

INVITED PAPER

## Three Biological Heresies

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**Abstract:** A science, like a religion, develops an orthodoxy, and those whose thought diverges from it become heretics. Although in the present age they are not likely to be burnt at the stake or forced by torture to recant, they can be penalized in various ways. Editors of scientific journals may reject their contributions; reviewers censure their books; universities are reluctant to give them professorships. Nevertheless, the scientific heretics of one age may become the revered pioneers of a later age. Among the biological heresies of our day are anthropomorphism, teleology, and intergroup selection. Anthropomorphism makes unproved assumptions about the psychic life of animals. Teleology, the doctrine that nature strives toward predetermined ends or goals, is rejected because mutations are random and the agents of selection, chiefly predation, disease, starvation, and climatic extremes, care not at all for the welfare of a species. Intergroup selection is in disfavor because individuals, rather than families or groups, are primarily screened by natural selection. This essay presents three arguments on the above subjects. Current evolutionary theory is consistent with the idea that animals may have minds with varying degrees of similarity with the human mind. Careful anthropocentric interpretations of biological observations should not be rejected *a priori*. We should keep an open mind towards the possible existence of unconscious programming towards an end, as known to exist in nucleic acid codification: much opposition to teleology is based on the inappropriate use of "purpose" and "end" as synonyms. Finally, the rejection of intergroup selection and the sole acceptance of individual selection in organic evolution is an oversimplification that neglects important phenomena such as coevolution and social interactions.

**Key words:** Anthropocentrism, teleology, group selection, individual selection, biological theory, evolution, philosophy.

A science, like a religion, develops an orthodoxy, and those whose thought diverges from it become heretics. Although in the present age they are not likely to be burnt at the stake or forced by torture to recant, they can be penalized in various ways. Editors of scientific journals may reject their contributions; reviewers censure their books; universities are reluctant to give them professorships. Nevertheless, the scientific heretics of one age may become the revered pioneers of a later age. When astronomical orthodoxy favored a geocentric Universe, Copernicus was a heretic whose book was not published until he lay dying.

When biological orthodoxy supported the fixity of species, Darwin was a heretic who hesitated to promulgate his theory of evolution until prompted to do so by receipt of a paper, expounding similar ideas, that Alfred Russel Wallace sent to him from the East Indies. Among the biological heresies of our day are anthropomorphism, teleology, and intergroup selection. Anthropomorphism makes unproved assumptions about the psychic life of animals. Teleology, the doctrine that nature strives toward predetermined ends or goals, is rejected because mutations are random and the agents of selection, chiefly predation, disease, starva-

and climatic extremes, care not at all for the welfare of a species. Intergroup selection is in disfavor because individuals, rather than families or groups, are primarily screened by natural selection.

**Anthropomorphism:** "Anthropomorphous" means manlike in form. Most of man's gods have been more or less anthropomorphic, often revoltingly so. In zoology, anthropomorphism is the ascription of human characteristics to animals. The literal meaning of the word, derived from the Greek nouns *anthropos* (human being, man) and *morphe* (form) would lead one to conclude that it refers to the physical configuration of nonhuman animals rather than to their psychic qualities. To point out that the bones of a bird's wing correspond closely to those of a human arm and hand is certainly anthropomorphism in this literal sense. Indeed, anatomists recognize a fundamental similarity in the skeletons of all terrestrial vertebrates. Nevertheless, biologists who emphasize these similarities are never accused of anthropomorphism in a depreciatory sense. Such resemblances provide the strongest evidence for the theory of evolution; to deny them is to undermine its foundations.

When we turn from the anatomy to the psychic life of animals, we find a very different attitude among biologists; to recognize psychic similarities, at least above such basic feelings as hunger, pain and sexual desire, is heresy. Are we to conclude, then, that some extranatural agent implanted the human mind in a body that evolved from earlier vertebrate forms? Proponents of this dualistic view of man's origin have not been lacking, but this is not biological orthodoxy. The more consistent view is that man's mind and his body evolved together. Both his physical structures and his psychic traits have antecedents among animals less richly endowed.

The difficulty is that psychic states are not observable as bones and organs are. Aside from our individual selves, consciousness is always an inference, never a datum. We infer the feelings of those closest to us by certain overt signs, vocal, facial, behavioral; we cannot prove by scientific procedures that they feel. The more unlike ourselves another creature is, the more precarious our inferences from its behavior become.

Our imagination is limited by our experience. It is difficult for us to imagine any feelings, affections, or enjoyments that might give value to another creature's life wholly different from those that have enhanced our own. An animal's psychic state may differ in intensity or tone from ours, but it cannot be utterly unlike anything that we have felt without becoming inconceivable by us. Among the experiences that might enrich the life of one of the more advanced animals, including many birds and mammals, are pleasure in spontaneous activity, such as flying and soaring by birds, gambling by quadrupeds, swimming by dolphins; the comfort of companionship in a perilous world; affection for mates, especially among animals continuously paired; emotional attachment to nests and dependent young; aesthetic response to beautiful colors and melodious sounds; a bird's delight in his own singing; the comfort of a snug dormitory nest on a chilly night; in a small minority of birds, joy in a tastefully decorated bower. Since all such satisfactions are of sorts that from time to time many of us experience, they are in this sense "anthropomorphic." Unless we ascribe to nonhuman animals certain psychic states that make life worth living to us, as likewise such debilitating passions as fear, anger, and hatred, we must view their lives as emotionally blank, with no zest in living.

We cannot prove that nonhuman animals enjoy living, are emotionally attached to mates and young, or are attracted by beauty; we can only seek indications and weigh probabilities. But instead of stigmatizing - I almost wrote "vituperating" - as anthropomorphic the attempt to demonstrate humanlike psychic qualities in animals, we should welcome every indication of their presence, and be grateful to naturalists who call attention to them. The probability that they occur should raise our estimate of the worth of animate life, making us feel less alone in a world overcrowded with organisms. If all nonhuman creatures are devoid of the psychic attributes called "anthropomorphic", it follows that during the immense age before man arose no gleam of joy, no warmth of affection, nothing to give living intrinsic value, brightened the existence of any of the myriad animals that swarmed over a hospitable planet. Devoid of anything that might give value to existence, Earth might as well have remained lifeless until the human lineage

abruptly acquired the psychic qualities that enhance our lives. We cannot prove beyond all doubt that this was not true, but to affirm the continuity of development of both anatomical and psychic characters accords well with evolutionary theory.

**Teleology:** The second frequently condemned heresy is teleology, the doctrine that natural processes are directed toward ends, that nature is pervaded by purpose. Since we humans are so purposeful, we spontaneously ascribe purpose to the animals around us, and often to nature as a whole. Thus, teleology might be considered an aspect of anthropomorphism, the ascription of human qualities to nonhuman things. The teleological thought of early man was firmly incorporated in religions that thrive to this day and was accepted by Classical philosophers. Aristotle (*Physics*, Bk. 2, Ch.3) recognized four categories of causes: material, formal, efficient, and final. The first, or material, cause is the matter of which anything is made. The second, or formal, cause is the archetype or the form that it will assume. The third, or efficient, cause is the mover, or agent, that shapes the material into form. The final cause is the end for which the object is created, the goal toward which a movement is directed. To take one of the examples that Aristotle gives, the material cause of a bowl is the silver of which it is made. Its formal cause is its design, perhaps an image in the silver-smith's mind, or a model that he copies. The efficient cause is the smith himself, who hammers it out with arms and hands. The final cause is the finished product, or the use for which it is intended. In general, the final cause is the end, for the sake of which something is made or done, as health is the end of the physician's art. A complex artifact may have multiple causes: a variety of materials may enter into its construction; different components may be planned by different designers; many workers may be needed to make its parts and assemble them; if it can serve in diverse ways, it may be said to have several final causes in the Aristotelian sense.

Only efficient causes can accomplish ends. Unless it find means, a purpose is as helpless as a hatchling sparrow. To be effective, a final

cause must find adequate material and efficient causes. An end capable of fulfillment becomes a selector of causes, itself a cause of the second order.

Modern technology is, of course, deeply concerned with final causes - the uses to which its inventions can be put, the profits they will bring to their manufacturers. Pure science concentrates upon the first two causes: matter and the forces that move or shape it. A form is viewed, not as a cause, but as a result of the action of forces upon matter. Final causes, ends for the sake of which things happen or are done, are commonly viewed as beyond the purview of science. This is true even in biology, which deals with the living world, where, if anywhere, we are inclined to look for purposes. Organs and tissues appear to be formed to serve definite ends; animals appear to act with a purpose. Since we are such purposeful, goal-oriented bipeds, our language is so rich in teleological expressions that a young student in a biological laboratory does well to be careful how he uses it. He will be safer from rebuke by a meticulous professor if he speaks of the function rather than the purpose of an organ. The harmless little preposition "to" has teleological implications: we study to learn; we work to earn money. To avoid so much as a suspicion of this heresy, the student should say "The plant grows upward and spreads its leaves in the sunshine", not "in order to spread its leaves..."

A major concern of contemporary biologists is evolution. I infer from the titles of many of their papers that many of them believe it more important to know how an animal evolved (usually a speculative question) than how it lives and acts (which often can be learned by patient observation). In discussions of evolution, which to the naive onlooker sometimes appears to be directed toward ends, purpose, design, of goal are strictly taboo; only material and efficient causes are admissible.

Contemporary theory recognizes three major steps in the evolution of species. The first is mutation, resulting from alterations in the arrangement of molecules in the genes that jointly determine the forms, colors, functioning, and innate behavior of organisms. Genes are distributed along the strands of deoxyribonucleic acid (DNA) which together form the "coil of life". Mutations are demonstrably caused by

hard radiations, certain chemicals, and thermal agitation of the molecules. Since their occurrence is random in the sense that they are not related to the needs of the organism, most of them prove to be harmful instead of beneficial.

The second step in the evolution of all organisms that reproduce sexually is recombination. In the formation of a germ cell -egg or sperm- the gene-bearing chromosomes, present in pairs in each parent's body, are separated randomly to form sets of unpaired chromosomes, thus halving their number. At fertilization, the set formed by the male parent is united with the set from the female parent in the nucleus of the egg cell, replicas of which the new organism will carry in all its tissues. The whole process is reminiscent of dealing out playing cards. (Skutch 1985, 1991).

The third step in evolution is natural selection, which by agents the most diverse -malfunction of organs, climatic extremes, malnutrition, predation - eliminates individuals poorly endowed by the foregoing random processes, like unlucky gamblers who receive poor hands of cards. However, natural selection does not consistently remove the poorly adapted and preserve the fittest to survive. Accidents occur; a well-endowed animal may fall prey to a predator, while an inferior individual that happens at the moment to be better concealed escapes it. From first to last, and most strongly in the first two steps, chance enters largely into this schema of evolution.

It is easy to understand how mutation and recombination, continued through long ages, might cause the great diversity of the living world. Natural selection is essentially destruction; it eliminates the poorly endowed while of promising mutants it takes no special care, such as an intelligent breeder of plants or animals gives to individuals that show improvement in the characters he desires. Although an organism may be better equipped to resist the stresses or to profit by the opportunities offered by a natural environment; the latter does nothing to favor the superior individual, as we might expect it to do if natural selection resembled the breeder's artificial selection, which is responsible for the misleading term. Although we detect nothing constructive in the orthodox account of evolution, when we survey its products, the plants and animals that fill the living world, their great diversity, their marvelous

adaptations to the most varied situations, the beauty of many of them, the intelligence of some, we recognize that construction has occurred. Causes must be adequate to produce the results attributed to them. What is lacking in the above synopsis of evolution? Could it be a final cause, or a purpose? To answer this question, we must look closely at final causes, which imply ends.

Aristotle's dictum (*Physics*. Bk. 2, Ch. 8) that it is absurd to suppose that purpose is not present because we do not observe the agent deliberating becomes the more convincing the more we reflect upon our personal experiences. Sometimes, after trying through much of a day to find a solution to a perplexing problem, I have fallen asleep without reaching a conclusion. Next morning, I awake with the answer clearly in mind. If we insist that a purpose was absent while I slept, nevertheless, it was then more effective than while I pondered my problem. Evidently, my purpose was not dormant even while I was unaware of it, but had become implicit rather than explicit.

We are never more acutely conscious of our purpose than when we painfully learn to perform a difficult task. As we become expert and our activity habitual, our purpose appears to migrate from our minds to our muscles, which without conscious guidance repeat familiar operations. We might say, paradoxically, that we become less purposeful as we become more proficient. Moreover, all our consciously directed activities are supported by the autonomic functions of our bodies, including the pulsations of the heart, circulation of the blood, and metabolism, without which we can accomplish nothing. Our explicit purposes shade into implicit purposes in a manner that makes it difficult to separate them sharply; the distinction between them, although conceptually clear, is not profound.

Our conscious purposes are often directed toward ends that are optional, attainable by alternative routes, expertly or by trial and error. The vital physiological processes that support them require such precise and unremitting control that nature has not entrusted them to flickering consciousness, but the way they integrate with and support our conscious purposes points to a common origin, the purposiveness of life. Our strongest, most abiding purposes, our yearning for happiness, fulfillment, or a satisfy-

ing existence, appear not to be originated so much as discovered by us. Deliberation defines and directs strivings that rise from profound depths, the cosmic foundations of the living world. Only the more inconstant and trivial of our purposes appear to spring from a source no deeper than our conscious minds.

The constructive element in evolution, needed to complement mutation, recombination, and selection, that we have been seeking appears to be of the nature of a final cause, an implicit purpose, the will of each creature to survive. It strives to make the best of its genetic endowment, however defective this may be, and to perfect itself according to its kind. The mutations it may have received were not designed to conform to its genetic constitution, but it adjusts them as best it can, like a mason fitting an oddly shaped tile into a mosaic. This will to grow and survive, however great the obstacles, is the only strong motive that we can detect in evolution. It is a phase of harmonization, the cosmic process that brings order into chaos, and in living organisms reveals itself most clearly as growth. This teleological movement is not directed toward specific ends, such as the production of a definite number of species of predetermined forms and attributes, but to the more inclusive end of increasing the organization of the cosmos and the values that arise from harmonious integration. The details are determined by the interplay of physical forces and the interactions of organisms.

A teleological impulsion might pervade the living world without becoming explicit in the minds of animals. We often wonder how far they are aware of the ends of their activities. Does a bird, for example, build with a mental image, innate or learned, of the nest she is trying to complete? Is she conscious that she is making it for eggs and nestlings? I believe that she is, and that other highly organized animals are cognizant of the ends of at least the more elaborate of their activities; but I can offer no proof beyond inferences from their behavior. But neither can those who declaim against teleological interpretations of nature and animal behavior prove that I am wrong. Pending greater insight, we should keep our minds open while we hold, tentatively, the more generous interpretation.

Much of the opposition to the teleological interpretation of nature, or at least certain of its

aspects, appears to spring from the practice (approved by Webster's dictionary) of using "purpose" and "end" as synonyms, and of equating teleology with conscious purpose. We should pay attention to the sentence from Aristotle's *Physics* already quoted. I do not know how it may be in the original Greek, but I surmise that the translation would more accurately convey the philosopher's meaning if we wrote: "It is absurd to suppose that a process is not teleological (or directed toward an end) because we do not detect a purpose", meaning by "purpose" a conscious intention, by "end" the result of a process or movement. The consistent use of "purpose" for consciously intended results, and of "end" for the result of a process, whether intended or not, would conduce to clarity and make a teleological world view more acceptable. "End" is the more inclusive category. All purposes, except possibly the most trivial, are directed toward ends, but not all ends are consequences of foreseeing purposes. Flowering is the end of a plant's growth, a teleological process, but not its purpose, unless we attribute thought to vegetation. Pervaded by harmonization, the cosmos has ends (possibly an inclusive end) but not purposes, except in the restricted areas where we can detect, or infer the presence of, foreseeing minds, as in humans and probably the more intelligent animals.

In a critical chapter on "The Multiple Meanings of Teleological", Ernst Mayr (1988) threw new light upon this difficult subject. In the programmed processes of organisms, which he calls "teleonomic", the great philosophical evolutionist recognizes "the teleological aspect of the living world". He tentatively defines "program" as "coded or prearranged information that controls a process (or behavior) leading it toward a given end". A program includes not only the blueprint but also the instructions of how to use the information it contains. Programs may be minutely detailed, as appears to be true of those that control embryological development, or open, subject to modification by learning, experience, or insights, as in the overt behavior of animals, or the more intelligent of them. These teleonomic programs are encoded in the DNA of the nuclei, where over the generations they were evolved, in relation to the organism's structure and needs, by the usual processes of mutation and selection. According to this interpretation, nest-building,

incubation, and the other parental activities of a bird are details of a teleonomic process whose end is the rearing of fledglings. The southward migration of a northern bird in autumn is likewise teleonomic, to avoid the rigors of a cold winter. These and similar activities do not necessarily involve conscious purposes but foresight might not be absent.

Although, not without opposition, liberal minded biologists attribute a degree of teleology to the living world, its ascription to the cosmos as a whole is vehemently rejected by many contemporary philosophers and, especially, workers in the physical sciences. Nevertheless, I believe we may recognize in inorganic nature something analogous to the programmed activities of organisms. Atoms are social beings with strong tendencies to join others. Their sociality is of two kinds, indiscriminating and discriminating. The former is manifest in gravitation which, aided by the medium that contains them, space, draws them together in great masses, irrespective of their kinds, and with an intensity determined only by the magnitude of these aggregations - the greater the crowd, the more eagerly the atoms appear to join it. The discriminating sociality, sometimes called "chemical affinity", impels atoms to unite closely with certain other atoms or combinations of them, while avoiding union with others. Operating on a grand scale, the indiscriminating sociality of atoms condenses vast clouds of cosmic gasses and dust into stars, planets, and their satellites. Only on the surfaces of some of these planets, neither too hot nor too cold, enveloped in an atmosphere neither too dense nor too rare, can atoms give full play to their selective sociality, forming a great variety of salts and crystals and, in a watery medium, the very complex molecules of living organisms.

The social atoms unite in formations of increasing amplitude, complexity, and coherence - the process of harmonization. Among those of greatest complexity are the strands of DNA that form the coils of life, which encode the programs for the teleonomic processes and activities of organisms. We may trace a continuous progression from the union of atoms in the simplest molecules to the much more complex molecules of organisms. If the activities of these creatures are teleonomic, the movements of the social atoms seeking companions must

be regarded as teleonomic in the same sense. One continuous movement runs through the Universe from its prime foundations to its most advanced formations. It is improbable that creatures so purposeful as we humans, composed of atoms widespread in the cosmos, activated by the same energy that courses through it everywhere, arose in a Universe devoid of teleology. Nevertheless, the programs encoded in the genes of organisms and that implicit in the sociality of atoms differ greatly. The former, products of a long evolution, are highly detailed, differ from species to species, and are probably rarely exactly the same in two individuals who are not identical twins. Atoms appear to be coeval with the Universe and their nature never changes. Their sociality determines only the general course of cosmic development, from the chaos of diffused cosmic dust to planetary systems of quite definite forms and movements, and on some planets a vast diversity of living creatures, whose forms and activities were not predetermined but resulted from their interactions with the lifeless and living components of their different environments, depending much on the chances of mutation.

As to the end or goal of the cosmic process, it appears to be to give value to the Universe. No matter how vast its spread, how many millions or trillions of galaxies or stars it contained, a Universe with no single being to enjoy its existence would, it seems, be so utterly valueless that nothing of importance would be lost if it were annihilated, leaving only nothingness. The cosmic process is best interpreted as an aeonian striving to increase the value of the Universe by producing creatures capable of enjoying their existence in it, but unhappily not without much suffering along the way. And this striving or seeking for value or significance appears to be a teleonomic process, programmed, in its general direction although not in its details, by the sociality of the atoms.

An objection to the view that the Universe is programmed to augment its value by producing creatures able to enjoy their lives is that, on present evidence, life is so thinly scattered through its immensity. Of the nine planets in our solar system, only Earth is known to support organisms, and billions of years passed before some of them rose to the psychic level of aesthetic appreciation and thirst for understanding. An answer to this objection is that a

Universe that is apparently eternal and possibly of infinite extent has had unlimited time to create, by slow evolution, beings with an advanced psychic life, and abundant resources to form millions of planetary systems, so that a few of them might give birth to living creatures. Possibly the atoms themselves are not devoid of a degree of feeling proportionate to their minute size, which is intensified and diversified as organization increases. The two-aspect or bipolar ontology, which I regard as the most satisfactory solution of the ancient problem of the relation of mind to matter, postulates that every particle has a physical side, public and the object of scientific study, and a psychic side, which like our own consciousness is private and unobservable by others. When the sentient atoms are arranged in a special pattern as in a brain, consciousness is intensified and the more advanced manifestations of psychic life develop. Although the foregoing solution of the basic problem of teleology has much to recommend it, we cannot prove it. Despite all our science and all our philosophy, the Universe guards its secrets well.

If we insist that teleology implies a conscious purpose widely diffused through the Universe, we are on precarious grounds; when we recognize a movement to increase the value of the cosmos, we are on firm ground, for this is what it demonstrably accomplishes, at least on Earth. The definite, consistently followed direction of a teleological process distinguishes it from random movements.

I would not conclude from this that biologists should be concerned with teleology and give more attention to final causes: To elucidate the material and efficient causes that have shaped and preserve organisms should keep these scientists sufficiently busy. The investigation of final causes is more pertinent to philosophy than to science. But scientists should be more tolerant of philosophers' often groping efforts to throw light upon obscure aspects of reality that since people became thoughtful they have most ardently wished to illuminate; just as philosophers should be tolerant of the sometimes illogical pronouncements of scientists.

**Intergroup Selection:** The third of the most frequently condemned biological heresies is

intergroup selection, often more briefly called "group selection". The orthodox view is that the natural selection of individuals, or their differential survival and reproduction, is adequate for the theory of evolution, or, more succinctly, individuals rather than groups are selected by natural agents. This insistence upon the adequacy of inter-individual selection has three weaknesses: it exaggerates the self-sufficiency of the individual, it neglects social interactions, and it underestimates the complexity of evolution- it is too simplistic.

Solitary animals, that associate with other adults only long enough to inseminate them or to be inseminated by them, are self-sufficient as to their survival but not as to their reproduction. Modern evolutionists assess the fitness of an organism by the number of its progeny; but no individual of a species that can reproduce only sexually is, in a strict logical sense, fit by this measure. It becomes fit only by choosing a partner in reproduction. Since each parent contributes an approximately equal number of genes to the progeny, their innate quality, or ability to survive and reproduce, will depend upon the adequacy of the parent that contributes most to their production and nurture, who is usually the female; although in a number of species the male contributes substantially to the care of his offspring, and in certain birds, amphibians, and fishes he is largely or wholly responsible for protecting and/or feeding them. This is the primary reason why to insist upon the adequacy of individual selection is an over-simplification of the problem of evolution. As though recognizing this, birds, more than most other animals, tend to be careful in the selection of their partners.

When we trace a lineage backward in time, we find that, in the absence of inbreeding, the number of ancestors increases geometrically with the number of generations -four grandparents, eight great-grandparents, and so forth. Each of these forebears has contributed genes which jointly determine the quality of the latest progeny; all are virtually involved in their birth. Likewise, when we project the transmission of an individual's genes forward through its descendants, we find that they tend to diffuse ever more widely through a population. The individual that succeeds in reproducing is but a link in a lengthening chain. Without the opportunity to mate with enough unrelated

individuals to prevent deleterious inbreeding and provide the genetic diversity that is the foundation of adaptability, a lineage may become extinct. When a dwindling species or race is tardily given protection from humans and encouraged to increase, as we might expect it to do rapidly because of reduced competition for resources, it sometimes fails to recover but continues to decline, as happened to the Heath Hen on Martha's Vineyard Island off the coast of Massachusetts. Lack of genetic diversity was one of the factors adduced for its extinction. The perpetuation of an interbreeding population, its capacity to evolve or to extend its range, depends upon its gene pool, the aggregate of genes of which every individual bears a selection but none the whole range of them. In contemporary ornithology the term "cooperative breeders" is applied to a group consisting of a reproductive pair with one or more non-breeding helpers. In a wider sense, all the members of an interbreeding population, or deme, form a single cooperatively breeding group, providing each other's progeny with mates, preventing debilitating inbreeding by exchanging genes. The number and quality of an individual's offspring -its fitness- depends upon the quality of the partners in reproduction that the species can provide for him or her.

Inter-individual selection helps to maintain, or to improve, the anatomical and physiological quality of a species by removing, by agents the most diverse, defective or substandard individuals. It is adequate to account for the extinction of races or species. In the absence of a natural catastrophe that wipes out a whole population at a stroke, or a drastic climatic or ecological change that extinguishes it, individuals may be eliminated one by one by predation, disease, or other natural agents, if not by man, until the last member of a species vanishes from Earth. But individual selection cannot account for the evolution of a race, which depends upon changes in the composition of its gene pool, a process in which many interbreeding individuals participate, but to which none can contribute alone.

The foregoing considerations apply to all organisms, plants as well as animals, that can reproduce only by the union of two individuals, or of their sexual cells, their gametes. In certain special situations, it is more obvious that evolution depends upon coordinated genetic changes

in interacting individuals. The first is in the field of social relations. Animals attract sexual partners by signs or signals, which may be visual, vocal, olfactory, or a combination of these. If a mutation in the appearance, sounds, or odors of one sex is not supplemented by a complementary mutation in the preference or reaction of the opposite sex, the former will fail to mate and leave progeny, with the result that its mutation will disappear from the gene pool. The gorgeous plumage of many male birds, which since Darwin has been attributed to sexual selection, could not have developed if the preferences of females had not evolved in the direction of the changes in the males' attire. Cooperation of a male and female in rearing their young, the two sexes playing complementary rather than identical roles -as in many birds and fewer mammals- could hardly have been perfected without coordinated evolution in a interbreeding population. The calls or other signals by which animals alert their companions to approaching danger would be meaningless if signal and response did not evolve together in a group of related animals. Releaser and innate releasing mechanism, social interactions the most diverse, point to the natural selection of groups as well as of individuals.

In recent decades ornithologist have been discovering an increasing number of avian species that breed in closely knit groups of parents and their self-supporting offspring, who aid their elders in defending the territory, feeding and protecting their younger siblings, and often, too, in building the nest and incubating the eggs. Sometimes the family is joined by individuals less closely related. Some of the species in which cooperative breeding is widespread can breed successfully as unassisted pairs; others cannot. Among the latter are White-winged Choughs in Australia, Yellow-billed Shrikes and apparently also White-browed Sparrow-Weavers in Africa, in all of which pairs without helpers raise so few young, or suffer such high mortality, that their species would become extinct in the absence of cooperative breeding (Skutch 1987). In these cases it is especially clear that the unit of selection is the cooperating group; or, in terms of fitness, we might say that the fitness of an individual is strictly dependent upon its membership in a group.

The prominence given to individual selection in contemporary discussions of evolu-



tion, the widespread rejection of group selection, ignores the significance of sexual reproduction. The genes of an individual lack evolutionary importance unless they are contributed to the gene pool of its species; and the first step in this incorporation is their mingling with the genes of a second individual. The pair rather than the individual appears to be the primary unit of selection that does not lead to extinction, but this is only a step toward the wider diffusion of their genes through a larger group of interbreeding organisms. The sharp distinction between individual selection and group selection erects an artificial boundary in a continuum. Natural selection has both a negative and a positive aspect. It acts like a sieve, which holds back, for rejection, coarser particles, while permitting the finer grains to pass - finer, in the present context, meaning fitter or more adequate to confront their environment. And these finer individuals gain their evolutionary significance by mingling their genetic endowments with those of their contemporaries.

For examples of pure individual selection, we must turn to organisms that reproduce with never the intervention of sex. Their progeny form clones, all of whose members bear precisely the same constellation of genes, so that differences in their survival must be attributed to external factors instead of intrinsic differences. When feasible, horticulturists and agriculturists frequently prefer vegetative propagation, which is often quicker and more efficient than reproduction by seeds, and has the great advantage that plants so multiplied nearly always "breed true". Many of the most valuable agricultural plants, including potatoes, cassava, sugarcane, and bananas are regularly propagated by vegetative parts; some of their varieties never set seed. Occasionally by a "sport", or bud variation, one of these cultivars produces a new and valuable variety, which must be propagated as a clone by vegetative means. Despite the vigor of many plants that can reproduce only asexually, they rarely spread widely without man's help; most would probably become extinct without his care. Among vertebrate animals, parthenogenesis is rare. Why has sexual reproduction, indirect and frequently wasteful, become so much more widespread among all the more highly evolved plants and animals than the more direct and

efficient methods of asexual multiplication? The reason appears to be that strict individual selection does not produce the genetic diversity that promotes adaptability to confront changing condition and the capacity for continuing evolution. Sexual reproduction and group selection have evolved because they promote evolution.

Darwin was aware of the inadequacy of individual selection. In *The Origin of Species* he wrote: "I did not appreciate how rarely single variations, whether slight or strongly marked, could be perpetuated". Farther along he elaborated: "But in the great majority of cases, namely, with all organisms which habitually unite for each birth, or which occasionally intercross, the individuals of the same species inhabiting the same area will be kept nearly uniform by intercrossing; so that many individuals will go on simultaneously changing, and the whole amount of modification at each stage will not be due to descent from a single parent ". And again: " Hence in order that a new species should suddenly appear..., it is almost necessary to believe, in opposition to all analogy, that several wonderfully changed individuals appeared simultaneously within the same district. This difficulty is avoided on the theory of gradual evolution, through the preservation of a large number of individuals, which varied more or less in any favourable direction, and of the destruction of a large number which varied in the opposite manner".

In these days when biology has become highly mathematical, the views of mathematical evolutionists have great weight, despite their disagreements. Many years after Darwin, Sewall Wright (1949) concluded that the subdivision of a species into partly isolated groups, or demes, between which there is limited interbreeding with resultant flow of genes "provides the largest store of variability both locally and within the species as a whole, and by providing for selection in which whole genetic complexes are the objects, frees evolution most completely from dependence on rare favorable mutations and makes possible the most rapid exploitation of an ecologic opportunity". Elsewhere (1940) he wrote: "A local population that happens to arrive at a genotype that is peculiarly favourable in relation to the general conditions of life of the species...will tend to increase in numbers and supply more than its share of migrants to other regions, thus grading them up

to the same type by a process that may be described as *intergroup selection*".

Another mathematical evolutionist whose writings are often quoted, R. A. Fisher (1958), denied the effectiveness of group selection, even in man, who for ages lived in small, mutually hostile groups to which Wright's model might apply, and until quite recently continued to exist in this manner in vast areas of Amazonian forests. "The selection of whole groups", he wrote, "is, however, a much slower process than the selection of individuals, and in view of the length of the generation in man the evolution of his higher mental faculties, and especially of the self-sacrificing element in his moral nature, would seem to require the action of group selection over an immense period". In answer to this objection, we might remember that the evolution of man from prehuman hominids required at least about two million years, or about a hundred thousand generations.

Until modifications that spring up in individuals become firmly established in a population, however long this might take, evolution has not occurred. Fisher denied that "the principle of Natural Selection" affords a rational explanation "for any properties of animals or plants which, without being individually advantageous, are supposed to be of service to the species to which they belong". This is no argument against group selection, which does not require self-sacrificing activities, but rather cooperation that benefits all participants, as in mutual defence, the search for food, the construction by groups of avian apartment houses in which many individuals nest and sleep, cooperative breeding, and among plants that grow gregariously, the maintenance of a habitat or microclimate in which they thrive better than when growing alone. Moreover, reproduction itself entails a sacrifice of the individual for the benefit of its species.

Group selection may transcend specific boundaries. The group favored by selection may consist of animals of two kinds who become mutually dependent, or of an animal and a plant, as occurs when a flower becomes specialized for pollination by one species of insect or bird, which in turn becomes highly modified for extracting nectar from that particular kind of flower. Unless the modifications of pollinator and flower keep pace with one another, such coevolution could not occur.

An inappropriate term can cause widespread confusion. Impressed by the results of man's selection of domestic animals and plants, Darwin chose the term "natural selection" for a superficially analogous process in wild nature. Artificial selection and natural selection differ profoundly. An intelligent breeder of plants or animals takes special care of individuals that vary in a desired direction; nature does nothing of the sort, without pampering the more fit, it ruthlessly eliminates the less fit. Not surprisingly, many of Darwin's early critics (like not a few later ones) were perplexed by the term "natural selection". On 6 June 1860, the year after the publication of *The Origin of Species by Means of Natural Selection: Or the Preservation of Favoured Races in the Struggle for Life*, he wrote to his friend, the geologist Charles Lyell: "I suppose 'natural selection' was a bad term; but to change it now, I think, would make confusion worse confounded". On 26 September, he confided to the botanist Asa Gray "If I had to write my book again I would use 'Natural Preservation' and drop 'selection' (Burkhardt *et al.* 1993). The substitution of 'natural preservation' for 'natural selection' might have precluded the stubbornly shortsighted insistence that natural selection is confined to individuals, because it is undeniable that groups, species, and larger categories of organisms are preserved along with the individuals that compose them.

Happily, as the behavior of animals is studied more deeply and perceptively, as more and more examples of cooperation among them are disclosed, as the coevolution of animals and plants is investigated, the attitude of the biological community toward some of the heresies appears to be softening. It is beginning to be realized that the gap between the emotions of man and those of other animals need not be as wide as that in their intellectual development. It is becoming apparent that the selection of individuals is only the first step in an extremely complex process that extends to groups of individuals and finally to whole species, and even to two or more mutually dependent species. When we recognize the continuity of development from lifeless matter through all stages of evolving life, we may finally perceive that purposeful activity is not confined to man. We may even go beyond this to recognize that, in postulating a teleological Universe, Aristotle,

the first great naturalist-philosopher of whom we have knowledge, was not wholly wrong.

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