changes too rapidly. Cumulation is affected by contingency; which variants actually appear will profoundly affect the subsequent response to selection.

Characters evolve through their effect on differential survival and reproduction, and in any population there are a large number of potential mutations that can affect fitness. This favors divergence among populations subject to identical selection because different populations will experience different mutations by chance, each population represents only a sample of all possible allele combinations, effects of a gene may depend upon the alleles present at other loci, and each episode of selection modifies the composition of the population. Any divergence of lines predisposes future selection in each to favor different mutations. Different lineages will accumulate different working combinations so that the effects of subsequent mutations on fitness will be different. The differences will continue to cumulate, with each line evolving higher fitness by different gene combinations. Thus the cumulation of different gene combinations is contingent upon history; long-term selection is Bayesian.

The Bayesian approach helps to avoid a misunderstanding exhibited by many nonevolutionists (including creationists) who argue that complex adaptations are "unlikely." Consider a cultured RNA gene sequence of length 218. There are 4^{218} or about 10^{128} different sequences of length 218. How long would we have to wait for a functional sequence to show up? A culture tube contains about 10^{16} molecules. The world's ocean could fill about 10^{22} culture tubes, containing altogether 10^{38} molecules. If we could change the sequence of every molecule every second, never allowing any sequence to be repeated, we would have tried out every possible sequence and found our best adapted molecule in $10^{128}/10^{38} = 10^{72}$ years, or about 10^{62} times the age of the universe. This is the non-evolutionist's version and overlooks two major considerations: only alterations that give rise to functional improvements are favored by selection, and new improvements build upon past improvements. We know that highly adapted molecules of RNA can evolve in culture within a week, insufficient time for something to turn up all at once. Components turn up sequentially; better ones replace the inferior ones, and then additional variants show up. Each altered sequence forms the basis for further improvement. This can proceed very rapidly, of the order of the single-position substitution rate, not the product of the probabilities of changing all sites at once. It is conditional rather than absolute probabilities that are important in evolution, just as we must work with relative rather than absolute fitnesses.

The cumulative nature of evolution places severe constraints on the kinds of organisms and adaptations that can evolve. The degree to and ways in which adaptedness can be improved depend upon the connectance of the genotypic space through which the population could travel. If it is very connected, then evolution can proceed rapidly, otherwise it will be slow or stagnate. But the contingent nature of the paths taken also explains the diversity of effects of selection on different populations in the same selective environment.

Although populations starting from a single base population diverge even under identical selection, selection lines starting from different base populations will become more similar through time if subject to the same selection. This is not a contradiction. First, there is convergence at the level of fitness and the trait function (phenotype) undergoing selection, but not at the level of physiology, development, and genetics. Second, there are just phases of selection; divergence occurs under sorting, but the lines will eventually converge in phenotype when enough mutations have occurred. The point here is that there are multiple genetic solutions to the same environmental challenge. Owing to cumulation and contingency of the evolutionary paths taken, evolutionary reversals may be unlikely at the genotypic level, even if likely at the phenotypic level.

Bell's literature survey suggests that populations of all kinds of organisms at all scales are kept in flux by continual change in the intensity and direction of selection. It is doubtful whether natural environments are uniform with respect to selection at any scale of time or space. Bell discusses many consequences of temporal and spatial heterogeneity, and they are especially interesting for multiple traits. Although particular combinations of traits are favored in one environment, different combinations may be newly superior if the environment changes, and response is limited by the strength of the genetic correlation between the traits. Adaptation to novel environments is hindered by existing genetic covariance structure. In contrast, in a constant environment adaptation is hindered by a lack of genetic covariance. The strengths of genetic covariances can evolve and may reflect the scale of temporal and spatial variance.

In addition to offering new views and taking up topics that have not heretofore been put in a genetic context, Bell discusses most of the active topics in the selection-oriented part of evolutionary biology, including the evolution of life cycles, life history, sex, gametes, recombination, epistasis, genetic variance, plasticity, specialization, and parasitism. In most cases he gives clear and interesting summaries, with excellent examples and questions to ponder. I recommend the books to anyone interested in almost any aspect of natural selection and its importance in evolution.

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