# Fisher's Reproductive Value

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## Definition

The expected contribution of genes made by an individual or class to generations in the distant future

Natural selection is driven by differences in individual reproductive success, but a simple count of the number of children that individuals produce is often insufficient to describe their Darwinian fitness. For example, in a well-mixed population with a female-biased sex ratio, a mother who produces only sons will tend to have more grandchildren than will a mother who instead produces an equal number of daughters. And simply counting the number of grandchildren may also be insufficient, as these too may differ in their quality in terms of how many children they will have. R. A. Fisher's theory of reproductive value resolves this conundrum by defining the fitness of individuals – or whole classes of individuals – in terms of their expected contribution of genes to generations in the distant future. This concept has broad application within Darwinian evolution and is particularly crucial for the understanding of social evolution.

An individual's reproductive value can be defined recursively, in terms of her share (typically one half, in a diploid population) of her children's aggregate reproductive value, with each child's reproductive value being their own share of their own children's aggregate reproductive value, and so on. Although this might appear to lead to an unresolvable infinite regress, reproductive value can be readily calculating using elementary linear algebra. Indeed, the mathematics of reproductive value directly mirrors that of Google's hugely successful *PageRank* algorithm, which quantifies the importance of a webpage on the Internet according to the aggregate importance of all the webpages that link to it (Fig. 1). Whereas *PageRank* is the relative probability that an Internet surfer who clicks on links entirely at random will, after some large amount of time, find themselves browsing a particular webpage, reproductive value is the relative probability that a gene chosen at random from the distant future will trace its ancestry to a particular individual or class in the present generation.

Fisher first introduced the concept of reproductive value in relation to age-structured populations, in the prelude to his derivation of the "fundamental theorem of natural selection" (Fisher 1930). The problem here is that while Fisher defined natural selection in terms of systematic change in the genetic constitution of a population, there are systematic changes associated with other factors, such as age. For instance, a neutral allele that is found only in post-
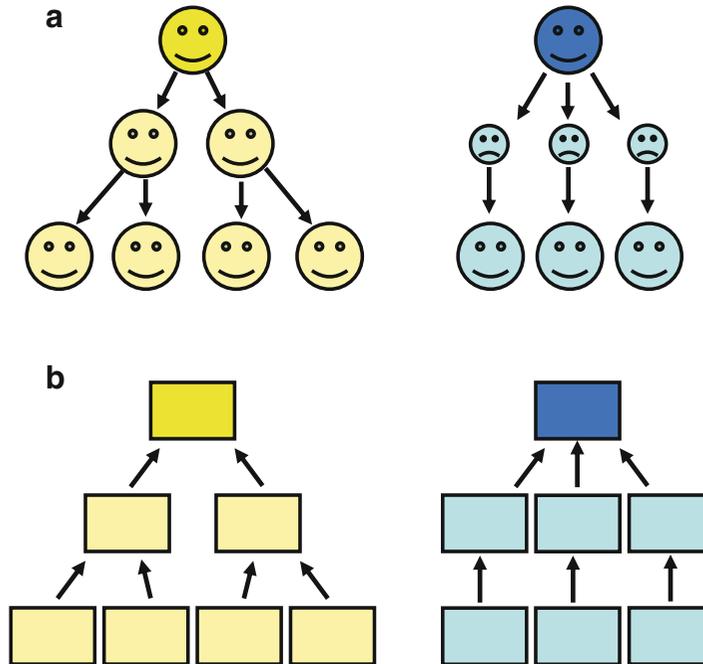
**Fisher's Reproductive Value, Fig. 1** Fisher's reproductive value and Google's *PageRank*. (**a**) Offspring number is not a good measure of Darwinian fitness, because offspring can vary in quality. Reproductive value provides a better measure, because it also describes the success of these offspring, the success of their offspring, and so on down the generations. The yellow individual has only two offspring, but these are of high quality, each leaving two offspring of their own. The blue individual has three offspring, but these are of low quality, leaving one offspring each. Calculation of reproductive value requires that we know how successful these grandoffspring will be but, all else being equal, the yellow individual has the highest reproductive value, as she leaves the most descendents. (**b**) The number of links pointing to a webpage is not a good measure of that webpage's importance, because linking webpages can vary in their own importance. Google's *PageRank* – so-called because it was developed by Larry Page, rather than because it ranks webpages per se – provides a better measure of importance, because it also describes how many links point to these linking webpages and so on through the whole of the Internet. The yellow webpage is only linked twice, but these are from important webpages that are also linked twice. The blue webpage is linked three times, but these are from unimportant webpages, each linked only once. Calculation of *PageRank* requires that we know how the whole Internet is linked together (see Page et al. 1999 for details) but, all else being equal, the yellow webpage has the highest *PageRank*, as it is altogether more linked to by the rest of the Internet

reproductive individuals will inexorably decline in its per capita frequency until it is lost from the population, not through the action of natural selection but rather on account of that age class leaving no descendants. Accordingly, Fisher corrected for such class effects by defining the population frequency of an allele as a weighted sum of its frequencies within each of the age classes, with the class reproductive values providing the weights. This recovered Darwin's (1859) stipulation that natural selection increases the frequency of beneficial variants, decreases the frequency of deleterious variants, and does not alter the frequency of neutral variants.

In the context of his treatment of age structure, Fisher (1930) made some cryptic remarks as to the potential for natural selection to have molded the relationship between age and incidence of natural death, on account of it having greater power to improve survival at those ages at which reproductive value is greater. Fisher appears to have mistakenly focused on the reproductive value of the individual, rather than the whole age class, but this was rectified by Peter Medawar (1952), who developed the idea into a fuller evolutionary

theory of senescence. Medawar's account emphasized the tension between natural selection and recurrent deleterious mutation, with the decline of class reproductive value with age weakening natural selection's ability to purge the population of mutations contributing to death in older age. Medawar also suggested that genes responsible for senescence might actually be favored by natural selection, on account of possible pleiotropic increases in fertility manifesting earlier in life, with the decrease in class reproductive value with age making the fertility of the young relatively more evolutionarily important than the survival of the old.

Fisher (1930) next used the notion of reproductive value to great effect in explaining why there is usually equal investment of parental resources into sons and daughters, building and improving upon arguments put forward by Charles Darwin and Carl Düsing (West 2009). On account of the total reproductive value of all newborn females being equal to that of all newborn males then, in the event of any population imbalance in the investment into females versus males, a unit of parental investment into the underinvested sex will on average yield a higher return of reproductive value. Accordingly, Fisher argued that natural selection favors those parents who act to correct any imbalance in the population's sex allocation and will thereby restore the equal investment into sons versus daughters. This "rarer-sex effect" lies at the heart of a very large body of theoretical and empirical work on sex allocation (West 2009).

The application of reproductive value to sex allocation illustrates how it provides not only a measure of how different individuals are differently valued by natural selection but also how they are differently valued by each other. On account of reproductive value considerations, a mother is favored to invest more heavily into sons than daughters when males are the rarer sex. Another factor that influences the valuation that one individual places on another is their degree of genetic relatedness, which is central to the theory of kin selection. Hamilton (1972) first incorporated the mathematics of reproductive value into kin selection theory to illuminate the biology of social insects, whose colonies exhibit age, sex, caste, and ploidy forms of class structure, and the modern theory of kin selection puts relatedness and reproductive value on equal conceptual footing, recognizing both as fundamental measures of value (Frank 1998). This development has been essential in moving the explanatory domain of formal kin selection theory beyond simple interactions between generic, interchangeable individuals and enabling its application to real-world biological systems in all their complexity.

The other major approach to social evolution is the group selection or multilevel selection approach. In contrast to what has been done in relation to kin selection, there has been very little interest in reproductive value in the context of multilevel selection. Yet the concept of reproductive value resolves several of the conundrums that plague that literature (Gardner 2015). For example, a long-standing dispute concerns whether it is better to conceive of a group's fitness being equal to the number of daughter individuals it produces (the "collective fitness 1" approach) versus the number of daughter groups it produces (the "collective fitness 2" approach), with this decision leading to different fitness estimates when daughter groups can contain different numbers of daughter individuals, and hence ambiguity as to how group selection is supposed to operate and what phenotypes it actually favors (Okasha 2006). The theory of reproductive value provides a resolution, by recasting the fitness of the group as its expected genetic contribution to the distant future – which can be alternatively viewed as its share of the aggregate of the reproductive values of its daughter individuals or daughter groups, with both aggregates yielding the same total reproductive value (Gardner 2015).

## Conclusion

Fisher's notion of reproductive value is a fundamental concept in the study of Darwinian adaptation and is of particular importance to the study of social evolution in which fitness consequences of social behaviors for multiple parties must be rendered in the same universal currency if they are to be properly understood.

## Cross-References

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