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Cooperation Varies with Genetic Relatedness

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Synonyms

Altruism; Assortment; Inclusive fitness; Kin discrimination; Kin recognition; Kin selection

Definition

A prediction from Hamilton's rule that altruism is more likely the more related the beneficiary is to the actor/donor. Here we briefly discuss the theoretical reasoning and focus on the empirical support for this prediction in humans.

Introduction

In the most general sense, cooperation occurs when one individual helps another. In evolutionary terms, helping means increasing the lifetime reproductive success of another individual. Genes are selected to produce behaviors that tend to increase their frequency in the population. They can do this via two routes, by inducing behaviors that increase either the reproductive success of their bearer (direct fitness), or the reproductive success of other individuals that tend to carry the same gene (indirect fitness). Hamilton realized this and that therefore natural selection, operating on genes, will lead to individuals that appear designed to maximize the sum of their direct and indirect fitness. Consequently, helping behaviors can evolve when helpers receiver personal benefits in return that surpass their initial costs (increasing their direct fitness), e.g., through exchaning favors (reciprocity). Helping behaviors can also evolve even if helpers never receive any benefits, providing they direct their help toward other individuals that tend to carry the same helping gene (altruism, increasing indirect fitness). The easiest way to help individuals that tend to carry the same helping gene is to help close genealogical relatives, and therefore kin can be selected to cooperate altruistically (Kurzban et al. 2015).

Whether a helping behavior between kin will be favored by natural selection depends on three things: the costs to the actor/donor (in terms of reduced lifetime reproductive success), the benefits to the recipient (in terms of increased), and the probability that the recipient carries the same helping gene. In evolutionary terms, the probability that the recipient carries the same gene for helping at the same locus is termed Relatedness. Relatedness is a statistical coefficient genetic describing the similarity between the actor and recipient, relative to the rest of the population (see entry for 'R = Coefficient of Relatedness).

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The relationship between these three terms is defined by Hamilton's rule, where C < Rb, which means the benefits have to be greater than the costs, even when discounted by relatedness. Therefore, the more related the recipient is, the more costly the helping behavior can be and still be favored. Hamilton's rule leads to the prediction that cooperation will occur more often between closer relatives than distant relatives. Studies of how human cooperation varies with relatedness typically, for convenience, estimate relatedness on a scale from 0 to 1 by calculating the coefficient of relationship between two individuals, e.g., siblings are related by 0.5. Not that this estimate does not incorporate factors such as inbreeding (see entry for 'R = Coefficient of Relatedness).

Empirical Challenges

Although Hamilton's rule is supported in nonhuman studies, ethical considerations make it difficult to test experimentally in humans. Therefore human studies are often observational or survey based, and/or typically concern low-cost behaviors. This can be problematic because low-cost behaviors can be under less natural selection pressure, can be favored toward close and distant kin, and can be favored between nonkin for direct benefits (e.g., reputation). Strong tests of Hamilton's rule compare how cooperation varies with the degree of relatedness. Weaker tests only ask if humans cooperate more with kin than nonkin. Although how much people should discriminate between close and distant kin will depend on the costs and benefits and the cues of relatedness available. Note that studies which only measure cooperation toward nonrelatives do not invalidate Hamilton's rule, because they are unable to test the relative importance of Hamilton's rule. Indirect support comes from studies that show a psychological mechanism for recognizing kin, although this mechanism can also result from incest avoidance (Lieberman et al. 2007).

Survey Data

Survey responses, either on line or in the laboratory, often show that individuals expect to be more cooperative toward closer kin (Burnstein et al. 1994; Korchmaros and Kenny 2001; Stewart-Williams 2007), or expect to receive more cooperation from closer kin (Burton-Chellew and Dunbar 2015). For instance they report that they are more likely to donate a kidney to closer kin, although the effect sizes are modest (Stewart-Williams 2007). Burton-Chellew and Dunbar (2015) showed that individuals reported they *expected to receive* more help from closer kin than distant kin in times of crisis. While people still respond that they would help nonrelatives, mostly best friends, the key finding is that cooperation is increased toward close kin in support of evolutionary theory. Complementary data comes from studies that investigate the proximate, psychological, mechanisms governing these behaviors, and they typically show that feelings of "emotional closeness" are an important mediator of helping behaviors (Korchmaros and Kenny 2001).

Observational Data

Survey data has its limitations because the costs may never be realized. An analysis of real helping behaviors came from Smith et al. (1987) who analyzed patterns of giving by relatedness in 1000 wills. They found that when individuals made their wills, they allocated a greater proportion to their closer relatives. Specifically they gave 46% to close relatives (r = 0.5), and just 8% when r = 0.25 and 1% when r = 0.125. However as these transfers occur after death it could be argued they are noncostly. Another prominent nonexperimental study on real costs in real time was by Bowles and Posel (2005). They analyzed how much money male migrant workers sent "home" (remittances) and how this varied with the relatedness of the recipient to the migrant worker. Overall, they found that including relatedness in the model improved the model's accuracy to predict the value of remittances, although other factors were important too. Likewise, many observational studies tend to find mixed support

for the role of relatedness and other factors such as reciprocity in explaining human cooperation, but as explained above, cooperation can be explained by both direct and indirect benefits. The key prediction is that because indirect benefits vary with degree of relatedness, cooperation is greater or more likely with closer relatives.

Experimental Data

Perhaps the first experimental test of how cooperation varies with relatedness in humans was by Madsen et al. (2007). Across three crosscultural studies, participants were asked to adopt a painful posture (an isometric skiing exercise) in exchange for monetary benefits that went to their various relatives. Control treatments included benefits that went to themselves, nonrelatives, and charities. The posture involved supporting one's weight in a way that worked the thigh muscles and rapidly became intensely painful (after ~60 s). The pain may signal muscle damage and thus may indicate a genuine cost in evolutionary terms. A willingness to endure pain on behalf of relatives may also translate into a willingness to pay genuine costs. The longer the participant maintained the posture (cooperated), the more money their relatives got. The results were generally supportive. Cooperation did vary positively with relatedness, although in one study this arguably required including the control measure of help toward oneself, where relatedness = 1, and there were potential sex differences.

Other Factors

Finally, the indirect benefits of helping relatives also depend on other factors that ideally need to be controlled for. First, the indirect benefits of helping a recipient will be greater when they stand to gain more. This will occur when they have a higher probability of future reproduction (more reproductive value), i.e., generally when they are younger, because the help is more likely to lead to increased reproduction. In both the studies of Madsen et al. and Smith et al., the results were more in line with theory once the reproductive value of the recipients was controlled for (Madsen et al. 2007; Smith et al. 1987). Second, competition occurs at different scales in populations, and relatives often have to compete, decreasing the benefits of kin-directed altruism. This is because helping one relative merely helps them to outcompete another relative, reducing the net gain (Borgerhoff Mulder 2007).

Conclusion

Studies generally find that very costly cooperation is greater toward kin than nonkin, which provides a weak test of Hamilton's rule. More studies are needed that directly test if and how individuals differentiate between close and distant kin.

Cross-References

- Altruism
- $C < Rb$
- Full Siblings Vs. Half Siblings
- Genetic Relatedness
- Hamilton's Rule and Theoretical Implications
- Manipulative Use Of Kin Terminology

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