Towards a Methodology of Teleonomy

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The problem of adaptation is the only one by which biology differs fundamentally from all other natural sciences. It's therefore surprising to see how little this basic problem has been studied. This deplorable situation is mainly due to three reasons, as many discussions with biologists have made clear to me:

1. Because of historical reasons, the question is thought to be contaminated with Aristotelian finality.
2. The claim of the theory of natural selection to explain historical events empirically remained misunderstood and its explanatory potential went unrecognized.
3. The main reason, however, seems to be the lack of a methodology. For instance, many biologists of our days still do not know that natural selection can be investigated experimentally. Consequently I shall try to outline below some avenues of approach to study the problem of 'adaptation'. Because of lack of space, theory, questioning and methodology must necessarily remain rather unsophisticated.

In 1859 the study of the problem of adaptation received a precise foundation, when DARWIN published his theory of natural selection. For approximately 70 years its core remained a concept falsely epitomized as 'survival of the fittest' and 'struggle for survival', two well-known clichés which DARWIN had adopted from H. SPENCER (see 5), and that still nowadays serve for an erroneous characterization of a misunderstood theory. The theory of natural selection, as it stands since the early Thirties, describes how all those characters of an organism are selected which ensure for its owners, as opposed to other members of the species, a higher reproductive success, i.e. it implies differential survival of genotypes in a population. The theory of natural selection consequently explains the survival of species, and the survival of the individual only inasmuch as it serves its reproductive success. Further misunderstandings and errors, which still nowadays hamper progress of evolutionary research, will be briefly dealt with in an appendix.

One of the major drawbacks, which prevented the general acceptance of the theory by the causally oriented evolutionists, was the alleged goal-directedness of selection. This goal-directedness gave rise to the confusion with Aristotelian teleology; it was overlooked that natural selection was the cause for the development of adaptations and not a causa finalis to be rejected with good reason. In recognition of this unfortunate, semantic historical burden of the study of adaptations, PITTEDRIGH coined for it the term 'teleonomy' in order to give the seemingly finalistic question of the 'what for?' of biological phenomena a strictly causal meaning. Accordingly, teleonomy thrives at the causal answer to the question of the nature and the operation of selection pressures (factors).

The proposal to redefine the old term of teleology in this way seems to me confusing.

Basic concepts

The identification of the responsible selection pressure which has shaped a given character of an organism is a necessary pre-requisite to unravel its function or biological significance.

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1 Altered version of a paper read at the 3rd German Speaking Ethological Conference 1972 at Radolfzell, Bodensee (Germany, Fed. Rep.)
6 M. EIGEN, Chemie in unserer Zeit 6, 1 (1972).
7 P. SCHUSTER, Chemie in unserer Zeit 6, 1 (1972).
If one looks at an adaptation at a given time one will not know anything about the speed of its evolutionary development. If, for the sake of simplicity, one leaves aside time, one can symbolize the co-action of several selection pressures simply by means of a vector symbolizing the strength and the direction of selection (Figure 1). The depth of the angle signifies the maximally attainable degree of perfection for a given adaptation. In the particular example chosen here, interaction between selection pressures was not considered. The direction of selection determines the nature of the adaptation. Given two selection factors acting in the same direction but with different strength, the answer of the adapting organism will be equally strong, irrespective of whether there are two (b) or only one (a) selective agent(s) at work, if the latter is as strong as the more effective of those working in unison; s'' cannot conceivably operate in the presence of s' because the species cannot 'perceive' it. In general this applies only if the individuals least adapted to s' are no longer affected by s''. This condition in turn depends on how much s' is smaller than s'' and on the individual variability of the adaptation achieved. In case s' would suddenly cease to operate, the adaptation coping with it would also be advantageous in coping with s''. From this follows: An adaptation arises only through the operation of the strongest of several selection factors acting in the same direction. This conclusion rules out the wide-spread but erroneous idea that every observed advantage would derive from the effect of selection. By contrast, one has to examine carefully whether an advantage has not been gained as a by-product of an adaptation to a stronger selective force. If, for instance both, cold and drought select a spherical shape, i.e. the most advantageous ratio of volume to surface, then approximation of a sphere would only be achieved by the stronger of two selective agents acting in the same direction.

If two selection pressures act against each other ('counter-selection'), a comprise solution is commonly arrived at which is capable of coping, though not perfectly, with both selective agents (c). This counter-action need not follow algebraic addition; instead selection pressures operating in different directions can interact with each other. Precise action in parallel (b) and precise counter-action (c) are but borderline cases along a scale with many possibilities of the direction of two or more selection pressures.

The effect of two equally strong selection pressures which act in the same direction upon the degree of perfection of an adaptation is as strong as any one of them alone (d). (In the latter case the adaptation would ceteris paribus arise more slowly than could be demonstrated by the inclusion of the time factor). Two predators with precisely identical hunting strategy effect a prey species only as strong as anyone of them: Doubling the number of individuals of one of them would replace the effect of the other one. Probably the case (d) under consideration would only be relevant for abiotic selection factors and would then occur perhaps only rarely; synecological relations, e.g. the pressure of several predators or competition with several similar species etc. would always tend to follow paradigm (b) since in no place are there two predators with identical hunting strategy and in no place, because of the competition exclusion principle by Gause, will competing species with precisely identical ecology occur.

Adaptation denotes both the evolutionary process as well as its end-product. In the following only the former meaning will apply. Adaptations may be obligatory or may be facultative, i.e. will only occur under certain environmental conditions. The most versatile 'organ' in this respect is the learning ability of animals.

DOBZHANSKY has distinguished between the adapt-edness of a population and the Darwinian fitness of the individual. The measures for both these aspects are very often correlated in one and the same population, yet there are exceptions. In the following only Darwinian fitness, as measured by reproductive success, will be discussed.

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Fig. 1. Diagram illustrating the effect of one or two selection pressures upon an adaptation in the state of maximally possible perfection. Direction and strength of the selection pressures are symbolized as vectors. For further explanation, see the text.

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