

*Essay Two*

*CAUSE AND EFFECT IN BIOLOGY*

BEING a practicing biologist, I feel that I cannot attempt the kind of analysis of cause and effect in biological phenomena that a logician would undertake. I would instead like to concentrate on the special difficulties presented by the classical concept of causality in biology. From the first attempts to achieve a unitary concept of cause, the student of causality has been bedeviled by these difficulties. Descartes's grossly mechanistic interpretation of life, and the logical extreme to which his ideas were carried by Holbach and de la Mettrie, inevitably provoked a reaction leading to vitalistic theories which have been in vogue, off and on, to the present day. I have only to mention (lames like Driesch (entelechy), Bergson (elan vital), and Lecomte du Ndiy, among the more prominent authors of the recent past. Though these authors may differ in particulars, they all agree in claiming that living beings and life processes cannot be causally explained in terms of physical and chemical phenomena. It is our task to ask whether this assertion is justified, and if we answer this question with "no," to determine the source of the misunderstanding.

Causality, no matter how it is defined in terms of logic, is believed to contain three elements: (i) an explanation of past events ("a posteriori causality"); (2) prediction of future events; and (3) interpretation of teleological—that is, "goal-directed"—phenomena.

The three aspects of causality (explanation, prediction, and teleology) must be the cardinal points in any discussion of causality and were quite rightly singled out as such by Nagel (1961). Biology can make a significant contribution to all three of them. But before I can discuss this contribution in detail, I must say a few words about biology as a science.

*Two Fields*

The word *biology* suggests a uniform and unified science. Yet recent developments have made it increasingly clear that biology is a most

complex area—indeed, that the word *biology* is a label for two largely separate fields which differ greatly in method, *Fragestellung*, and basic concepts. As soon as one goes beyond the level of purely descriptive Structural biology, one finds two very different areas, which may be designated functional biology and evolutionary biology. To be sure, the two fields have many points of contact and overlap. Any biologist working in one of these fields must have a knowledge and appreciation of the other field if he wants to avoid the label of a narrow-minded specialist. Yet in his own research he will be occupied with problems of either one or the other field. We cannot discuss cause and effect in biology without first having characterized these two fields.

### *FUNCTIONAL BIOLOGY*

The functional biologist is vitally concerned with the operation and interaction of structural elements, from molecules up to organs and whole individuals. His ever-repeated/question is "How?" How does something operate, how does it function? The functional anatomist who studies an articulation shares this method and approach with the molecular biologist who studies the function of a DNA molecule in the transfer of genetic information. The functional biologist attempts to isolate the particular component he studies, and in any given study he usually deals with a single individual, a single organ, a single cell, or a single part of a cell. He attempts to eliminate, or control, all variables, and he repeats his experiments under constant or varying conditions until he believes he has clarified the function of the element he studies.

The chief technique of the functional biologist is the experiment, and his approach is essentially the same as that of the physicist and the chemist. Indeed, by isolating the studied phenomenon sufficiently from the complexities of the organism, he may achieve the ideal of a purely physical 'or chemical experiment. In spite of certain limitations of this method, one must agree with the functional biologist that such a simplified approach is an absolute necessity for achieving his particular objectives. The spectacular success of biochemical and biophysical research justifies this direct, although distinctly simplistic, approach.

### *EVOLUTIONARY BIOLOGY*

The evolutionary biologist differs in his method and in the problems in which he is interested. His basic question is "Why?" When we say "why" we must always be aware of the ambiguity of this term. It may mean "How come?" but it may also mean the finalistic "What for?" When the evolutionist asks "Why?" he or she always has in mind the historical

"How come?" Every organism, as an individual and as a member of a species, is the product of a long history, a history which indeed dates back more than 3,000 million years. As Max Delbruck (1949) has said, "A mature physicist, acquainting himself for the first time with the problems of biology, is puzzled by the circumstance that there are no 'absolute phenomena' in biology. Everything is time-bound and space-bound. The animal or plant or micro-organism he is working with is but a link in an evolutionary chain of changing forms, none of which has any permanent validity." There is hardly any structure or function in an organism that can be fully understood unless it is studied against this historical background. To find the causes for the existing characteristics, and particularly adaptations, of organisms is the main preoccupation of the evolutionary biologist. He is impressed by the enormous diversity of the organic world. He wants to know the reasons for this diversity as well as the pathways by which it has been achieved. He studies the forces that bring about changes in faunas and floras (as in part documented by paleontology), and he studies the steps by which the miraculous adaptations so characteristic of every aspect of the organic world have evolved.

We can use the language of information theory to attempt still another characterization of these two fields of biology. The functional biologist deals with all aspects of the decoding of the programmed information contained in the DNA of the fertilized zygote. The evolutionary biologist, on the other hand, is interested in the history of these programs of information and in the laws that control the changes of these programs from generation to generation. In other words, he is interested in the causes of these changes.

But let us not have an erroneous concept of these programs. It is characteristic of them that the programming is only in part rigid. Such phenomena as learning, memory, nongenetic structural modification, and regeneration show how "open" these programs are. Yet, even here there is great specificity, for instance with respect to what can be "learned," at what stage in the life cycle "learning" takes place, and how long a memory engram is retained. The program, then, may be in part quite unspecific, and yet the range of possible variation is itself included in the specifications of the program. The programs, therefore, are in some respects highly specific; in other respects they merely specify "reaction norms" or general capacities and potentialities.

Let me illustrate this duality of programs by the difference between two kinds of birds with respect to "species recognition." The young cowbird is raised by foster parents—let us say, in the nest of a song

sparrow or warbler. As soon as it becomes independent of its foster parents, it seeks the company of other young cowbirds, even though it has never seen a cowbird before! In contrast, after hatching from the egg, a young goose will accept as its parent the first moving (and preferably also calling) object it can follow and become "imprinted" to. What is programmed is, in one case, a definite "gestalt," in the other, merely the capacity to become imprinted to a "gestalt." Similar differences in the specificity of the inherited program are universal throughout the organic world.

### *The Problem of Causation*

Let us now get back to our main topic and ask: Is *cause* the same thing in functional and evolutionary biology?

Max Delbruck (1949), again, has reminded us that as recently as 1870 Helmholtz postulated "that the behavior of living cells should be accountable in terms of motions of molecules acting under certain fixed force laws." Now, says Delbruck correctly, we cannot even account for the behavior of a single hydrogen atom. As he also says, "Any living cell carries with it the experiences of a billion years of experimentation by its ancestors."

Let me illustrate the difficulties of the concept of causality in biology by an example. Let us ask: What is the cause of bird migration? **Or** more specifically: Why did the warbler on my summer place in New Hampshire start his southward migration on the night of the 25th of August?

I can list four equally legitimate causes for this migration:

- (1) *An ecological cause.* The warbler, being an insect eater, must migrate, because it would starve to death if it should try to winter in New Hampshire. '
- (2) *A genetic cause.* The warbler has acquired a genetic constitution in the course of the evolutionary history of its species which induces it to respond appropriately to the proper stimuli from the environment. On the other hand, the screech owl, nesting right next to it, lacks this constitution and does not respond to these stimuli. As a result, it is sedentary.
- (3) *An intrinsic physiological cause.* The warbler flew south because its migration is tied in with photoperiodicity. It responds to the decrease in day length and is ready to migrate as soon as the number of hours of daylight have dropped below a certain level.

(4) *An extrinsic physiological cause.* Finally, the warbler migrated on the 25th of August because a cold air mass, with northerly winds, passed over our area on that day. The sudden drop in temperature and the associated weather conditions affected the bird, already in a general physiological readiness for migration, so that it actually took off on that particular day.

Now, if we look over the four causations of the migration of this bird once more, we can readily see that there is an immediate set of causes of the migration, consisting of the physiological condition of the bird interacting with photoperiodicity and drop in temperature. We might call these the *proximate* causes of migration. The other two causes, the lack of food during winter and the genetic disposition of the bird, are the *ultimate* causes. These are causes that have a history and that have been incorporated into the system through many thousands of generations of natural selection. It is evident that the functional biologist would be concerned with analysis of the proximate causes, while the evolutionary biologist would be concerned with analysis of the ultimate causes. This is the case with almost any biological phenomenon we might want to study. There is always a proximate set of causes and an ultimate set of causes; both have to be explained and interpreted for a complete understanding of the given phenomenon.

Still another way to express these differences would be to say that proximate causes govern the responses of the individual (and his organs) to immediate factors of the environment, while ultimate causes are responsible for the evolution of the particular DNA program of information with which every individual of every species is endowed. The logician will, presumably, be little concerned with these distinctions. Yet, the biologist knows that many heated arguments about the "cause" of a certain biological phenomenon could have been avoided if the two opponents had realized that one of them was concerned with proximate and the other with ultimate causes. I might illustrate this by a quotation from Loeb (1916): "The earlier writers explained the growth of the legs in the tadpole of the frog or toad as a case of adaptation to life on land. We know through Gudernatsch that the growth of the legs can be produced at any time even in the youngest tadpole, which is unable to live on land, by feeding the animal with the thyroid gland."

Let us now get back to the definition of "cause" in formal philosophy and see how it fits with the usual explanatory "cause" of functional and evolutionary biology. We might, for instance, define cause as a nonsufficient condition without which an event would not have happened, or as

a member of a set of jointly sufficient reasons without which the event would not happen. Definitions such as these describe causal relations quite adequately in certain branches of biology, particularly in those which deal with chemical and physical unit phenomena. In a strictly formal sense they are also applicable to more complex phenomena, and yet they seem to have little operational value in those branches of biology that deal with complex systems. I doubt that there is a scientist who would question the ultimate causality of all biological phenomena—that is, that a causal explanation can be given for past biological events. Yet such an explanation will often have to be so unspecific and so purely formal that its explanatory value can certainly be challenged. In dealing with a complex system, an explanation can hardly be considered very illuminating that states: "Phenomenon A is caused by a complex set of interacting factors, one of which is *b*." Yet often this is about all one can say. We will have to come back to this difficulty in connection with the problem of prediction. However, let us first consider the problem of teleology.

### *The Problem of Teleology*

No discussion of causality is complete which does not come to grips with the problem of teleology. This problem had its beginning with Aristotle's classification of causes, one of the categories being the "final" causes. This category is based on the observation of the orderly and purposive development of the individual from the egg to the "final" stage of the adult. Final cause has been defined as "the cause responsible for the orderly reaching of a preconceived ultimate goal." All goal-seeking behavior has been classified as "teleological," but so have many other phenomena that are not necessarily goal-seeking in nature.

Aristotelian scholars have rightly emphasized that Aristotle—by training and interest—was first and foremost a biologist, and that it was his preoccupation with biological phenomena which dominated his ideas on causes and induced him to postulate final causes in addition to the material, formal, and efficient causes. Thinkers from Aristotle to the present have been challenged by the apparent contradiction between a mechanistic interpretation of natural processes and the seemingly purposive sequence of events in organic growth, reproduction, and animal behavior. Such a rational thinker as Bernard (1885) has stated the paradox in these words.

There is, so to speak, a preestablished design of each being and of each organ of such a kind that each phenomenon by itself depends upon the general forces of nature, but when taken in connection with the others it

seems directed by some invisible guide on the road it follows and led to the place it occupies.

We admit that the life phenomena are attached to physicochemical manifestations, but it is true that the essential is not explained thereby; for no fortuitous coming together of physicochemical phenomena constructs each organism after a plan and a fixed design (which are foreseen in advance) and arouses the admirable subordination and harmonious agreement of the acts of life . . . Determinism can never be [anything] but physicochemical determinism. The vital force and life belong to the metaphysical world.

What is the  $x$ , this seemingly purposive agent, this "vital force," in organic phenomena? It is only in our lifetime that explanations have been advanced which deal adequately with this paradox.

The many dualistic, finalistic, and vitalistic philosophies of the past merely replaced the unknown  $x$  by a different unknown,  $y$  or  $z$ , for calling an unknown factor *entelechia* or *elan vital* is not an explanation. I shall not waste time showing how wrong most of these past attempts were. Even though some of the underlying observations of these conceptual schemes are quite correct, the supernaturalistic conclusions drawn from these observations are altogether misleading.

Where, then, is it legitimate to speak of purpose and purposiveness in nature, and where it is not? To this question we can now give a firm and unambiguous answer. An individual who—to use the language of the computer—has been "programmed" can act purposefully. Historical processes, however, *cannot* act purposefully. A bird that starts its migration, an insect that selects its host plant, an animal that avoids a predator, a male that displays to a female—they all act purposefully because they have been programmed to do so. When I speak of the programmed "individual," I do so in a broad sense. A programmed computer itself is an "individual" in this sense, but so is, during reproduction, a pair of birds whose instinctive and learned actions and interactions obey, so to speak, a single program.

The completely individualistic and yet also species-specific DNA program of every zygote (fertilized egg cell), which controls the development of the central and peripheral nervous systems, of the sense organs, of the hormones, of physiology and morphology, is the *program* for the behavior computer of this individual.

Natural selection does its best to favor the production of programs guaranteeing behavior that increases fitness. A behavior program that guarantees instantaneous correct reaction to a potential food source, to a potential enemy, or to a potential mate will certainly give greater fitness

in the Darwinian sense than a program that lacks these properties. Again, a behavior program that allows for appropriate learning and the improvement of behavior reactions by various types of feedback gives greater likelihood of survival than a program that lacks these properties.

The purposive action of an individual, insofar as it is based on the properties of its genetic code, therefore is no more nor less purposive than the actions of a computer that has been programmed to respond appropriately to various inputs. It is, if I may say so, a purely mechanistic purposiveness.

We biologists have long felt that it is ambiguous to designate such programmed, goal-directed behavior "teleological," because the word *teleological* has also been used in a very different sense, for the final stage in evolutionary adaptive processes (see Essay 3).

The development or behavior of an individual is purposive; natural selection is definitely not. When MacLeod (1957) stated, "What is most challenging about Darwin./however, is his re-introduction of purpose into the natural world," he chose the wrong word. The word *purpose* is singularly inapplicable to evolutionary change, which is, after all, what Darwin was considering. If an organism is well adapted, if it shows superior fitness, this is not due to any purpose of its ancestors or of an outside agency, such as "Nature" or "God," that created a superior design or plan. Darwin "has swept out such finalistic teleology by the front door," as Simpson (1960) has rightly said.

We can summarize this discussion by stating that there is no conflict between causality and teleonomy, but that scientific biology has not found any evidence that would support teleology in the sense of various vitalistic or finalistic theories (Simpson 1960; 1950; Koch 1957). All the so-called teleological systems which Nagel discusses (1961) are actually illustrations of teleonomy.

### *The Problem of Prediction*

The third great problem of causality in biology is that of prediction. In the classical theory of causality the touchstone of the goodness of a causal explanation was its predictive value. This view is still maintained in Bunge's modern classic (1959): "A theory can predict to the extent to which it can describe and explain." It is evident that Bunge is a physicist; no biologist would have made such a statement. The theory of natural selection can describe and explain phenomena with considerable precision, but it cannot make reliable predictions, except through such trivial and



meaningless circular statements as, for instance: "The fitter individuals will on the average leave more offspring." Scriven (1959) has emphasized quite correctly that one of the most important contributions to philosophy made by the evolutionary theory is that it has demonstrated the independence of explanation and prediction.<sup>1</sup>

Although prediction is not an inseparable concomitant of causality, every scientist is nevertheless happy if his causal explanations simultaneously have high predictive value. We can distinguish many categories of prediction in biological explanation. Indeed, it is even doubtful how to define "prediction" in biology. A competent zoogeographer can predict with high accuracy what animals will be found on a previously unexplored mountain range or island. A paleontologist likewise can predict with high probability what kind of fossils can be expected in a newly accessible geological horizon. Is such correct guessing of the results of past events genuine prediction? A similar doubt pertains to taxonomic predictions, as discussed in the next paragraph. The term *prediction* is, however, surely legitimately used for future events. Let me give four examples to illustrate the range of predictability.

(1) *Prediction in classification.* If I have identified a fruit fly as an individual of *Drosophila melanogaster* on the basis of bristle pattern and the proportions of face and eye, I can "predict" numerous structural and behavioral characteristics which I will find if I study other aspects of this individual. If I find new species with the diagnostic key characters of the genus *Drosophila*, I can at once "predict" a whole set of biological properties.

(2) *Prediction of most physicochemical phenomena on the molecular level.* Predictions of very high accuracy can be made with respect to most biochemical unit processes in organisms, such as metabolic pathways, and with respect to biophysical phenomena in simple systems, such as the action of light, heat, and electricity in physiology.

In examples 1 and 2 the predictive value of causal statements is usually very high. Yet there are numerous other generalizations or causal statements in biology that have low predictive values. The following examples are of this kind.

(3) *Prediction of the outcome of complex ecological interactions.* The statement, "An abandoned pasture in southern New England will be replaced by a stand of grey birch (*Betula populifolia*) and white pine (*Pinus strobus*)" is often correct. Even more often, however, the replacement may be an almost solid stand of *P. strobus*, or *P. strobus* may be missing altogether

and in its stead will be cherry (*Prunus*), red cedar (*Juniperus virginianus*), maples, sumac, and several other species.

Another example also illustrates this unpredictability. When two species of flour beetles (*Tribolium confusum* and *T. castaneum*) are brought together in a uniform environment (sifted wheat flour), one of the two species will always displace the other. At high temperatures and humidities, *T. castaneum* will win out; at low temperatures and humidities, *T. confusum* will be the victor. Under intermediate conditions the outcome is indeterminate and hence unpredictable (Park 1954).

(4) *Prediction of evolutionary events.* Probably nothing in biology is less predictable than the future course of evolution. Looking at the Permian reptiles, who would have predicted that most of the more flourishing groups would become extinct (many rather rapidly), and that one of the most undistinguished branches would give rise to the mammals? Which student of the Cambrian fauna would have predicted the revolutionary changes in the marine life of the subsequent geological eras? Unpredictability also characterizes small-scale evolution. Breeders and students of natural selection have discovered again and again that independent parallel lines exposed to the same selection pressure will respond at different rates and with different correlated effects, none of them predictable.

As is true in many other branches of science, the validity of predictions for biological phenomena (except for a few chemical or physical unit processes) is nearly always statistical. We can predict with high accuracy that slightly more than 500 of the next 1,000 newborns will be boys. We cannot predict the sex of a particular child prior to conception.

#### *Reasons for Indeterminacy in Biology*

Without claiming to exhaust all the possible reasons for indeterminacy, I can list four classes. Although they somewhat overlap each other, each deserves to be treated separately.

(i) *Randomness of an event with respect to the significance of the event.* Spontaneous mutation, caused by an "error" in DNA replication, illustrates this cause for indeterminacy very well. The occurrence of a given mutation is in no way related to the evolutionary needs of the particular organism or of the population to which it belongs. The precise results of a given selection pressure are unpredictable because mutation, recombination, and developmental homeostasis are making indeterminate contributions to the response to this pressure. All the steps in the determination

of the genetic contents of a zygote contain a large component of this type of randomness. What we have described for mutation is also true for crossing over, chromosomal segregation, gametic selection, mate selection, and early survival of the zygotes. Neither underlying molecular phenomena nor the mechanical motions responsible for this randomness are related to their biological effects.

(2) *Uniqueness of all entities at the higher levels of biological integration.* In the uniqueness of biological entities and phenomena lies one of the major differences between biology and the physical sciences. Physicists and chemists often have genuine difficulty in understanding the biologist's stress on the unique, although such an understanding has been greatly facilitated by developments in modern physics. If a physicist says "ice floats on water," his statement is true for any piece of ice and any body of water. The members of a class usually lack the individuality that is so characteristic of the organic world, where each individual is unique; each stage in the life cycle is unique; each population is unique; each species and higher category is unique; each interindividual contact is unique; each natural association of species is unique; and each evolutionary event is unique. Where these statements are applicable to man, their validity is self-evident. However, they are equally valid for all sexually reproducing animals and plants. Uniqueness, of course, does not entirely preclude prediction. We can make many valid statements about the attributes and behavior of man, and the same is true for other organisms. But most of these statements (except for those pertaining to taxonomy) have purely statistical validity. Uniqueness is particularly characteristic for evolutionary biology. It is quite impossible to have for unique phenomena general laws like those that exist in classical mechanics.

(3) *Extreme complexity.* The physicist Elsasser stated in a recent symposium: "[An] outstanding feature of all organisms is their well-nigh unlimited structural and dynamical complexity." This is true. Every organic system is so rich in feedbacks, homeostatic devices, and potential multiple pathways that a complete description is quite impossible. Furthermore, the analysis of such a system would require its destruction and would thus be futile.

(4) *Emergence of new qualities at higher levels of integration.* It would lead too far to discuss in this context the thorny problem of "emergence." All I can do here is to state its principle dogmatically: "When two entities are combined at a higher level of integration, not all the properties of the new entity are necessarily a logical or predictable consequence of the properties of the components." This difficulty is by no means confined to

biology, but it is certainly one of the major sources of indeterminacy in biology. Let us remember that indeterminacy does not mean lack of cause, but merely unpredictability.

All four causes of indeterminacy, individually and combined, reduce the precision of prediction.

One may raise the question at this point whether predictability in classical mechanics and unpredictability in biology are due to a difference of degree or of kind. There is much to suggest that the difference is, in considerable part, merely a matter of degree. Classical mechanics is, so to speak, at one end of a continuous spectrum, and biology is at the other. Let us take the traditional example of the gas laws. Essentially they are only statistically true, but the population of molecules in a gas obeying the gas laws is so enormous that the actions of individual molecules become integrated into a predictable—one might say "absolute"—result. Samples of 5 or 20 molecules would show definite individuality. The difference in the size of the studied "populations" certainly contributes to the difference between the physical sciences and biology.

### Conclusions

Let us now return to our initial question and try to summarize some of our conclusions on the nature of the cause-and-effect relations in biology.

- (1) Causality in biology is a far cry from causality in classical mechanics.
- (2) Explanations of all but the simplest biological phenomena usually consist of sets of causes. This is particularly true for those biological phenomena that can be understood only if their evolutionary history is also considered. Each set is like a pair of brackets which contains much that is unanalyzed and much that can presumably never be analyzed completely.
- (3) In view of the high number of multiple pathways possible for most biological processes (except for the purely physicochemical ones) and in view of the randomness of many of the biological processes, particularly on the molecular level (as well as for other reasons), causality in biological systems is not predictive, or at best is only statistically predictive.
- (4) The existence of complex programs of information in the DNA of the germ plasm permits teleonomic purposiveness. On the other hand, evolutionary research has found no evidence whatsoever for a goal-

seeking" of evolutionary lines, as postulated in that kind of teleology which sees "plan and design" in nature. The harmony of the living universe, so far as it exists, is an a posteriori product of natural selection.

Finally, causality in biology is not in real conflict with the causality of classical mechanics. As modern physics has also demonstrated, the causality of classical mechanics is only a very simple, special case of causality. Predictability, for instance, is not a necessary component of causality. The complexities of biological causality do not justify embracing nonscientific ideologies, such as vitalism or finalism, but should encourage all those who have been trying to give a broader basis to the concept of causality.

#### NOTES

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i. Various philosophers have published seeming refutations of Scriven's claims. No doubt my views on prediction at that time were rather simplistic. I have since revised them considerably (Mayr 1982:57-59). The philosophical problems of prediction have been well stated by Grünbaum (1963:114—149).

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