

MOLECULAR SELECTION<sup>1</sup>

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ABSTRACT: I propose that natural selection at the molecular level be recognized as such.

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Natural selection is a very general process. It is most concisely defined as differential replication or reproduction, which includes such aspects as mortality because a dead organism no longer produces offspring. To incorporate such aspects as differential persistence (apart from reproduction) and change in size or resource control (Cook, 1980; Harper, 1977), I have generalized this a little, into differential expansion (Van Valen, 1976). The word "differential" is meant to imply a dependence on properties of the units considered, rather than random processes of change. Other side comments, such as the process of natural selection being different from any response to it, are often necessary to avoid confusion. There are many hundreds, probably several thousands, of described cases of selection under natural conditions, but as few of them have ever been reviewed many people think such cases are rare.

The units of natural selection can occur at many levels and need not even be biological. Thus the natural selection of ideas is becoming more widely accepted (Pulliam and Dunford, 1980; Cavalli-Sforza and Feldman, 1981) and the decrease of the number of atoms of uranium in the Earth (both absolutely and with reference to a standard such as iron) over geologic time also exemplifies this process.

The paradigmatic kind of natural selection is that among individual organisms. This was what Darwin emphasized, although Lyell (1832) had earlier explained the differences among the biotas of different geological ages by selection among species. Other kinds of natural selection have on occasion been excluded from the domain of natural selection. Darwin (1871) himself did this for sexual selection, which mechanistically is an aspect of the fertility component of individual selection (Van Valen, 1983). It has also been done at least for meiotic selection (Sandler and Novitski, 1957), gametic selection (Dunn, 1957), and selection among whole species and lineages (Stanley, 1975). Competition among local species populations or their regional metapopulations is also natural selection although rarely so regarded.

Internal causes of change in the composition of the genome within single individuals have recently been called "molecular drive" (Dover, 1982), although the author of this term considers it partly inappropriate (Dover et al., 1982). It has two sorts of problems. One is that it explicitly lumps together directional and random causes, which at other levels are distinguished as selection and drift. The other problem is that, by conceptually removing selection within a genome from selection at other levels, it implies a distinction in kind rather than in level.

I therefore suggest that selection among parts of the genome be called molecular selection and that random changes among such units be called molecular drift. Each is an aspect of intra-genome evolution, although they can occur

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also outside genomes (Mills et al., 1973). Processes on all levels and time-scales of evolution interact with each other (Lewontin, 1970; Van Valen, 1976); the interactions commonly but not always produce compromises among the optima of each level or time-scale when these optima differ. Such compromises occur also for different component vectors, like fertility and mortality schedules, within single levels. But only by the interaction of different levels or time-scales can polymorphisms or their equivalent be maintained by constant vectors of opposite direction.

Biased gene conversion, or expansion of a family of transposons, is selective. The relevant DNA increases or decreases both absolutely and as a proportion of the total genome, by differential replication. Its fitness within the genome differs from that of the background DNA. And if both processes somehow occurred on the same piece of DNA, their selective vectors would merge and not support a polymorphism. Such vectors are propensities or expectations; change due to sampling error despite a directional expectation of 0 is drift. As on other levels (Lewontin, 1970; Van Valen, 1975), detailed analysis of molecular selection (Lamb and Helmi, 1982; Strachen et al., 1982; Ohta, 1983) requires parameters specific to the processes involved, but this should not override their basic unity.

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