An approximate criterion for increase of a gene for a social action is $br-c>0$, where b is conferred benefit, c is cost of the action, and r is Sewall Wright's Coefficient of Relationship of interactants. *Inclusive fitness*, based on the criterion, is proposed as a guide in social reasoning. [The *SCI*® and *SSCI*® indicate that this paper has been cited in over 1,335 publications, making it this journal's most-cited paper.]

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This paper (part one of a consecutive pair) was the first that I published apart from one short note embodying the same idea.[1] The note came out the year before but was written after the main work; in spite of one rejection, it had, through its shortness, a swifter editorial passage.

The theme of all three—the condition for the evolution of genetical altruism—began for me while I was an undergraduate reading natural sciences at the University of Cambridge in 1958. I discovered R.A. Fisher's *The Genetical Theory of Natural Selection* in the St John's College Library and immediately realised that this was the key to the understanding of evolution that I had long wanted. I became a Fisher freak and neglected whole courses in my efforts to grasp the book's extremely compressed style and reasoning. I quickly noticed, however, that Fisher's arguments implied a basically different interpretation of adaptation from what I was hearing from most of my lecturers and reading in other books. Was adaptation mainly for the benefit of species (the lecturers' view) or for the benefit of individuals (Fisher's view)? Clearly it was Fisher who had thought out his Darwinism properly; where interpretations differed, therefore, he must be right—but were the others *always* wrong? I started on what seemed the key theme in this puzzle—*altruism*. Did it exist? Could one evolve it in a model?

What had been a distraction in undergraduate days became, in 1960, a problem of funds and survival once I had my BA. Most whom I consulted could not see that a problem existed; those that could see something averred that what little was worth saying about it had certainly all been said by J.B.S. Haldane, although none could tell me where. That both Haldane and Fisher had said things, albeit few and special, was true, as I saw later after a lot of reading.

I found some interest in my ideas, surprisingly, at the London School of Economics (LSE) and an oppor-tunity there for graduate study. Isolation and disinterest in my theme continued, however, in spite of additional enrollment at University College, London, after I had begun to be too genetical for LSE.

And as I look back, the attack that I began on deriving a general measure of relatedness was indeed extremely circuitous and ill conceived. I even delved into anthropological literature in the hope of seeing from the way people actually behaved some hint of the quantitative measure that I needed. All this led nowhere. It would have been sensible, at some point, to have asked Fisher (whose department I had trained in) for rays of guidance, but I hated to expose my evident naivety in writing. Fisher had retired a few years back and was working (and, in 1962, dying) in Australia; Haldane was in India and also was soon to die.

All I wanted was a measure of relationship that would enable me to generalise from the case of altruism to sibs that I had already worked out. Invariance that had appeared in the criterion for altruism with respect to gene frequency in the case of sibs had seemed a gift from God, and I did not expect to see it repeated in the more complex trial cases I had moved on to. So it was with joy and almost with incredulity that I at last found emerging out of acres of my tedious and usually wrong algebra for the case of uncles, and then for the case of cousins, the same invariance as I had found before. Shortly after this I saw how I could generalise still further and could invoke (slightly incorrectly, as I and others saw later[2]) Sewall Wright's Coefficient of Relationship for my measure. Finally, I saw how I could formulate a new concept of biological fitness—*inclusive fitness*—that would serve as a guide to reasoning in social situations.

My manuscript had a rather slow passage with the *Journal of Theoretical Biology (JTB)*, largely because of the many biological applications that I wanted to include to illustrate the idea's usefulness. Realising that it was going to take a long time to get it through, I wrote the shorter paper. I had an urgent need to get something published because I had given up on the idea of getting a PhD out of my work and needed some published achievement to back my hunt for further research opportunities. An editor's acceptance would also encourage me personally because of my main fear about my work: that I was simply a crank.

At its first submission, to *Nature*, my short paper was rejected by return of post (possibly my address, "Department of Sociology, LSE," weighed against it), but then, on the next attempt, it was accepted by *American Naturalist*. Shortly, I learned that the long manuscript would be accepted by *JTB* subject to rearranging and writing as two; this slowed it because the rewriting had to be done in the midst of a trip to Brazil that I had arranged to try to check some of the predictions arising from the ideas. In the end the first part had the math and the second the biological discussion,[3] including that of the evolution of kin recognition, which is one of the growth areas for citations today.[4]

1. Hamilton W D. The evolution of altruistic behavior. *Amer. Naturalist* 7:354-6, 1963. (Cited 140 times.)
2. Grafen A. A geometric view of relatedness. *Oxford Surv. Evol. Biol.* 2:28-89, 1985. (Cited 5 times.)
3. Hamilton W D. The genetical evolution of social behaviour. II. *J. Theor. Biol.* 7:17-52, 1964. (Cited 315 times.)
4. Fletcher D J C & Michener C D, eds. *Kin recognition in animals.* Chichester, England: Wiley, 1987. 465 p.