

Jack Lester King

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Jack King died June 29, 1983, after a short illness. He was a member of the editorial board of *Evolutionary Theory* (as well as one of the editors of the *Journal of Molecular Evolution* and will be remembered by different sets of people for different qualities.

He published little, usually saving his work for later improvement and several times finding it published by others, but he made two important discoveries. The first (1966 and later) was that reasonable epistatic interaction at the level of fitness can greatly ameliorate the problem of various kinds of genetic load. He and others followed up on his seminal 1966 paper, which has been unduly neglected as the source of this work. Load theory is conceptually difficult and is still one of the most commonly misrepresented areas of population genetics. Jack's partial solution, if empirically as well as theoretically correct, has various and far-reaching ramifications, which he was working on at the time of his death. They may be published in due course, although the lack of a manuscript makes this awkward and any paper will not do justice to this work, which he presented in seminars at Chicago and elsewhere.

His best-known work was a 1969 paper with Jukes. The title (coined by King), "Non-Darwinian evolution", was reasonably accurate as well as provocative. *Science* had initially rejected the paper, one referee saying that it was obviously false and another that it was trivially true. By its eventual publication the authors had had to eliminate their suggestion that most isozyme polymorphisms were neutral, which is, however, a common view today.

The paper gave the first adequate presentation of the neutralist theory of molecular evolution. In 1968, while King and Jukes were still writing, Kimura had published a paper that also advocated this view, but ironically his argument for it was that nucleotide substitutions in structural genes occur so often that if most were selectively caused the genetic load would be impossibly large. (For a single locus the substitutional load is the same for neutral and adaptive changes, unlike the situation with selection.) He had apparently not realized the implications of King's 1966 paper. The neutralist view is still often misunderstood; some people even think that stabilizing (purifying) selection is evidence against it, when in fact this is an integral part.

King himself never believed that most features of the visible phenotype evolved nonadaptively. Adaptation is as obvious (to most people) now as it was two centuries ago. Indeed, several years later he remarked that he was as ambivalent as I was about the scope of the neutral theory itself. His final view (King, 1983) was that "the controversy continued unresolved for a decade, apparently because both sides were essentially correct in the matters they were arguing about while both were mistaken in the ideas they held in common. Eventually, Kimura himself showed [as did King in a manuscript] that the genes that determine polygenic variation may often, under stabilizing selection, have such small individual net advantages or disadvantages as to be effectively neutral. Such genes determine phenotypic variation, and may bring about adaptation, by their massed effects, while their individual fates are subject only to mutation and drift. The neutral theory is now part of the accepted framework of evolutionary genetics."

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Jack was born in Oakland in 1934 and spent his life in California. All his university training was at Berkeley, where he received a Ph.D. in 1963 and remained until he joined the faculty at Santa Barbara in 1969. He became, as he described it, "a graduate student in biochemistry" after his 1969 paper with Jukes, in order to know more than the population-genetics side. He was quiet, almost self-effacing, but vigorous and did not like to be wrong. His often elegant results were perhaps related to his habit of thinking at length and writing infrequently. He was, however, the spark behind a well-received general text in biology, for which he was working on the second edition at the time of his death.

He cared about people, perhaps even those who abused him, and gave much attention to both his family and teaching. He was generous in his consultation for the research of others; his 1980 paper on contingency tables resulted from such consultation, but usually there was little recognition. His wife, Ethel, eight children, and two grandchildren survive him.

One of Jack's unpublished manuscripts appears in this issue; it may be possible to have other work published later. I thank Tom Jukes, Ethel King, Sam Sweet, and Jerry Westby for information and comments.

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