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Weak altruism, strong group selection

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Throughout its history, the group selection controversy has been dominated by two major themes. The first involves the selection of groups in a metapopulation as a process analogous to the selection of individuals within single groups. The second involves altruistic behaviors that benefit others at the expense of the individual actor. Usually it is assumed that the two themes are fully compatible and that altruistic behaviors are the primary outcome of group selection. In this essay I point out some inconsistencies between the two themes. I also show that, by following the first theme to its natural conclusions, it is reasonable to expect strong group selection to operate in random associations, without any genetic relatedness among group members.

The theme of altruism

Evolutionists define altruism as any trait that increases the fitness of others at the expense of the actor's fitness. The simplest model of altruism posits two haploid types, *A* and *S*, in a group of size N and in frequencies p and (1−p) respectively (Wilson 1975, 1980). Altruistic *A*-types exhibit a behavior that has an effect d on themselves and an effect r on all others in the group. The absolute fitness of *A* and *S* types are then:

$$W_A = Z + d + (Np\text{-}1)r \tag{1}$$

$$W_S = Z + Npr \tag{2}$$

Both types have a baseline fitness of Z. Each *A*-type receives the effect of its own behavior and also is recipient for the (Np-1) other *A*-types in the group. *S*-types do not exhibit the behavior and are recipients for all Np *A*-types. The *A*-types increase in frequency within the group whenever $W_A > W_S$, which reduces to the inequality $d > r$.

This inequality reveals an ambiguity in the verbal definition of altruism. Do the words "increase" and "expense" refer to *relative* fitness within the group or to the *absolute* fitness of the donor and recipient? In the former case, a positive effect on self ($d>0$) can be altruistic if the effects on others are even greater ($r>d$). In the latter case, the effect on self must be negative ($d<0$) to count as altruistic. To distinguish between these definitions, Wilson (1979, 1980) coined the terms *weak altruism* and *strong altruism*.

It is obvious from (1) and (2) that both weak altruism and strong altruism are selected against in single groups. When many groups are considered in a metapopulation model, however, altruism can evolve because relatively altruistic groups contribute more to the global population than do relatively selfish groups. The conditions for the *A*-type to spread in one kind of metapopulation (to be described in detail below) is:

$$d > r\left[-N\left(\frac{\sigma^2}{1-p} + \frac{\sigma^2}{p}\right) + 1\right] \tag{3}$$

where p is the frequency of *A* in the global population and σ^2 is the variance in p among groups (Wilson 1980). When $\sigma^2 = 0$ then (3) reverts to the conditions for selection within a single group ($d>r$). With random associations the types are binomially distributed into groups, $\sigma^2 = p(1-p)/N$, and inequality (3) simplifies to $d>0$. Thus, weak altruism ($r>d>0$) can evolve in random associations but strong altruism cannot. The evolution of strong altruism requires nonrandom associations of types, such that $\sigma^2 > p(1-p)/N$.

Although no one disputes the mathematics outlined above, some authors have argued that traits for which $d>0$ are not altruistic in any sense and certainly do not require the process of group selection for their evolution (Dawkins 1979, Grafen 1980, 1984, Maynard Smith 1982, Nunney 1985). For example, Grafen (1980) states

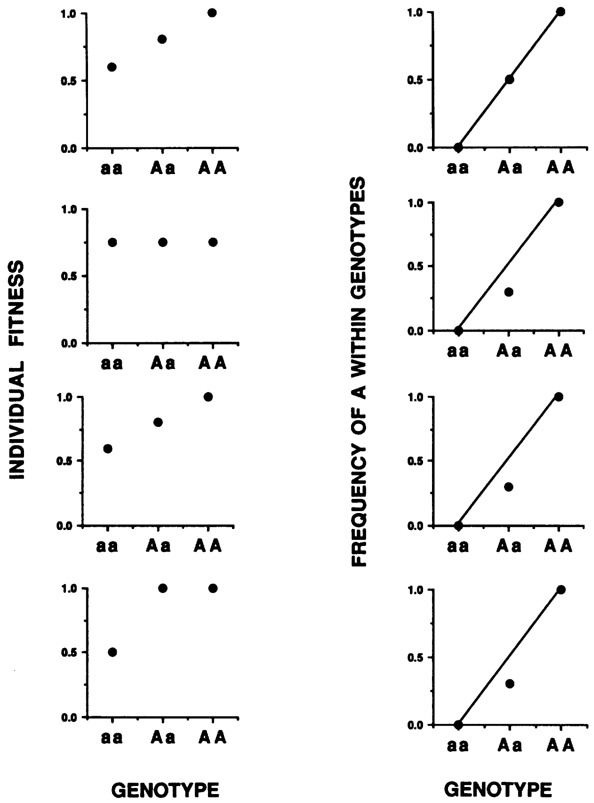

Fig. 1. Four examples of within- and between-individual selection. The left column shows the relative fitness (y-axis) of each genotype (x-axis) at a single diploid locus. The right column shows the frequency of the *A* allele (y-axis) within each genotype (x-axis) after within-individual selection. The genotypes can be thought of as groups of alleles in which the frequency of *A* prior to within-individual selection is 0, 0.5, and 1 respectively. Within-individual selection can occur only in genotypes that are polymorphic for the two alleles (i.e., heterozygotes) and favors the *a* allele when $g<0.5$ (below the 45° line). Row 1 shows directional between-individual selection for the *A* allele without opposing within-individual selection ($W_{aa}=0.6$, $W_{Aa}=0.08$, $W_{AA}=1.0$, $g=0.5$). Row 2 shows within-individual selection for the *a* allele without opposing between-individual selection ($W_{aa}=W_{Aa}=W_{AA}=0.75$, $g=0.3$). Row 3 shows a conflict between levels of selection in which the *a* allele evolves to fixation despite deleterious effects at the individual level, assuming Hardy-Weinberg equilibrium ($W_{aa}=0.6$, $W_{Aa}=0.08$, $W_{AA}=1.0$, $g=0.3$). Row 4 shows a conflict between levels of selection that results in a stable polymorphism ($W_{aa}=0.5$, $W_{Aa}=1$, $W_{AA}=1$, $g=0.3$).

that "the random groups case ... corresponds to the orthodox, individual selection model." These authors maintain that the process of group selection begins with above-random variance in p, allowing the evolution of traits that decrease the absolute fitness of the actor.

The theme of group selection as a process analogous to individual selection

Inequality (3) is derived from a metapopulation model with the following specific assumptions:

a) Many local groups of size N are formed from a global pool of dispersers composed of p *A*-types and (1−p) *S*-types. The expected frequency of *A* in local groups is p. The variance in p among groups depends on the details of colonization, but conforms to the binomial distribution for random associations.

b) Individuals interact within local groups according to Eqs (1) and (2). Absolute fitness depends on the number of *A*-types and therefore varies between groups as a function of local p-values. Interactions alter the frequency of *A* within groups and also alter the overall size of the group, relative to other groups.

c) After interacting, all individuals (or their descendants, if the groups persist for multiple generations) disperse back into the global pool. Global gene frequency change is determined by local gene frequencies after selection and the relative sizes of the groups.

d) The cycle of group formation, interactions within groups, and dispersal is repeated many times.

This model is termed "intrademic group selection (IGS)" because the groups are isolated only with respect to fitness-determining interactions and not with respect to gene flow (Wade 1978). The groups are often termed "trait groups" because they must be defined in reference to particular traits (Wilson 1975, 1977a,b, 1980).

Several authors have observed that the relationship between individuals and groups in IGS models is identical to the relationship between genes and individuals in standard diploid or polyploid population genetics models (Holt 1983, Maynard Smith 1987, Wilson and Sober 1988, Wilson 1989). In other words, single alleles in the gamete stage form into zygote "groups" during which fitness is determined, followed by dissociation back into a gametic pool. Genetic interactions can alter the frequency of alleles within zygotes (i.e., meiotic drive or selection of cytoplasmic elements) and also can alter the fitness of zygotes, relative to other zygotes (i.e., standard Darwinian selection). As Maynard Smith (1987: 124) put it, "individuals are merely temporary trait groups".

Because group selection has always been envisioned as a process analogous to individual selection, the point-for-point similarity between IGS models and population genetic models is instructive. Consider, for example, the question of whether group selection can operate among randomly composed groups. The overwhelming

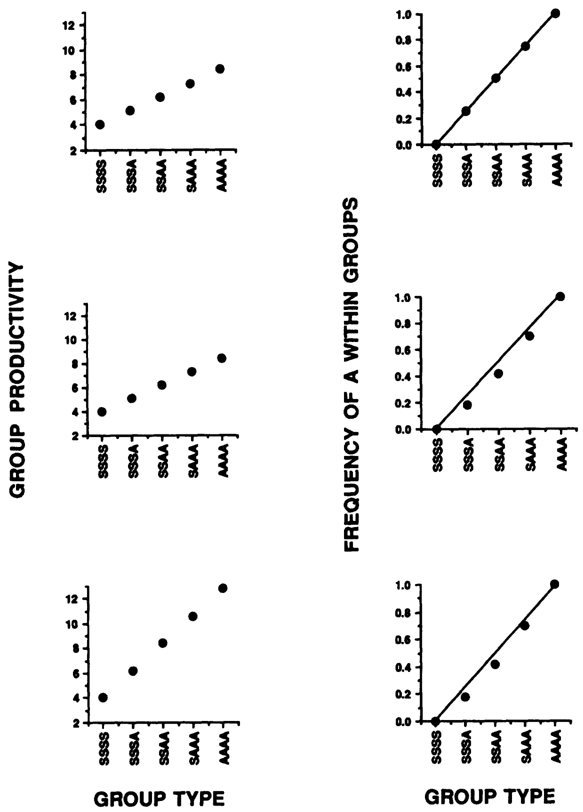

Fig. 2. Three examples of within- and between-group selection. A group size of N=4 yields 5 "group types" (x-axis), analogous to the genotypes of tetraploid organisms. The left column shows the relative productivity of the entire group. The right column shows the frequency of haploid *A*-types within groups after within-group selection. As for genes in individuals, within-group selection can occur only in polymorphic groups and favors the *S*-type when the points lie below the 45° line. Row 1 shows directional between-group selection for the *A* type without opposing within-group selection. Row 2 shows a conflict between levels of selection in which the *S*-type evolves to fixation despite deleterious effects at the group level, assuming random associations. Row 3 shows another conflict in which the *A*-type prevails in random associations, because between-group selection is stronger than in row 2. When defined in terms of altruism, the *A* type is nonaltruistic in row 1, strongly altruistic in row 2, and weakly altruistic in row 3.

majority of population genetics models assume that alleles are randomly distributed into zygotes, such that the genotypes exist in Hardy-Weinberg equilibrium. Non-random associations of alleles have been studied (e.g., inbreeding) but they have never been used as the defining criterion for individual selection. If group selection is a process analogous to individual selection, then what can possibly be the justification for using nonrandom associations of individuals in groups as the defining criterion for group selection? This is our first hint that the two themes of the group selection controversy are not entirely compatible.

More insight can be gained by inspecting the way that levels of selection are treated for genes in individuals. The left hand column of graphs in Fig. 1 shows the relative number of offspring produced by three genotypes of a diploid organism (W), caused by standard Darwinian processes such as differential survival and reproduction. The right hand column shows the allele frequency within single genotypes after selection, caused by such processes as meiotic drive (Cosmides and Tooby 1981, Werren et al. 1988). Since the *AA* and *aa* genotypes represent "monomorphic populations" of alleles, allele frequency change can occur only in the "polymorphic" *Aa* heterozygote. Global evolutionary change is determined by a) the frequency of the three genotypes, b) the relative fitness of the three genotypes, and c) the change in allele frequency within heterozygote genotypes. For example, if alleles are randomly distributed into individuals and g is the frequency of the *A* allele in heterozygotes after selection then the global frequency of *A* after selection (p′) is:

$$p' = \frac{p^2W_{AA}+2p(1-p)gW_{Aa}}{p^2W_{AA}+2p(1-p)W_{Aa}+(1-p)^2W_{aa}} \tag{4}$$

Row 1 represents the standard case in which the *A* allele evolves by increasing the fitness of the genotype in which it resides ($W_{AA}>W_{Aa}>W_{aa}$) while no evolution occurs within heterozygotes (g=0.5). Row 2 represents a case in which the alleles have no effect on the fitness of genotypes ($W_{AA}=W_{Aa}=W_{aa}$) but the *a* allele nevertheless evolves by increasing the frequency of *a* gametes produced by heterozygotes (g<0.5).

One common way that these two examples of natural selection are distinguished is with the terms "individual-level selection" and "gene-level selection" (e.g., Futuyma 1986: 153). These terms identify the level at which differential fitness is driving the evolutionary process. Another semantic framework is provided by Williams (1966, 1986) and Dawkins (1976, 1982), who use the term "gene-level selection" to describe both rows 1 and 2, and indeed all examples of natural selection that result in gene frequency change. This single term has the advantage of emphasizing that only genes have the permanence to serve as "bookkeeping" devices (Williams 1986), but it fails to identify the units that actually differ in fitness, thereby causing evolutionary change (Sober 1984). To make this crucial distinction, Dawkins coined the term "vehicles of selection" (= the "interactors" of Hull 1980). Thus, the individual is the vehicle of selection in row 1 while the gene is the vehicle of selection in row 2. Since Dawkins' term "vehicle" is identical to the previous term "level", the two semantic frameworks are not as different as they initially appear (Wilson and Sober 1988).

To encourage precision and to facilitate the description of higher levels of selection (see below:, I will use the terms "between individual/within group selection" for row 1 and "between gene/within individual selection" for row 2. If only two levels of selection are being considered, these may be shortened to "between-individual" and "within-individual" selection.

Although rows 1 and 2 show the two levels of selection in their pure forms, a single trait can be selected at both levels simultaneously. Assuming Hardy-Weinberg equilibrium, the *a* allele evolves to fixation in row 3 by within-individual selection despite deleterious effects at the between-individual level. For row 4, the opposing levels of selection maintain the alleles in a stable polymorphism. These observations are mundane for genes in individuals but provide a useful basis for comparison, as we shall see.

If group selection is a process analogous to individual selection, we should be able to take the framework outlined above for genes in individuals and apply it directly to individuals in groups. Fig. 2 shows examples for groups of N=4 haploid individuals, which generates 5 different "group-types" analogous to the five genotypes of a tetraploid organism. The left-hand column shows the relative productivity of groups and the right-hand column shows changes in type-frequency within groups. As with genes in individuals, global evolutionary change is determined by a) the frequencies of the five group-types, b) the relative productivity of the group-types, and c) the frequency of *A* within group-types after selection.

In row 1, *A*-types possess a trait that increases the fitness of everyone in the group equally (d=r>0). This should be classified as pure "between group/within metapopulation" selection (between-group selection for short), and yet because d=r it doesn't even qualify as weak altruism. In rows 2 and 3, between-group selection favoring the *A*-type is opposed by "between-individual/within-group" selection (within-group selection for short) favoring the *S*-type. The within-group component is the same for both rows but the between-group component is greater in row 3. Nevertheless, row 2 constitutes a case of *strong* altruism that requires above-random variance in p for the *A*-type to evolve, while row 3 constitutes a case of *weak* altruism that requires only a binomial distribution for *A* to evolve. More generally, any strongly altruistic trait can be converted to weak altruism by intensifying the between-group component of selection.

Clearly, the relationship between the two themes of the group selection controversy is not as simple as it is usually taken to be. Between-group selection is required for the evolution of both weak and strong altruism, but the degree of altruism cannot be used as an index for the importance of between-group selection in the evolution of a trait. The group-level analog of standard between-individual selection–a trait that benefits a group as a collective, including the individuals expressing the trait–cannot even be described in terms of altruism. *Increasing* the between-group component of selection can have the effect of making a trait *less* altruistic. A trait can be weakly altruistic, but evolve by strong group selection.

The evolution of group-level superorganisms in random associations

In standard population genetics models, the random distribution of alleles into individuals provides sufficient variation for between-individual selection to operate. Mechanisms such as inbreeding, that increase genetic variation between individuals, accelerate the spread of favorable alleles but certainly are not necessary for the process of between-individual selection.

The same reasoning can be applied to individuals in groups as follows: Many trait groups in nature consist of small numbers of individuals, comparable to the numbers of alleles in polyploid organisms. Indeed, the burgeoning field of evolutionary game theory is equivalent to an IGS model with trait groups of size N=2, the group-level analog of diploidy (Wilson 1983, 1989). Consider a haploid *A*-type that increases the fitness of all individuals in its trait group, including itself (d=r>0). The random allocation of individuals into groups creates a distribution of group-types in which group fitness correlates directly with the number of *A*-types in the group, allowing the trait to evolve by between-group selection. Mechanisms such as associations among kin, that increase variation between groups, accelerate the spread of group-beneficial traits but they enter group selection theory exactly as inbreeding enters population genetic theory and do not have the conceptual primacy attributed to them by models founded on the theme of strong altruism. Envisioning group selection as a process analogous to individual selection therefore makes it quite reasonable that, in certain ecological situations, random associations of individuals can be molded into functionally organized groups–superorganisms in the same sense that individuals are organisms (Wilson and Sober 1988).

Rissing et al. (1989) have provided a possible example in the desert leaf cutting ant *Acromyrmex versicolor*. After highly synchronized mating swarms, new colonies are formed in clusters such as under the canopy of trees that provide shelter from the harsh thermal environment. The trait groups in this case are the new colonies, which usually are founded by more than one female (mean number of foundresses=2.5, s.d.=2.42, N=64). Unlike the queens of most ant species, who raise the first generation of workers from fat reserves, *A. versicolor* queens must forage for leaves to initiate a new fungus garden. This task is not shared equally by the co-foundresses but rather by a single queen who becomes a specialized forager. From the standpoint of the colony it makes good sense for one individual to forage because efficiency is enhanced through experience. Above-ground foraging is a dangerous activity, however, that substantially reduces the fitness of the specialized forager relative to her colony-mates. In other words, it is selected against within groups.

In the social insects, division of labor with resulting differences in survival and reproduction is usually explained in terms of kin selection (Hamilton 1964) and/or social dominance (West-Eberhard 1978). In *A. versicolor,* however, co-funding queens appear to be unrelated and the specialized forager is not socially subordinate to the others. How then can such seemingly altruistic behavior be maintained in the population?

The answer appears to involve an exceptionally strong form of between-group selection. As soon as the first generation of workers emerges, they raid the brood of other new colonies. Ultimately, only a single colony within the cluster will survive to grow to maturity. Any trait that increases the size of the first worker force and its speed of emergence will increase the likelihood of colonies expressing the trait prevailing over other colonies. The trait benefits all queens within the colony, however, including those that do not express the trait. To use the language of Dawkins, the colony is the vehicle of selection. Returning to the comparison with genes in individuals, the situation is similar to an allele that increases the fitness of a heterozygote, including the other allele that does not express the trait. Superimposed on the group-level benefit, however, is the individual-level cost of the trait that causes it to be selected against within groups.

When both levels of selection are taken together, it is obvious that strong within-group selection against the trait can be countered by even stronger between-group selection for the trait, even in random associations. Specifically, consider a mutant (A) invading a metapopulation of unspecialized queens (S). Assume that queens in all-S colonies forage equally while A forages disproportionately often in colonies with one A and $(N-1)$ S. Let $x < 1$ equal A's probability of survival relative to S in colonies of all-S and let $y > 1$ equal A's effect on her colony's chances of prevailing over the other colonies. Globally, the fitness of A will exceed the fitness of S when $xy > 1$. Thus, within-group selection against the trait (represented by x) can be arbitrarily low as long as between-group selection for the trait (represented by y) is sufficiently high.

The inequality $xy>1$ signifies that A's absolute effect on itself – including both the individual-level cost of foraging and the group-level benefit of brood raiding – must be positive for A to evolve from mutation frequency. Thus, if the trait evolves in random associations it can never be labelled as strongly altruistic, no matter how low the fitness of the specialized forager relative to her colony mates. This merely illustrates how completely the concept of strong altruism fails to represent the intensity of between- and within-group selection that is operating on the system. As in Fig. 2c, the altruism is "weak" because between-group selection is sufficiently *strong* to overwhelm within-group selection, given the variation provided by random associations.

Although A can invade the metapopulation when $xy>1$, it cannot spread to fixation. Consider a metapopulation of specialized foragers (A) invaded by S. Assume that a random process causes one queen to become the forager in colonies of all-A but that S never forages in colonies that contain at least one A. When S is rare it enjoys all the benefits of specialized foraging without the costs, and will spread until the advantages of freeloading within mixed groups are balanced by the disadvantage of being in groups composed entirely of S. This is a group-level analog to the genetic phenomenon of dominance, in which the phenotypic expression of the trait is not increased by adding a second allele (see Wilson 1977b and Dugatkin 1990 for other biological examples). If the group-level benefit is characterized by dominance but the same trait is selected against within groups, a polymorphism is expected in the global population, similar to the fourth row of Fig. 1 for genes in individuals. We might therefore predict that some *A. versicolor* queens refuse to become specialized foragers and that their "defection" is not punished by colony mates, as might be expected from game theory models. Rather, their "punishment" comes from occasionally existing in groups that contain no specialized foragers.

While such a polymorphism would be stable by itself, it might also be vulnerable to invasion by other types and therefore unstable from the standpoint of ESS theory. In particular, "guarded" A-types that become specialized foragers and punish defectors might replace "unguarded" A-types that do not regulate the behavior of others. The final social system might resemble the human practice of drawing straws, in which the specialized forager is selected by a random process and enforced by threat of punishment. This kind of social system reduces within-group selection against the costly behavior, concentrating natural selection at the between-group level. It might therefore be regarded as a group-level analog to the genetic and developmental mechanisms that suppress within-individual selection (Buss 1987, Wilson and Sober 1988). It is important to emphasize, however, that such an elaborate system is not *required* for specialized foraging to evolve, but rather can *itself* evolve as a modification of simpler unguarded behaviors that are maintained at an intermediate frequency by between-group selection.

Division of labor with corresponding differences in survival and reproduction is a milestone in the transition from groups *of* organisms to groups *as* organisms. Commonly it is thought to require a high degree of relatedness among group members. The existence of specialized foragers in *A. versicolor* suggests that the essential ingredient is strong between-group selection, which can occur even in random associations.

Conclusion

The theme of group selection as a process analogous to individual selection was eloquently expressed by G. C. Williams (1966: 92).

> It is universally conceded by those who have seriously concerned themselves with this problem that such group-related adaptations must be attributed to the natural selection of alternative groups of individuals and that the natural selection of alternative alleles within populations will be opposed to this development. I am in entire agreement with the reasoning behind this conclusion. Only by a theory of between-group selection could we achieve a scientific explanation of group-related adaptations. However, I would question one of the premises on which the reasoning is based. Chapters 5 to 8 will be primarily a defense of the thesis that group-related adaptations do not, in fact exist. A *group* in this discussion should be understood to mean something other than a family and to be composed of individuals that need not be closely related.

Despite the universal consensus reported by Williams, the theme of group selection as a process analogous to individual selection was soon eclipsed by the theme of altruism and the subtle but important differences between the two themes were seldom discussed. Following the first theme to its natural conclusions is elementary but requires fundamental changes in some widely held beliefs about the evolutionary process. Between-group selection becomes an essential ingredient of models (such as game theory) that are commonly regarded as alternatives to group selection. Above-random associations (such as kin groups) lose their conceptual primacy and become products of the same forces of within- and between-group selection that operate in random associations. Many traits that appear individually advantageous by the criterion of strong altruism must be reinterpreted as group-level adaptations. Most importantly, even randomly composed groups can sometimes be regarded as superorganisms in the same sense that individuals are organisms. Not only are individuals trait groups of genes, but trait groups of individuals can be "organisms without walls" (Holt 1983).

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