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Lewontin R C & Kojima K. The evolutionary dynamics of complex polymorphisms. *Evolution* 14:458-72, 1960.
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This paper gives the general theoretical equations for treating natural selection operating on two genes simultaneously when the linkage between those genes is taken into account. It reveals conditions under which the genetic composition of the population is significantly affected by the complication of linkage and solves the general equations for a simplified pattern of selection. Previous theoretical work on selection had neglected the effect of genetic linkage. [The *SCI*® and *SSCI*® indicate that this paper has been cited in over 190 publications.]

Excessive Citations? A Case from Genetics

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The high frequency of citation of our paper seems at first glance to be unproblematical. It is usually cited as the founding paper in what has become a minor industry in theoretical population genetics, the study of multilocus selection problems taking account of the recombination of genes. But a second look reveals some complications that illuminate the way in which papers gain or lose influence.

The paper was the result of an equal collaboration between an assistant professor beginning his research career (R.C. Lewontin) and an advanced and very mature graduate student (K. Kojima). Kojima had already embarked on his research career at the National Institute of Genetics in Mishiuca, Japan, and had come to the US to acquire the prestige of an American PhD, a not uncommon practice in the early 1950s.

As a consequence of giving my first course of lectures in theoretical population genetics, I came to realize that there was a hole in population genetic theory. Aside from a throwaway remark by R.A. Fisher[1] in *The Genetical Theory of Natural Selection*, the theory of selection ignored completely the fact that genes are organized on chromosomes and so have limited recombination. In 1955 and early 1956, I worked on the exact theory of selection of linked genes and developed the basic equations for handling this problem, with some rather surprising results. But the equations could not be solved in closed form (and still have not been solved in general) so I put the results aside without publishing the basic material. Then, at the end of 1956, a paper by M. Kimura[2] appeared in which he analyzed theoretically a case of mimicry in butterflies involving two loci, in the context of Fisher's earlier discussion of the evolution of linkage between polymorphic loci. In this paper, Kimura gave the time-continuous form of the equations that I had developed and then solved them for a very special simplified case.

Impelled by Kimura's "scoop," I took up the problem again. Kojima had been working, quite independently, on a multilocus selection problem, not taking linkage into account, for his thesis. As we often discussed theoretical problems in general, and his thesis in particular, it was natural for us to collaborate on the general linkage/selection problem. Abandoning any hope of finding a general closed solution to my equations, we settled for the most general set of parameters for

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which we could find solutions and published a general theoretical paper on the evolution of linked genes under selection.

Nothing further appeared on this subject for two years when, in 1962, a "review" paper, "Linkage and recombination in evolution" by W.F. Bodmer and P.A. Parsons,[3] appeared that again derived the exact equations for a slightly more general model. While this review cited both Kimura's and our paper, there was considerable original and new work in it. The field then developed rapidly, producing PhD theses and numerous publications that included contributions by nearly every active theoretical population geneticist.

In view of Kimura's earlier publication and the somewhat more general model produced by Bodmer and Parsons, why is Lewontin and Kojima cited 181 times to Kimura's 118 and Bodmer and Parsons's 157 through 1986?

We can rule out Merton's "Matthew effect," by which the best-known author receives the most citations.[4] Kimura is surely the most eminent and best-known theoretician now alive, and Bodmer (now Sir Walter), a person of immense visibility in science. Nor does it lie in accessibility. Both Lewontin and Kojima, and Kimura, were published in the same journal. The answer, I believe, lies in two important factors at work in citation frequency: context and hindsight.

The general equations in the Kimura paper were imbedded in the context of a specific natural historical problem of limited interest. Even the title of Kimura's paper seems to promise only a specific model of a specific system. Moreover, no general *claims* are made for the result, but only the remark that a specific case has been found that substantiates a remark of Fisher's. Thus, it is left to the reader to see the general context into which the completely general equations given by Kimura might fit. Bodmer and Parsons, at the other extreme, gave their equations in the context of a review paper and explicitly referred to the previous derivation of the general equations by Lewontin and Kojima, thus obscuring the originality of their own contribution. In contrast, the very title of the Lewontin and Kojima paper makes an ambitious and sweeping claim for the domain of the investigation. The content of the paper itself is constantly cast in the most inclusive terms, and a previously unappreciated phenomenon requiring attention in the future is announced. Thus, Lewontin and Kojima *demand* citation in any future work on this subject.

The other factor arises from the later research history of the authors. Bodmer[5] made only one other contribution to this subject, albeit a very important one, five years after his first; while Kimura returned to the subject once, only to minimize the importance of the joint effects of selection and linkage.[6] In contrast, I made the issue a major subject of my subsequent theoretical research, being an author or coauthor of 10 further papers and two book chapters on the question, as well as sponsoring doctoral theses and postdoctoral research on linkage and selection. Thus, I became identified with the subject matter and so my early paper becomes an automatic citation.

[Since it is of general interest, this commentary appears in all *Current Contents*® editions this week. A follow-up essay on citation behavior will appear in a few weeks.]

1. **Fisher R A.** *The genetical theory of natural selection.* Oxford, England: Clarendon Press, 1930. 272 p. (Cited 1,685 times since 1945.)
2. **Kimura M.** A model of a genetic system which leads to closer linkage by natural selection. *Evolution* 10:278-87, 1956. (Cited 125 times through August 1988.)
3. **Bodmer W F & Parsons P A.** Linkage and recombination in evolution. *Advan. Genet.* 11:1-100, 1962. (Cited 180 times through August 1988.)
4. **Merton R K.** The Matthew effect in science. *Science* 159:56-63, 1968. (Cited 210 times.)
5. **Bodmer W F & Felsenstein J.** Linkage and selection: theoretical analysis of the deterministic two locus random mating model. *Genetics* 57:237-65, 1967. (Cited 110 times.)
6. **Kimura M.** The attainment of quasi-linkage equilibrium when gene frequencies are changing by natural selection. *Genetics* 52:875-90, 1965. (Cited 60 times.)

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