



# **The SAGE Encyclopedia of Theory in Psychology**

**Hamilton, W. D.**

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William Donald (“Bill”) Hamilton (1936–2000) was an English biologist who is best known for his theory of *inclusive fitness*, which formalized how natural selection acts on traits that are “social” in the sense that they have effects on other parties besides the trait-bearing individuals themselves. The theory, which constituted Hamilton’s PhD thesis at the University of London, has been of great interest to psychologists and other social scientists trying to integrate their fields with biological understandings of social evolution. This entry reviews Hamilton’s theory of inclusive fitness and its contribution to the field of psychology.

### Inclusive Fitness Theory

In evolutionary biology, the Darwinian “fitness” of an individual or a trait refers to its intrinsic capacity to increase its representation in subsequent generations. It is thus the quantity that natural selection tends to maximize, and every evolved trait should, in principle, be explicable in terms of its contributions to the fitness of those with the trait.

Since Charles Darwin, biologists had equated fitness with personal reproduction: The attributes that enable individuals to produce the most descendants are obviously the attributes that will come to prevail numerically. However, as Darwin himself realized, this interpretation of natural selection could not readily explain cases in which animals apparently fail to maximize reproduction, helping others instead. Most female ants, for example, work to help their “queen” reproduce, and never lay an egg of their own. This is an extreme example, but helping others at some potential cost to oneself is common, and all forms of costly help raise the same theoretical “problem of altruism”: How can such behavior arise and persist in creatures shaped by natural selection?

In 1964, Hamilton solved this conundrum by recognizing that selection favors social action that facilitates the replication of the actor’s particular genes, regardless of whether those genetic replicas reside in the actor’s descendants or in other kin. Fitness must therefore be defined more inclusively, to encompass not only effects on reproduction but also “nepotistic” effects on other relatives, who have an above-average probability of carrying copies of the actor’s genes. More specifically, according to “Hamilton’s rule,” altruistic action that imposes a cost ( $c$ ) on the actor’s expected reproduction can nevertheless increase under natural selection if  $rb > c$ , where  $r$  is a measure of the genetic relatedness of the actor to a beneficiary of his or her action, and  $b$  is the expected reproductive benefit that the latter gains thereby. (Another common name for inclusive fitness theory is *kin selection*, but this term has engendered confusion, particularly with respect to whether “kin selection” parallels “natural selection” in referring to an evolutionary process or instead refers to the nepotistic discrimination that is an expected consequence of that evolutionary process.)

Most contemporary students of animal behavior consider Hamilton’s theory the cornerstone of understanding how social behavior evolves. So do evolutionary psychologists who have used the theory to predict, explain, and further explore the circumstances under which people help or harm one another.

### Other Contributions of Relevance to Psychology

Social evolution remained a focus of Hamilton’s work after 1964, and three of his subsequent theoretical contributions have particular relevance for psychologists.

Why do parents sometimes invest resources inequitably between daughters and sons?

Assume that the sexes garner equal shares of the parenthood of future generations. If either sex chronically received less parental investment (PI) in total, that sex would provide more long-term fitness per unit of PI and thus be less costly. This would create selection pressure for parents to reallocate more resources to the better investment, thus driving the sex ratio of investment back to unity. By this reasoning, the only “evolutionarily stable” parental strategy is equal investment in daughters and sons, and this was the prevailing theory. But in 1967, Hamilton described cases in nature where PI in the two sexes remains highly unequal and explained them as resulting from the fact that the marginal fitness gains from incremental investment may differ between the sexes. This insight paved the way for the influential theory of Robert Trivers, explaining why preference for sons is sometimes correlated with rank or status, and for much further work on discriminative PI in humans, mainly by anthropologists.

In another highly influential paper in 1981, Robert Axelrod and Hamilton outlined conditions that provide an escape from the social trap of a “Prisoner’s Dilemma.” In this game’s theoretical paradigm, mutually beneficial cooperation can be thwarted by individual incentives to defect, but Axelrod and Hamilton’s analysis showed that cooperative play can be stabilized when interactions with familiar acquaintances recur with no predictable end point and when defection is then punished. Much theoretical and empirical work has built on their insights.

In the 1970s, the idea that mate choice can evolve to recruit “good genes” for one’s offspring was rejected by most biologists, on the grounds that “good genes” would soon become universal, obviating selection for choosiness. In 1982, Hamilton and Marlene Zuk proposed, however, that the coevolution of parasites and their hosts could maintain the genetic benefits of mate choice because the particular genes that promote health would vary over generations. This theory launched another fruitful field of research.

For these and other accomplishments, Hamilton has often been called the most important evolutionary theorist since Darwin. For a fuller account of his career, contributions, and eccentricities, see Alan Grafen’s 2004 article in the *Biographical Memoirs of Fellows of the Royal Society of London*.

**See also** [Close Relationships](#); [Cooperation](#); [Culture and Social Relations](#); [Evolutionary Psychological Perspectives on Human Nature](#); [Critical Evaluation of](#); [Human Nature](#); [Mating Strategy Evolution and Development](#); [Natural Selection](#); [Parent-Offspring Relations](#)

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### Further Readings

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