



THE CONTROVERSY OF GROUP SELECTION THEORY

By Momoko Price

Though Darwin's original theory of evolution and natural selection stresses the role of selective forces acting on individuals of varying fitness, group-oriented 'altruistic' behaviours within the animal kingdom, such as worker castes in social insects and alarm cries in bird flocks, have been documented repeatedly which at a glance appear to completely contradict traditional evolutionary theory (Williams, 1971). They pose a challenge to evolutionary biologists, because the theory of natural selection in its simplest form favours selfish individual behaviours over altruistic ones: Individuals who invest the most effort into their own reproduction and survival should leave the most offspring and therefore have the greatest success of passing on their genes over other competing individuals. *Group selection theory* was originally postulated to account for behaviours observed in both human and animal societies that appear to benefit the group, even when it results in poor individual fitness.

The theory of group selection states that selective forces can in fact act on competing groups of individuals, not just competing individuals (Thompson, 2000). Behaviours theoretically arise which contribute to the persistence of a group of individuals over time, though the individual expressing the behaviour may suffer lower fitness relative to other group members. Historically, many biologists (including Darwin himself) recognized this as a problem (Ruse, 2002), because it seems obvious that those who do not suffer the individual negative fitness effects of altruism will eventually out-compete the lone wolf who decides to "act for the good of the group". It follows logically that altruistic traits could never fix in a population (or if they did, could be easily overtaken by invading selfish traits). However, inflexible support of this logic never managed to account for the evolution of many unusual, less-than-selfish behaviours observed in nature, including phenomena as widespread and persistent as sexual reproduction (since gene-shuffling with an unrelated individual would be tantamount to throwing away half your genes in favour of someone else's). The ongoing battle to resolve group selection theory with traditional theories of natural selection has inspired evolutionary biologists to look beyond selection acting solely at the individual level and begin investigating how selective forces can act at multiple levels of biological organization, resulting in the possibility of counter-intuitive interactions between populations, individuals, and genes.

A controversial issue often attacked when discussing group selection is the mechanism of inheritance: if the 'altruistic' individuals eventually die out due to lower fitness, how can the altruistic trait continue to persist? W.D Hamilton was the first to address this issue, and he created a model whose central theme was this: the cost of any 'altruistic' trait expressed by an individual against itself must be smaller than its beneficial effect on another individual in the group, an effect better conserved by a high level of relatedness between the two individuals. Mathematically this idea is expressed as:

$$rb > c$$

where r is the proportion of shared genes between the individuals;
 b is the benefit to the recipient, and
 c is the cost to the altruistic individual.

Hamilton's Rule as it is now known, became the basis of *kin selection* or *inclusive fitness*, a theory which claims that seemingly altruistic traits that benefit others continue to be passed on in spite of lower individual fitness (in terms of survival and reproduction) by the shared genes between individuals of varying levels of relatedness (Hamilton, 1964). An 'altruistic' individual's genes can continue to be represented in future generations through the reproduction of non-offspring relatives, which benefit from the altruistic individual's sacrifice.

Kin selection theory seems quite intuitive once one realizes that brothers, sisters, parents and offspring of a central individual all share the same proportion of genes (0.5). If it seems natural for parents to protect their young, according to kin selection it is just as plausible for an individual to protect the same number of brothers or sisters or a proportionally larger number of increasingly distant relatives. But this begs the question of whether or

not this is, in fact, truly group selection. According to Hamilton's rule, relatedness towards an 'altruistic' individual still plays a role in driving selection on the group. Though the direct reproduction of this individual's genes may be somewhat crippled through its lower individual fitness, it is still investing effort into the inheritance of its genes through alternative lineages.

So is it possible for selective forces to favour traits that benefit the group if members are unrelated? Evolutionary biologist D.S. Wilson argued that it is indeed possible, so long as certain group-structuring conditions are met: the global population must be divided into temporarily isolated but periodically interacting subgroups with varying compositions of one or more group-selected traits – subgroups which he called *trait-groups*. According to his model (Wilson, 1975), because individuals expressing the group trait can confer benefits to the preservation an entire subgroup, though perhaps to the detriment of its own personal fitness, the overall preserving effect of this trait on the subgroup (regardless of the relatedness of its members) can in effect drive selection in favour of the trait at the global population level– in other words, though it may appear at the subgroup level that the trait confers lower fitness, due to population structuring effects the absolute proportion of the trait is actually increasing over time.

But again, the question arises: is this truly 'group selection'? It seems that no matter how one tries to interpret it, at the centre of it all, the overall frequency of a supposed 'altruistic' allele or trait must increase or stabilize over time for it to persist (and therefore must have competitive overall fitness), regardless of the array of alternative mechanisms by which this can occur. Though original Darwinian natural selection theory, due at least in part to the constraints of human perspective and the comparably limited understanding of biology of the time, stressed selection acting on the 'individual', it has become more and more apparent since the works of Mendel that the real target of selection is neither the 'individual' nor the 'group', (essentially human abstractions that are never truly passed from generation to generation), but genes and alleles themselves.

The debate among biologists on the legitimacy of group selection theory continues unabated today, (Wilson, 2005 and Foster et al., 2005), and the ongoing struggle to resolve interpretations of how selection acts at the 'organismal' or 'superorganismal' (or even cellular or molecular) level is certain to challenge the limits of human perspective for a long time to come. This struggle to find a resolution, a seamlessly 'unified' selection theory that bridges the gap from the smallest nucleic acid to the largest populations, is essentially at the heart of smaller controversial issues like group selection, and is part of the reason why these heated topics have persisted since Darwin started it all.

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