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HOW TO CARRY OUT THE ADAPTATIONIST PROGRAM?

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To have been able to provide a scientific explanation of adaptation was perhaps the greatest triumph of the Darwinian theory of natural selection. After 1859 it was no longer necessary to invoke design, a supernatural agency, to explain the adaptation of organisms to their environment. It was the daily, indeed hourly, scrutiny of natural selection, as Darwin had said, that inevitably led to ever greater perfection. Ever since then it has been considered one of the major tasks of the evolutionist to demonstrate that organisms are indeed reasonably well adapted, and that this adaptation could be caused by no other agency than natural selection. Nevertheless, beginning with Darwin himself (remember his comments on the evolution of the eye), evolutionists have continued to worry about how valid this explanation is. The more generally natural selection was accepted after the 1930s, and the more clearly the complexity of the genotype was recognized, particularly after the 1960s, the more often the question was raised as to the meaning of the word *adaptation*. The difficulty of the concept adaptation is best documented by the incessant efforts of authors to analyze it, describe it, and define it. Since I can do no better myself, I refer to a sample of such efforts (Bock and von Wahlert 1965; Bock 1980; Brandon 1978; Dobzhansky 1956, 1968; Lewontin 1978, 1979; Muller 1949; Munson 1971; Stern 1970; Williams 1966; Wright 1949). The one thing about which modern authors are unanimous is that adaptation is not teleological, but refers to something produced in the past by natural selection. However, since various forms of selfish selection (e.g., meiotic drive, many aspects of sexual selection) may produce changes in the phenotype that could hardly be classified as "adaptations," the definition of adaptation must include some reference to the selection forces effected by the inanimate and living environment. It surely cannot have been anything but a lapse when Gould wanted to deny the designation "adaptation" to certain evolutionary innovations in clams, with this justification: "The first clam that fused its mantle margins or retained its byssus to adulthood may have gained a conventional adaptive benefit in its local environment. But it surely didn't know that its invention would set the stage for future increases in diversity" (Gould and Calloway 1980, p. 395). Considering the strictly a posteriori nature of an adaptation, its potential for the future is completely irrelevant, as far as the definition of the term adaptation is concerned.

A program of research devoted to demonstrate the adaptedness of individuals and their characteristics is referred to by Gould and Lewontin (1979) as an "adaptationist program." A far more extreme definition of this term was suggested by Lewontin (1979, p. 6) to whom the adaptationist program "assumes without further proof that all aspects of the morphology, physiology and behavior of organisms are adaptive optimal solutions to problems." Needless to say, in the ensuing discussion I am not defending such a sweeping ideological proposition.

When asking whether or not the adaptationist program is a legitimate scientific approach, one must realize that the method of evolutionary biology is in some ways quite different from that of the physical sciences. Although evolutionary phenomena are subject to universal laws, as are most phenomena in the physical sciences, the explanation of the history of a particular evolutionary phenomenon can be given only as a "historical narrative." Consequently, when one attempts to explain the features of something that is the product of evolution, one must attempt to reconstruct the evolutionary history of this feature. This can be done only by inference. The most helpful procedure in an analysis of historical narratives is to ask "why" questions; that is, questions (to translate this into modern evolutionary language) which ask what is or might have been the selective advantage that is responsible for the presence of a particular feature.

The adaptationist program has recently been vigorously attacked by Gould and Lewontin (1979) in an analysis which in many ways greatly pleases me, not only because they attack the same things that I questioned in my "bean bag genetics" paper (Mayr 1959), but also because they emphasize the holistic aspects of the genotype as I did repeatedly in discussions of the unity of the genotype (Mayr 1970, chap. 10; 1975). Yet I consider their analysis incomplete because they fail to make a clear distinction between the pitfalls of the adaptationist program as such and those resulting from a reductionist or atomistic approach in its implementation. I will try to show that basically there is nothing wrong with the adaptationist program, if properly executed, and that the weaknesses and deficiencies quite rightly pointed out by Gould and Lewontin are the result of atomistic and deterministic approaches.

In the period after 1859 only five major factors were seriously considered as the causes of evolutionary change, or, as they are sometimes called, the agents of evolution. By the time of the evolutionary synthesis (by the 1940s), three of these factors had been so thoroughly discredited and falsified that they are now no longer considered seriously by evolutionists. These three factors are: inheritance of acquired characters, intrinsic directive forces (orthogenesis, etc.), and saltational evolution (de Vriesian mutations, hopeful monsters, etc.). This left only two evolutionary mechanisms as possible causes of evolutionary change (including adaptation), chance, and selection forces. The identification of these two factors as the principal causes of evolutionary change by no means completed the task of the evolutionist. As is the case with most scientific problems, this initial solution represented only the first orientation. For completion it requires a second stage, a fine-grained analysis of these two factors: What are the respective roles of chance and of natural selection, and how can this be analyzed?

Let me begin with chance. Evolutionary change in every generation is a two-

step process, the production of genetically unique new individuals and the selection of the progenitors of the next generation. The important role of chance at the first step, the production of variability, is universally admitted (Mayr 1962), but the second step, natural selection, is on the whole viewed rather deterministically: Selection is a non-chance process. What is usually forgotten is what an important role chance plays even during the process of selection. In a group of sibs it is by no means necessarily only those with the most superior genotypes that will reproduce. Predators mostly take weak or sick prey individuals but not exclusively so, nor do localized natural catastrophies (storms, avalanches, floods, etc.) kill only inferior individuals. Every founder population is largely a chance aggregate of individuals and the outcome of genetic revolutions, initiating new evolutionary departures, may depend on chance constellations of genetic factors. There is a large element of chance in every successful colonization. When multiple pathways toward the acquisition of a new adaptive trait are possible, it is often a matter of a momentary constellation of chance factors as to which one will be taken (Bock 1959).

When one attempts to determine for a given trait whether it is the result of natural selection or of chance (the incidental byproduct of stochastic processes), one is faced by an epistemological dilemma. Almost any change in the course of evolution might have resulted by chance. Can one ever prove this? Probably never. By contrast, can one deduce the probability of causation by selection? Yes, by showing that possession of the respective feature would be favored by selection. It is this consideration which determines the approach of the evolutionist. He must first attempt to explain biological phenomena and processes as the product of natural selection. Only after all attempts to do so have failed, is he justified in designating the unexplained residue tentatively as a product of chance.

The evaluation of the impact of selection is a very difficult task. It has been demonstrated by numerous selection experiments that selection is not a phantom. That it also operates in nature is a conclusion that is usually based only on inference, but that is increasingly often experimentally confirmed. Very convincing was Bates' demonstration that the geographic variation of mimics parallels exactly that of their distasteful or poisonous models. The agreement of desert animals with the variously colored substrate also strongly supports the power of selection. In other cases the adaptive value of a trait is by no means immediately apparent.

As a consequence of the adaptationist dilemma, when one selectionist explanation of a feature has been discredited, the evolutionist must test other possible adaptationist solutions before he can resign and say: This phenomenon must be a product of chance. Gould and Lewontin ridicule the research strategy: "If one adaptive argument fails, try another one." Yet the strategy to try another hypothesis when the first fails is a traditional methodology in all branches of science. It is the standard in physics, chemistry, physiology, and archeology. Let me merely mention the field of avian orientation in which sun compass, sun map, star navigation, Coriolis force, magnetism, olfactory clues, and several other factors were investigated sequentially in order to explain as yet unexplained aspects of orientation and homing. What is wrong in using the same methodology in evolution research?

At this point it may be useful to look at the concept of adaptation from a historical point of view. When Darwin introduced natural selection as the agent of adaptation, he did so as a replacement for supernatural design. Design, as conceived by the natural theologians, had to be perfect, for it was unthinkable that God would make something that was less than perfect. It was on the basis of this tradition that the concept of natural selection originated. Darwin gave up this perfectionist concept of natural selection long before he wrote the *Origin*. Here he wrote, "Natural selection tends only to make each organic being as perfect as, or slightly more perfect than, the other inhabitants of the same country with which it has to struggle for existence. And we see that this is the degree of perfection attained under nature" (1859, p. 201). He illustrated this with the biota of New Zealand, the members of which "are perfect . . . compared with another" (p. 201), but "rapidly yielding" (p. 201) to recent colonists and invaders. After Darwin, some evolutionists forgot the modesty of Darwin's claims, but other evolutionists remained fully aware that selection cannot give perfection, by observing the ubiquity of extinction and of physiological and morphological insufficiencies. However, the existence of some perfectionists has served Gould and Lewontin as the reason for making the adaptationist program the butt of their ridicule and for calling it a Panglossian paradigm. Here I dissent vigorously. To imply that the adaptationist program is one and the same as the argument from design (satirized by Voltaire in *Candide*) is highly misleading. When *Candide* was written (in 1759), a concept of evolution did not yet exist and those who believed in a benign creator had no choice but to believe that everything "had to be for the best." This is the Panglossian paradigm, the invalidity of which has been evident ever since the demise of natural theology. The adaptationist program, a direct consequence of the theory of natural selection, is something fundamentally different. Parenthetically one might add that Voltaire misrepresented Leibniz rather viciously. Leibniz had not claimed that this is the best possible world, but only that it is the best of the possible worlds. Curiously one can place an equivalent limitation on selection (see below). Selection does not produce perfect genotypes, but it favors the best which the numerous constraints upon it allow. That such constraints exist was ignored by those evolutionists who interpreted every trait of an organism as an ad hoc adaptation.

The attack directed by Gould and Lewontin against unsupported adaptationist explanations in the literature is fully justified. But the most absurd among these claims were made several generations ago, not by modern evolutionists. Gould and Lewontin rightly point out that some traits, for instance the gill arches of mammalian embryos, had been acquired as adaptations of remote ancestors but, even though they no longer serve their original function, they are not eliminated because they have become integral components of a developmental system. Most so-called vestigial organs are in this category. Finally, it would indeed be absurd to atomize an organism into smaller and smaller traits and to continue to search for the ad hoc adaptation of each smallest component. But I do not think that this is the research program of the majority of evolutionists. Dobzhansky well expressed the proper attitude when saying: "It cannot be stressed too often that natural selection does not operate with separate 'traits.' Selection favors genotypes . . . The reproductive success of a genotype is determined by the totality of

the traits and qualities which it produces in a given environment” (1956, p. 340). What Dobzhansky described reflects what I consider to be the concept of the adaptationist program accepted by most evolutionists, and I doubt that the characterization assigned to the adaptationist program by Gould and Lewontin, “An organism is atomized into traits and these traits are explained as structures optimally designed by natural selection for their functions” (p. 585), represents the thinking of the average evolutionist.

By choosing this atomistic definition of the adaptationist program and by their additional insistence that the adaptive control of every trait must be “immediate,” Gould and Lewontin present a picture of the adaptationist program that is indeed easy to ridicule. The objections cited by them are all based on their reductionist definition. Of course, it is highly probable that not all secondary byproducts of relative growth are “under immediate adaptive control.” In the case of multiple pathways it is, of course, not necessary that every morphological detail in a convergently acquired adaptation be an ad hoc adaptation. This is true, for instance, in the case cited by them, of the adaptive complex for a rapid turnover of generations that evolved at least three times independently in the evolution of the arthropods. Evolution is opportunistic and natural selection makes use of whatever variation it encounters. As Jacob (1977) has said so rightly: “Natural selection does not work like an engineer. It works like a tinkerer.”

Considering the evident dangers of applying the adaptationist program incorrectly, why are the Darwinians nevertheless so intent on applying it? The principal reason for this is its great heuristic value. The adaptationist question, “What is the function of a given structure or organ?” has been for centuries the basis for every advance in physiology. If it had not been for the adaptationist program, we probably would still not yet know the functions of thymus, spleen, pituitary, and pineal. Harvey’s question “Why are there valves in the veins?” was a major stepping stone in his discovery of the circulation of blood. If one answer turned out to be wrong, the adaptationist program demanded another answer until the true meaning of the structure was established or until it could be shown that this feature was merely an incidental byproduct of the total genotype. It would seem to me that there is nothing wrong with the adaptationist program, provided it is properly applied.

Consistent with the modern theory of science, adaptationist hypotheses allow a falsification in most cases. For instance, there are numerous ways to test the thesis that the differences in beak dimensions of a pair of species of Darwin’s finches on a given island in the Galapagos is the result of competition (Darwin’s character divergence). One can correlate size of preferred seeds with bill size and study how competition among different assortments of sympatric species of finches affects bill size. Finally, one can correlate available food resources on different islands with population size (Boag and Grant 1981). As a result of such studies the adaptationist program leads in this case to a far better understanding of the ecosystem.

The case of the beak differences of competing species of finches is one of many examples in which it is possible, indeed necessary, to investigate the adaptive significance of individual traits. I emphasize this because someone might conclude

from the preceding discussion that a dissection of the phenotype into individual characters is inappropriate in principle. To think so would be a mistake. A more holistic approach is appropriate only when the analysis of individual traits fails to reveal an adaptive significance.

What has been rather neglected in the existing literature is the elaboration of an appropriate methodology to establish adaptive significance. In this respect a recent analysis by Traub (1980) on adaptive modifications in fleas is exemplary. Fleas are adorned with a rich equipment of hairs, bristles, and spines, some of which are modified into highly specialized organs. What Traub (and various authors before him) found is that unrelated genera and species of fleas often acquire convergent specializations on the same mammalian or avian hosts. The stiffness, length, and other qualities of the mammalian hair are species specific and evidently require special adaptations that are independently acquired by unrelated lineages of fleas. "The overall association [between bristles and host hair] is so profound that it is now possible to merely glance at a new genus or species of flea and make correct statements about some characteristic attributes of its host" (Traub 1980, p. 64). Basically, the methodology consists in establishing a tentative correlation between a trait and a feature of the environment, and then to analyze in a comparative study, other organisms exposed to the same feature of the environment and see whether they have acquired the same specialization. There are two possible explanations for a failure of confirmation of the correlation. Either the studied feature is not the result of a selection force or there are multiple pathways for achieving adaptedness.

When the expanded comparative study results in a falsification of the tentative hypothesis, and when other hypotheses lead to ambiguous results, it is time to think of experimental tests. Such tests are not only often possible, but indeed are now being made increasingly often, as the current literature reveals (Clarke 1979). Only when all such specific analyses to determine the possible adaptive value of the respective trait have failed, is it time to adopt a more holistic approach and to start thinking about the possible adaptive significance of a larger portion of the phenotype, indeed possibly of the Bauplan as a whole.

Thus, the student of adaptation has to sail a perilous course between a pseudoexplanatory reductionist atomism and stultifying nonexplanatory holism. When we study the literature, we find almost invariably that those who were opposed to nonexplanatory holism went too far in adopting atomism of the kind so rightly stigmatized by Gould and Lewontin, while those who were appalled by the simplistic and often glaringly invalid pseudoexplanations of the atomists usually took refuge in an agnostic holism and abandoned all further effort at explanation by invoking best possible compromise, or integral component of Bauplan, or incidental byproduct of the genotype. Obviously neither approach, if exclusively adopted, is an appropriate solution. How do Gould and Lewontin propose to escape from this dilemma?

While castigating the adaptationist program as a Panglossian paradigm, Gould and Lewontin exhort the evolutionists to follow Darwin's example by adopting a pluralism of explanations. As much as I have favored pluralism all my life, I cannot follow Darwin in this case and, as a matter of fact, neither do Gould and

Lewontin themselves. For Darwin's pluralism, as is well known to the historians of science, consisted of accepting several mechanisms of evolution as alternatives to natural selection, in particular the effects of use and disuse and the direct action of external conditions on organisms. Since both of these subsidiary mechanisms of Darwin's are now thoroughly refuted, we have no choice but to fall back on the selectionist explanation.

Indeed, when we look at Gould and Lewontin's "alternatives to immediate adaptation," we find that all of them are ultimately based on natural selection, properly conceived. It is thus evident that the target of their criticism should have been neither natural selection nor the adaptationist program as such, but rather a faulty interpretation of natural selection and an improperly conducted adaptationist program. Gould and Lewontin's proposals (1979, pp. 590–593) are not "alternatives to the adaptationist program," but simply legitimate forms of it. Such an improved adaptationist program has long been the favored methodology of most evolutionists. There is a middle course available between a pseudoexplanatory reductionist atomism and an agnostic nonexplanatory holism. Dobzhansky (1956) in his stress on the total developmental system and adjustment to a variable environment and my own emphasis on the holistic nature of the genotype (1963, chap. 10; 1970, chap. 10 [considerably revised]; 1975) have been attempts to steer such a middle course, to mention only two of numerous authors who adopted this approach. They all chose an adaptationist program, but not an extreme atomistic one.

Much of the recent work in evolutionary morphology is based on such a middle-course adaptationist program, for instance Bock's (1959) analysis of multiple pathways and my own work on the origin of evolutionary novelties (1960). A semiholistic adaptationist program often permits the explanation of seemingly counter-intuitive results of selection. For instance, the large species of albatrosses (*Diomedea*) have only a single young every second year and do not start breeding until they are 6 to 8 yr old. How could natural selection have led to such an extraordinarily low fertility for a bird? However, it could be shown that in the stormy waters of the south temperate and subantarctic zones only the most experienced birds have reproductive success and this in turn affects all other aspects of the life cycle. Under the circumstances the extraordinary reduction of fertility is favored by selection forces and hence is an adaptation (Lack 1968).

The critique of Gould and Lewontin would be legitimate to its full extent if one were to adopt (1) their narrow reductionist definition of the adaptationist program as exclusively "breaking an organism into unitary traits and proposing an adaptive story for each considered separately" (p. 581) and (2) their characterization of natural selection, in the spirit of natural theology, as a mechanism that must produce perfection.

Since only a few of today's evolutionists subscribe to such a narrow concept of the adaptationist program, Gould and Lewontin are breaking in open doors. To be sure, it is probable that many evolutionists have a far too simplistic concept of natural selection: They are neither fully aware of the numerous constraints to which natural selection is subjected, nor do they necessarily understand what the target of selection really is, nor, and this is perhaps the most important point, do

they appreciate the importance of stochastic processes, as is rightly emphasized by Gould and Lewontin.

Darwin, as mentioned above, was aware of the fact that the perfecting of adaptations needs to be brought only to the point where an individual is "as perfect as, or slightly more perfect than" any of its competitors. And this point might be far from potentially possible perfection. What could not be seen as clearly in Darwin's day as it is by the modern evolutionist, is that there are numerous factors in the genetics, developmental physiology, demography, and ecology of an organism that makes the achievement of a more perfect adaptation simply impossible. Gould and Lewontin (1979) and Lewontin (1979) have enumerated such constraints and so have I (Mayr 1982) based in part on independent analysis.

Among such constraints, the following seem most important.

1. *A capacity for nongenetic modification.*—The greater the developmental flexibility of the phenotype, the better a species can cope with a selection pressure without genetic reconstruction. This is important for organisms that are exposed to highly unpredictable environmental conditions. When the phenotype can vary sufficiently to cope with varying environmental challenges, selection cannot improve the genotype.

2. *Multiple pathways.*—Several alternative responses are usually possible for every environmental challenge. Which is chosen depends on a constellation of circumstances. The adoption of a particular solution may greatly restrict the possibilities of future evolution. When the ancestor of the arthropods acquired an external skeleton, his descendants henceforth had to cope with frequent molts and with a definite limitation on body size. Yet, to judge from the abundance and diversity of arthropods in the water and on land, it was apparently a fortunate choice in other respects.

3. *Stochastic processes.*—An individual with a particular genotype has only a greater probability of reproductive success than other members of its population, but no certainty. There are far too many unpredictable chance factors in the environment to permit a deterministic outcome of the selection process. With the benefit of hindsight, one might come to the conclusion that selection has sometimes permitted a less perfect solution than would have seemed available. Virtually all evolutionists have underestimated the ubiquity and importance of stochastic processes. The kind of constraints to which natural selection is subjected, becomes even more apparent when we look at the process of selection more closely.

4. *The target of selection* is always a whole individual, rather than a single gene or an atomized trait, and an individual is a developmentally integrated whole, "fundamentally not decomposable into independent and separately optimized parts" (Gould and Lewontin, p. 591). For this reason, adaptation is by necessity always a compromise between the selective advantages of different organs, different sexes, different portions of the life cycle, and different environments. Even if the human chin is not the direct product of an ad hoc selection pressure, it is indirectly so as the compromise between two growth fields each of which is under the influence of selection forces.

A pleiotropic gene or gene complex may be selected for a particularly advantageous contribution to the phenotype even if other effects of this gene complex are slightly deleterious. To uncouple the opposing effects if apparently not always easy.

Since it is sufficient when an individual is competitively superior to most other individuals of its population, it may achieve this by particular features, indeed sometimes by a single trait. In that case natural selection "tolerates" the remainder of the genotype even when some of its components are more or less neutral or even slightly inferior.

5. *Cohesion of the genotype.*—Development is controlled by a complex regulatory system, the components of which are often so tightly interconnected with each other, that any change of an individual part, a gene, could be deleterious. For instance, it is apparently less expensive in the development of a mammal to go through a gill arch stage than to eliminate this circuitous path and to approach the adult mammalian stage more directly. Allometry is another manifestation of regulatory systems. A selectively favored increase (or decrease) of body size may result in a slightly deleterious change in the proportions of certain appendages. Selection will determine the appropriate compromise between the advantages of a changed body size and the disadvantages of correlated changes in the proportion of appendages. The capacity of natural selection to achieve deviations from allometry has been established by numerous investigations. It was realized by students of morphology as far back as Étienne Geoffroy St. Hilaire, that there is competition among organs and structures. Geoffroy expressed this in his *loi de balancement*. The whole is a single interacting system. Organisms are compromises among competing demands. Wilhelm Roux, almost 100 years ago, referred to the competitive developmental interactions as the *struggle of parts* in organisms. The attributes of every organism show to what an extent it is the result of a compromise. Every shift of adaptive zones leaves a residue of morphological features that are actually an impediment. Reductionists have asked, Why has selection not been able to eliminate these weaknesses? The answer would seem to be that these are inseparable parts of a whole which, as a whole, is successful.

There are chance components in all these processes, but it must be stated emphatically that selection and chance are not two mutually exclusive alternatives, as was maintained by many authors from the days of Darwin to the earlier writings of Sewall Wright and to the arguments of some anti-Darwinians of today. Actually there are stochastic perturbations ("chance events") during every stage of the selection process.

The question whether or not the adaptationist program ought to be abandoned because of presumptive faults can now be answered. It would seem obvious that little is wrong with the adaptationist program as such, contrary to what is claimed by Gould and Lewontin, but that it should not be applied in an exclusively atomistic manner. There is no better evidence for this conclusion than that which Gould and Lewontin themselves have presented. Aristotelian "why" questions are quite legitimate in the study of adaptations, provided one has a realistic conception of natural selection and understands that the individual-as-a-whole is a complex genetic and developmental system and that it will lead to ludicrous

answers if one smashes this system and analyzes the pieces of the wreckage one by one.

A partially holistic approach that asks appropriate questions about integrated components of the system needs to be neither stultifying nor agnostic. Such an approach may be able to avoid the Scylla and Charybdis of an extreme atomistic or an extreme holistic approach.

SUMMARY

1. The adaptationist program attempts to determine what selective advantages have contributed to the shaping of the phenotype.

2. Evolutionary change falls far short of being a perfect optimization process. Stochastic processes and other constraints upon selection prevent the achievement of perfect adaptedness. Evolutionists must pay more attention to these constraints than they have in the past. However, as already stressed by Darwin (1859, p. 201) there is no selective premium on perfect adaptation.

3. Even though the adaptationist program has been occasionally misapplied, particularly in an uncontrolled reductionist manner, its heuristic power justifies its continued adoption under appropriate safeguards. The application of the adaptationist program has led to important discoveries in many branches of biology.

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