrinology will continue to play a peripheral role, since it is concerned with the cruder tuning devices of nervous activity. To pass from this level and reach the next really distinct discipline, we must travel all the way up to the society and the population. Not only are the phenomena best described by families of models different from those of cellular and molecular biology, but the explanations become largely evolutionary. There should be nothing surprising in this

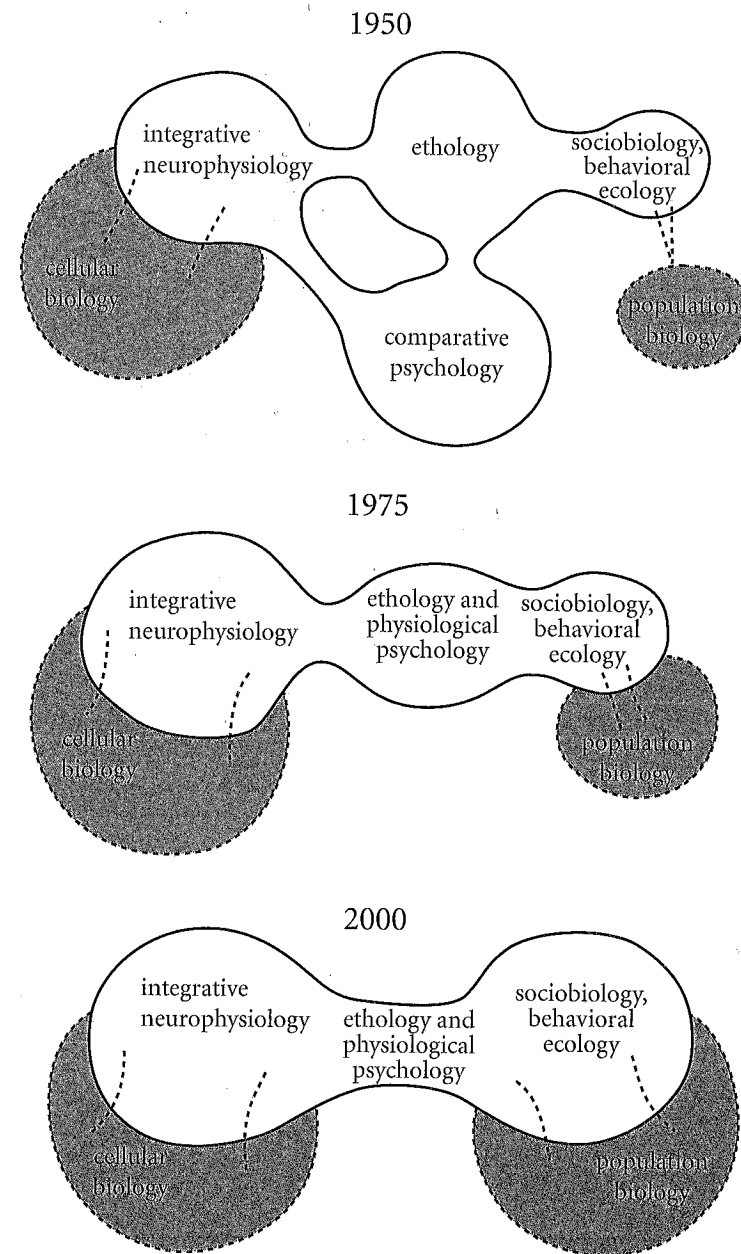


Figure 23.2 A subjective conception of the relative number of ideas in various disciplines in and adjacent to behavioral biology to the present time and as it might be in the future.

distinction. It is only a reflection of the larger division that separates the two greater domains of evolutionary biology and functional biology. As Lewontin (1972) has truly said: "Natural selection of the character states themselves is the essence of Darwinism. All else is molecular biology."

Man: From Sociobiology to Sociology

Let us now consider man in the free spirit of natural history, as though we were zoologists from another planet completing a catalog of social species on Earth. In this macroscopic view the

humanities and social sciences shrink to specialized branches of biology; history, biography, and fiction are the research protocols of human ethnology; and anthropology and sociology together constitute the sociobiology of single primate species.

Ethics

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. The subject at present consists of several oddly disjunct conceptualizations. The first is *ethical intuitionism*, the belief that the mind has a direct awareness of true right and wrong that it can formalize by logic and translate into rules of social action. The purest guiding precept of secular Western thought has been the theory of the social contract as formulated by Locke, Rousseau, and Kant. In our time the precept has been reweaved into a solid philosophical system by John Rawls (1971). His imperative is that justice should be not merely integral to a system of government but rather the object of the original contract. The principles called by Rawls "justice as fairness" are those which free and rational persons would choose if they were beginning an association from a position of equal advantage and wished to define the fundamental rules of the association. In judging the appropriateness of subsequent laws and behavior, it would be necessary to test their conformity to the unchallengeable starting position.

The Achilles heel of the intuitionist position is that it relies on the emotive judgment of the brain as though that organ must be treated as a black box. While few will disagree that justice as fairness is an ideal state for disembodied spirits, the conception is in no way explanatory or predictive with reference to human beings. Consequently, it does not consider the ultimate ecological or genetic consequences of the rigorous prosecution of its conclusions. Perhaps explanation and prediction will not be needed for the millennium. But this is unlikely – the human genotype and the ecosystem in which it evolved were fashioned out of extreme unfairness. In either case the full exploration of the neural machinery of ethical judgement is desirable and already in progress. One such effort, constituting the second mode of conceptualization, can be

called *ethical behaviorism*. Its basic proposition, which has been expanded most fully by J. E. Scott (1971), holds that moral commitment is entirely learned, with operant conditioning being the dominant mechanism. In other words, children simply internalize the behavioral norms of the society. Opposing this theory is the *developmental-genetic conception* of ethical behavior. The best-documented version has been provided by Lawrence Kohlberg (1969). Kohlberg's viewpoint is structuralist and specifically Piagetian, and therefore not yet related to the remainder of biology. Piaget has used the expression "genetic epistemology" and Kohlberg "cognitive-developmental" to label the general concept. However, the results will eventually become incorporated into a broadened developmental biology and genetics. Kohlberg's method is to record and classify the verbal responses of children to moral problems. He has delineated six sequential stages of ethical reasoning through which an individual may progress as part of his mental maturation. The child moves from a primary dependence on external controls and sanctions to an increasingly sophisticated set of internalized standards (see Table 23.1). The analysis has not yet been directed to the question of plasticity in the basic rules. Intracultural variance has not been measured, and heritability therefore not assessed. The difference between ethical behaviorism and the current version of developmental-genetic analysis is that the former postulates a mechanism (operant conditioning) without evidence and the latter presents evidence without postulating a mechanism. No great conceptual difficulty underlies this disparity. The study of moral development is only a more complicated and less tractable version of the genetic variance problem. With the accretion of data the two approaches can be expected to merge to form a recognizable exercise in behavioral genetics.

Even if the problem were solved tomorrow, however, an important piece would still be missing. This is the *genetic evolution of ethics*. I argue that ethical philosophers intuit the deontological canons of morality by consulting the emotive centers of their own hypothalamic-limbic system. This is also true of the developmentalists, even when they are being their most severely objective. Only by interpreting the activity of the emotive centers as a biological adaptation can the meaning

Table 23.1 The classification of moral judgment into levels and stages of development. (Based on Kohlberg, 1969.)

Level	Basis of moral judgment	Stage of development
I	Moral value is defined by punishment and reward	1. Obedience to rules and authority to avoid punishment 2. Conformity to obtain rewards and to exchange favors
II	Moral value resides in filling the correct roles, in maintaining order and meeting the expectations of others	3. Good-boy orientation: conformity to avoid dislike and rejection by others 4. Duty orientation: conformity to avoid censure by authority, disruption of order, and resulting guilt
III	Moral value resides in conformity to shared standards, rights, and duties	5. Legalistic orientation: recognition of the value of contracts, some arbitrariness in rule formation to maintain the common good 6. Conscience or principle orientation: primary allegiance to principles of choice, which can overrule law in cases where the law is judged to do more harm than good

of the canons be deciphered. Some of the activity is likely to be outdated, a relic of adjustment to the most primitive form of tribal organization. Some of it may prove to be *in statu nascendi*, constituting new and quickly changing adaptations to agrarian and urban life. The resulting confusion will be reinforced by other factors. To the extent that unilaterally altruistic genes have been established in the population by group selection, they will be opposed by allelomorphs favored by individual selection. The conflict of impulses under their various controls is likely to be widespread in the population, since current theory predicts that the genes will be at best maintained in a state of balanced polymorphism. Moral ambivalence will be further intensified by the circumstance that a schedule of sex- and age-dependent ethics can impart higher genetic fitness than a single moral code which is applied uniformly to all sex-age groups. The argument for this statement is the special case of the Gadgil-Bossert distribution in which the contributions of social interactions to survivorship and fertility schedules are specified. Some of the differences in the Kohlberg stages could be explained in this manner. For example, it should be of selective advantage for young children to be self-centered and relatively disinclined to perform altruistic

acts based on personal principle. Similarly, adolescents should be more tightly bound by age-peer bonds within their own sex and hence unusually sensitive to peer approval. The reason is that at this time greater advantage accrues to the formation of alliances and rise in status than later, when sexual and parental morality become the paramount determinants of fitness. Genetically programmed sexual and parent-offspring conflict of the kind predicted by the Trivers models are also likely to promote age differences in the kinds and degrees of moral commitment. Finally, the moral standards of individuals during early phases of colony growth should differ in many details from those of individuals at demographic equilibrium or during episodes of overpopulation. Metapopulations subject to high levels of r extinction will tend to diverge genetically from other kinds of populations in ethical behavior.

If there is any truth to this theory of innate moral pluralism, the requirement for an evolutionary approach to ethics is self-evident. It should also be clear 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 – these, of course, are the current condition of mankind.

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The Evolution of Cooperation

Robert Axelrod and William D. Hamilton

The theory of evolution is based on the struggle for life and the survival of the fittest. Yet cooperation is common between members of the same species and even between members of different species. Before about 1960, accounts of the evolutionary process largely dismissed cooperative phenomena as not requiring special attention. This position followed from a misreading of theory that assigned most adaptation to selection at the level of populations or whole species. As a result of such misreading, cooperation was always considered adaptive. Recent reviews of the evolutionary process, however, have shown no sound basis for a pervasive group-benefit view of selection; at the level of a species or a population, the processes of selection are weak. The original individualistic emphasis of Darwin's theory is more valid (1, 2).

To account for the manifest existence of cooperation and related group behavior, such as altruism and restraint in competition, evolutionary theory has recently acquired two kinds of extension. These extensions are, broadly, genetical kinship theory (3) and reciprocation theory (4, 5). Most of the recent activity, both in field work and in further developments of theory, has been on the side of kinship. Formal approaches have

varied, but kinship theory has increasingly taken a gene's-eye view of natural selection (6). A gene, in effect, looks beyond its mortal bearer to interests of the potentially immortal set of its replicas existing in other related individuals. If interactants are sufficiently closely related, altruism can benefit reproduction of the set, despite losses to the individual altruist. In accord with this theory's predictions, apart from the human species, almost all clear cases of altruism, and most observed cooperation, occur in contexts of high relatedness, usually between immediate family members. The evolution of the suicidal barbed sting of the honeybee worker could be taken as paradigm for this line of theory (7).

Conspicuous examples of cooperation (although almost never of ultimate self-sacrifice) also occur where relatedness is low or absent. Mutualistic symbioses offer striking examples such as these: the fungus and alga that compose a lichen; the ants and ant-acacias, where the trees house and feed the ants which, in turn, protect the trees (8); and the fig wasps and fig tree, where wasps, which are obligate parasites of fig flowers, serve as the tree's sole means of pollination and seed set (9). Usually the course of cooperation in such symbioses is smooth, but sometimes the partners

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