Genetic Relatedness

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Synonyms

Coefficient of relatedness; Coefficient of relationship; Genetic relatedness; Relatedness coefficient; Relatedness parameter

Definition

The probability that an allele in one individual is also found in another individual.

Introduction

Relatedness is an important parameter in kin selection or more generally inclusive fitness theory. One significant puzzle in the history of evolutionary theorizing is the evolution of altruism. Kin selection, with the use of the relatedness parameter, often denoted by r, permits to solve this puzzle.

The Puzzle of Altruism

A classical approach to natural selection tells us that only traits which confer a heritable fitness (reproductive) advantage to their bearer will evolve by natural selection. For instance, suppose a population of organisms which vary in height and in which the taller an organism is the higher its reproductive output. We could imagine that the organisms are giraffes and that giraffes which are taller have access to leaves on the top of trees while smaller giraffes do not. Because of this access to more resources, taller giraffes can produce more offspring than smaller ones. If taller giraffes produce taller offspring, everything else being equal, so that height is heritable, then tallness will evolve by natural selection. Under this picture of evolution by natural selection, following the three conditions of variation, difference in fitness, and heritability (Lewontin 1970), only traits that are beneficial to the individual bearer of these traits can evolve by natural selection.

Following this Darwinian scheme, we should thus expect to see only traits that confer a fitness advantage to their bearer in nature, since every time a mutation conferring a disadvantage emerges in the population it should be eliminated by natural selection (assuming what is known as genetic drift can be ignored). Thus, in our example, we should not expect giraffes to get smaller over time on average, because small giraffes have a lower probability to reproduce than tall giraffes. Although this Darwinian scheme seems

impeccable, it is contradicted by empirical evidence: everywhere one looks, one finds traits costly to the individual. Think about the ultimate sacrifice of a worker in an ant colony. The worker defends the colony, takes care of the offspring produced by the queen, or gathers food, and yet it never has the chance to reproduce; only the queen does. Ants and termites, for which the reproductive activity of the colony is typically carried by a single female, have been estimated to represent only 2% of the total number of species of insects. Yet, their biomass is estimated to represent more than a quarter of the total animal biomass (Wilson 1990). Eusocial insects are evolutionary very successful despite contradicting the classical scheme for Darwinian evolution.

Solving the Puzzle

As described by Dawkins (1976), one solution to the problem of altruism proposed by some biologists has been to say that, although a costly trait does not provide any advantage to the individual that bears it, it nevertheless provides an advantage to its group or species. In fact, if workers suddenly stopped defending the hive, taking care of the larvae, or bringing food, the colony would soon disappear. But this explanation faces the problem that any worker unwilling to pay the reproductive cost paid by other workers would get an evolutionary advantage over individuals paying the cost. In fact, following this logic, a worker deciding to reproduce instead of paying the cost of gathering food, taking care of the larvae or defending the nest, would soon produce workers like it with the same properties, all of which would have a (short term) evolutionary advantage over sterile workers. Thus, the "good of the group" proposal cannot be the whole story, for, following its rationale, groups would irremediably be subverted by selfish individuals.

William Hamilton (1936–2000) was the first one to give a formal solution to the problem of altruism without relying on a form of the good of the group argument (Hamilton 1963, 1964a, b). His solution is reductionist in that it requires taking the perspective of a gene borne by an individual, also known as the "gene's eye view," which was made famous by George Williams's *Natural Selection and Adaptation* (1966) and even more so by Richard Dawkins' *The Selfish Gene* (1976). Before Hamilton, some evolutionists, including J. S. B. Haldane and Darwin himself, seem to have gestured to the same solution to the puzzle of altruism, but not as rigorously as Hamilton did.

Hamilton's solution to the problem of altruism is that an allele incurring a fitness cost to its bearer can be compensated for if another individual with the same allele receives a benefit from the first individual which is equal or superior to the cost that it incurred. For instance, suppose an individual "actor" with an allele **A** helps another individual "recipient" with the same allele by providing the recipient with some resources. In doing so the actor pays a cost in terms of offspring it can produce. It is altruistic. We could imagine that without helping the recipient, the actor would produce three offspring while if it helps the recipient it can only produces two offspring. We could further suppose that the recipient, without any help from the actor, would be unable to produce any offspring, but produce two offspring when it receives some help. In this setting, if we compare the number of **A** alleles present in the offspring population when the actor helps the recipient to the situation in which it does not, the outcome will be four offspring (each with a single copy of the **A** allele) rather than three, respectively. Even though the actor produces fewer offspring when it helps the recipient, it is evolutionarily advantageous from the point of view of allele **A** that the actor helps the recipient. Helping the recipient will, after all, permit an increase in the number of copies of **A** when compared to the situation in which no help is provided. More formally, because the benefit obtained by the recipient "b" is higher than the cost "c" incurred by the actor – so that $b - c > 0$ – the altruistic behavior, if it is heritable, can evolve (i.e., successfully "invade" the population).

Although this reasoning provides a solution to the problem of altruism, there is a complication. We assumed in the example that the recipient has allele **A** with certainty. Yet, from the point of view

of the actor, there is typically no guarantee that the recipient has allele **A**. Suppose that the actor helps the recipient, yet the recipient does not have allele **A**. In such a case, being altruistic is evolutionary disadvantageous since the *guaranteed* number of copies of **A** in the offspring generation is, then, two rather than three.

The coefficient of relatedness r measures the probability from the point of view of the actor with a given allele (say **A**) that the recipient also has this allele. The more technical definition of r is slightly different since it takes into account the average probability of sharing an allele in the population, but this need not to concern us here (for details see Bourke 2011, p. 31). The reason r stands for "relatedness" is that one common cause of having a copy of the same allele is being related by descent, as in actors and recipients belonging to the same family. But the modern understanding of r is more general than that as we will see below.

Using r in Hamilton's Rule

For a population in which social interaction is dictated by family structure, it can be evolutionarily advantageous to be an altruist. Whether it is evolutionarily advantageous from the point of a view of an allele not only depends on the cost of the actor and benefit of the recipient, as we saw earlier, but also on the probability that the recipient receiving the benefit bears the same allele as the actor which is measured by r. Modifying the rule for the evolution of altruism given earlier ($b - c > 0$) by considering relatedness, we obtain $rb - c > 0$, which is known as "Hamilton's rule."

If we take our going example and assume that the actor and the recipient are full siblings, then because the benefit obtained by the recipient is two offspring and the relatedness is 0.5, it is not more advantageous, from the point of view of allele **A**, for the actor to help the recipient. In fact, in both cases, on average, the number of copies of **A** at the offspring generation will be 3. We have $rb - c = 0$

since $0.5 \times 2 - 1 = 0$. In a different situation in which the cost of one offspring paid by the actor would lead to a benefit of three offspring for the recipient (a full sibling), the altruistic behavior could evolve. In fact, we have $rb - c > 0$ since $0.5 \times 3 - 1 = 0.5$. With the actor and the recipient being first cousins, altruism is however disadvantageous. In fact, assuming the previous cost of one offspring for the actor but a benefit of three offspring for the recipient, because r is now 0.125 instead of 0.5, we have $rb - c < 0$ ($0.125 \times 3 - 1 = -0.625$).

Although a classical context in which relatedness plays a role is family, this is not the only one. It has been imagined that individuals with the same allele could recognize one another even without being related. This is known as the "green-beard effect" (Dawkins 1976; Gardner and West 2010). Even though empirically, "greenbeards" seem to be limited to a small number of cases and mostly not relevant for human evolution (Gardner and West 2010), their possibility shows that relatedness, following its most general definition, does not solely measure the extent to which individuals socially interacting are related by descent. It is much more general than that. Note also that it does not require recognition between individuals. Individuals might be altruistic towards one another because they live in the same place rather than because they know they are siblings. All these subtleties mean that despite the simplicity of Hamilton's rule, relatedness is a concept one should manipulate with care.

Conclusion

Relatedness is an important concept in evolutionary theory. Embedded within inclusive fitness theory, it extends a solution to one of the most important puzzles in evolutionary theory, namely, the evolution of altruism. Together with reciprocal altruism proposed by Trivers (1971), inclusive fitness theory is one of several evolutionary mechanisms for explaining the formidable level of cooperation in humans.

Cross-References

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