Inclusive fitness

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Definition

Inclusive fitness is a method of measuring evolutionary success. It is the ability of an individual to transmit genes to the next generation, including genes shared with relatives. In accordance with this rule, an individual's inclusive fitness can depend, in part, on altruistic behavior and cooperation. The term *inclusive fitness* was introduced in 1964 by William Donald Hamilton, an English evolutionary biologist. Hamilton distinguishes two types of fitness: a) direct fitness, defined as the number of offspring produced directly by an individual, regardless of who rears, supports, or rescues the offspring, and b) indirect fitness, defined as the number of related individuals produced, multiplied by the degree of relatedness of those individuals. Inclusive fitness is defined as an individual's direct fitness plus an individual's indirect fitness.

In the above-mentioned definition, one offspring is defined as an individual's own child, which shares 50% the individual's genes, in sexually reproducing species. Following this logic, a sibling's child, which shares 25% of the individual's genes, is half an offspring equivalent, and a cousin's child, which shares 6% of the individual's genes, is an eighth of an offspring. From a gene-centered perspective, evolutionary success is achieved when a gene has a relatively high number of copies in the population. It can be achieved by producing one's own direct offspring, and/or by helping kin produce offspring.

Introduction

Hamilton's calculations showed that passing a gene to one's offspring is not the only way of successfully transmitting it to the population. Another way of transmitting copies of a gene is by promoting survival and reproduction of those sharing copies of the gene by descent. The latter process is called *kin selection theory*, or *inclusive fitness theory*, and it is a key mechanism affecting the evolution of social behavior. For example, yellow-bellied marmots put themselves in danger and attract a predator's attention by producing loud calls warning their social group (usually consisting of related individuals) about danger (Blumstein, Steinmetz, & Armitage, 1997). This seemingly counterproductive behavior has evolved because ensuring the survival of kin will increase an individual's overall, inclusive fitness.

Hamilton's rule

The introduction of the concept of inclusive fitness helped to explain the prevalence of behaviors often perceived as altruistic. Hamilton argued that supporting kin increases one's evolutionary success by the mechanism of inclusive fitness, not direct fitness. For example, in ground squirrels, calls warning others about approaching predators occur most frequently if relatives of the calling individual were around (Milius, 1998), in red squirrels, females adopt orphans only when they are related to them; adoptions were never observed for non-kin (Gorrell, McAdam, Coltman, Humphries, & Boutin, 2010), and in humans, when declaring willingness to help children, close relatives are preferred over distant relatives, and distant relatives are preferred over unrelated children (Antfolk, Karlsson, Söderlund, & Szala, 2017). That means that natural selection favors organisms behaving in a way that leads to increases in inclusive fitness, and also ensures that the helper's "altruistic" gene (or complex of genes) is more widely present in the next generation. Hamilton developed a simple formula ($c < rb$) for calculating whether a gene "for" altruistic behavior will become more widespread in the population. The formula calculates

whether the actor's reproductive costs incurred by displaying altruism is lower than the degree of relatedness times the reproductive benefit to the recipient. If it is, then it will be beneficial for the actor and, therefore, help in spreading the relevant gene(s) in a population.

Another concept important for understanding inclusive fitness is the *green-beard effect*, a thought experiment explaining selective altruism, a way of recognizing behaviors considered altruistic, expressed by unrelated individuals willing to provide support. The idea of the green-beard effect is that a gene or genes (i.e. those coding the hypothetical green beard) must produce a recognizable phenotype that is preferentially treated by individuals with the same gene.

Cross-References:
Genes
Altruism
William Donald Hamilton
Fitness
Population
Reproduction
Kin selection
Social behavior
Predator
Green Beard
Phenotype

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