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**INCLUSIVE FITNESS AND THE SOCIOBIOLOGY OF  
THE GENOME**

by Herbert Gintis

Inclusive fitness theory provides conditions for the evolutionary success of a gene. These conditions ensure that the gene is selfish in the sense of Dawkins (1976): genes do not and cannot sacrifice their own fitness on behalf of the reproductive population. Therefore, while natural selection explains the appearance of design in the living world (Dawkins 1996), inclusive fitness theory does not explain how. Indeed, Hamilton's rule is equally compatible with the evolutionary success of prosocial altruistic genes and antisocial predatory genes, whereas only the former, which account for the appearance of design, predominate in successful organisms.

Inclusive fitness theory, however, permits a formulation of the central problem of sociobiology in a particularly poignant form: how do interactions among loci induce utterly selfish genes to collaborate, or to predispose their carriers to collaborate, in promoting the fitness of their carriers? Inclusive fitness theory because it abstracts from synergistic interactions among loci, does not answer this question.

Fitness-enhancing collaboration among loci in the genome of a reproductive population requires suppressing alleles that decrease, and promoting alleles that increase the fitness of its carriers. Suppression and promotion are effected by regulatory networks of genes, each of which is itself utterly selfish. This implies that genes, and a fortiori individuals in a social species, do not maximize inclusive fitness but rather interact strategically in complex ways. It is the task of sociobiology to model these complex interactions.