# On Group Selection

The question is not whether group selection occurs. We all know it occurs continually, in all clades of life. We know this because all that is required is for the genetic relationships of different groups -- of any units in the hierarchical organization of life -- to change as a result of differential survival of the groups themselves, or of any of their genetic components. The useful question is the extent to which group selection, at any particular level, accounts for the traits of individuals or groups, as opposed to selection at levels that would tend to fix traits other than those which might be fixed by group selection. Whenever group selection and other levels of selection tend to fix the same traits we are not informed significantly by pondering the question of potency of selection at different levels.

The criterion of group selection that is most deserving of attention, therefore, is the *strength* of any indicated level of group selection, *compared to the strength of selection at other levels*. We already know that the conditions for potent selection always exist at and below the level of individual organisms because of the very traits that define organisms (see below). This means that whenever group selection of organisms is weak, it is likely to be inconsequential in the effort to account for the traits of organisms.

At any given intensity of selection, rates of evolution depend on amounts of heritable variation and generation time. For group selection to be strong, then, the first requirement is that the units comprising the group -- whether, for example, genes comprising a genome or individuals comprising a social group -- cannot easily or frequently change groups. If units comprising a group can pass easily between groups, heritable variation between groups will constantly be eroded. The second requirement is that groups not last long (have a long generation time), compared to other units in the hierarchy of organization of life that might also be under selection. For example, selection among groups that last longer than the individual units comprising the group will, on this feature alone, be less potent than selection among the units themselves.

From these considerations we see that selection is likely to be strongest at levels no higher than that of the individual organism. The most potent levels of selection in ordinary organisms are (1) group selection of genes within genomes and (2) individual-level selection among organisms. This description should be understood to include the fact that individual organisms come to vary in heritable ways via mutational and recombinational changes at lower levels, either the individual gene or larger fragments of the genome such as chromosomes or bits of chromosomes.

To maximize the probability of finding potent group selection above the level of the individual organism (genome), we should, paradoxically, look for groups that have the characteristics of organisms: (1) they are either reliably and repeatedly separated in space and time beyond distances that allow exchange of organisms (thus

interbreeding and loss of heritable differences), or else each group possesses more or less impenetrable boundaries, (2) they have the same generation time as organisms, and (3) they tend to be founded either by genetically different individuals from the group or in such a way as to cause significant sampling error that results in the foundresses that emigrate from (are produced by) a single group having significant heritable differences.

Some investigators seeking potent group selection on the traits of individuals have in fact invoked it by referring to just such populations, or by creating them in the laboratory. An example would be a species in which individual foundress females establish their broods at considerable distances from one other (as in isolated bits of suitable habitat), and in which the broods then spend only one generation or less in the new habitat (the bits of habitat are also of brief duration), once again breaking up into individual foundresses. More specifically, an example might be a parasite in which each separate host organism is inhabited only by the offspring of a single female parasite. Of course, the groups in such a case would be the offspring of a single female, so that evolutionary outcomes could be understood as the product of individual selection among the foundresses. Thus, foundresses that produce broods of appropriate size which do well in the habitats chosen by the foundress, and within which sibling cooperation takes a form maximally advantageous to the reproduction of the brood as whole, will tend to win the selective race. To avoid the explanation of selection among genetically different foundresses, which obviates the usefulness of invoking group selection and may cause a group selection explanation to confuse analyses of the situation, or predictions from it, one would have to go to two or more foundresses. But this change necessarily reduces the amount of heritable difference between groups, thus slowing rates of selection at the level of two foundresses in relation to individual selection of foundresses and among their individual offspring within the combined groups. An effort to bypass this problem has involved reference to long-lasting groups that produce migrant individuals each generation. Unless all members of the group tend to produce equal numbers of migrants, however, as happens with genes in genomes, group selection cannot be the appropriate explanation: it does not allow for effects of selection among the individuals within groups to become the migrants, hence in the end the only surviving products of the group.

There is a particular complication in all cases in which group selection can be invoked as explicitly different from individual selection (i.e., in cases different from the single foundress example above). Adaptive outcomes of group selection, at least early in the process, will tend to increase the duration of the group. Increased group durations amount to increased generation time, also slowing rates of selection at the group level in relation to rates at the level of individuals within groups.

Despite circumstances that militate against the likelihood of group selection being effective, existence of evolutionary oddities shows that conditions allowing unusual combinations of events do happen. Thus, the odd case of effective group selection of individuals may be encountered, even when generation time of groups is several or

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many times that of individuals within groups. Any situation requiring a group selection explanation is likely to entail at most only brief and infrequent moments of possibilities for changing groups: meiosis is such a moment for genes living in genomes. Thus, there can be no doubt that today genes in genomes are group-selected, most potently (or completely) in secondarily asexual genomes. At the level of groups of organisms, or groups of their groups, however, the arguments just posed suggest that the burden of proof will always lie with the investigator who proposes a group selection explanation, and that this burden will be onerous for every single case. Any such cases, moreover, are likely to present exceptional -- not ordinary -- appearances to the observer from the start.

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What follows here is just notes, or ideas, directed mainly at the question of where in nature we can find instances of intergroup selection that are "in progress" or seemingly "incomplete" (at least compared to genomes). Such instances can tell us something about the stages through different kinds of group selection might have passed, how many such cases actually exist, therefore how frequently group selection happens, and in how many different kinds of situations group selection is potent.

We already know that potent group selection of organisms is in general weaker than group selection of genes in genomes, not merely on theoretical grounds, but as well because there are so few groups of organisms with the characteristics of organisms that derive from essentially complete cooperation of the genes in the genome: e.g., ontogenies, adult reproductive periods, and senescence leading to finite lives. The closest cases may be the so-called eusocial forms, which have non-reproducing individuals that act like somatic cells, restricted reproductive units, quasi-ontogenies (definable growth and change periods before reproduction), and special reproductive periods (as colonies). The known eusocial forms of this type tend to comprise nuclear families. They also tend to outlive their relatives that lack eusociality, and they apparently do not senesce. Such societies are known to have evolved around 20 times, evidently under extremely stringent conditions. The rarity of eusocial forms and unique nature of the organism -- its dramatic nature is easily overlooked by us because it is so universal and commonplace, and because we happen to be organisms ourselves -- suggests that once group selection becomes potent it is likely to produce quick changes, such that the history of eusociality and the organism may both be obscured. In order to make this conclusion most likely we should have to locate evidence that there are no blocks to further evolution toward an organism-like condition.

Consider species as groups of organisms, and any other such groups that become absolutely isolated from one another, meaning they cannot exchange genetic materials. If such groups go extinct differentially because of their differences, then even if the differences arise because of selection among the individuals within species, group selection plays a role in the nature of the species that exist (remain) at any given time. But if the conspecific individuals that only reproduce with one another are otherwise not social, selection at the two levels will not conflict. What yields

survival at the individual level will promote it at the group level. If, on the other hand, different species compete directly, then selection may become quite different at the two levels, and group selection can play an important role. This is why I said in 1979 or so that humans are a perfect model for effective group selection because different human groups sometimes behave toward one another as if they were different species. However, even if only via captured women, they also interbreed, eroding the amount of heritable difference between groups and reducing the potency of group selection. Some people did not realize that when I said what I did, I meant to emphasize that humans may be the best we can do, this essentially having to mean that group selection of individuals when all members of the group have the expectation of reproducing is highly unlikely.

There are two ways for groups to be altered toward equality of reproduction of their component units: (1) direct reproduction of all units with suppression of differences in reproduction among them (as apparently with genes in genomes) and (2) restriction of reproduction to one or a few units in groups of units identical or so closely related that indirect reproduction of somatic cells approximates that of the direct reproducing units (eusocial units, organisms).

Should we expect both of these kinds of groups to erect barriers to membership? Are there any examples of (1) above? Do (i) and (2) actually converge on one another?

Is it possible that in the earliest stages of potent intergroup selection most directions of change become the opposite of what they'll be later if group selection remains potent?

Consider longer life (generation time), external and internal barriers to immigration, equality of reproduction (via both everyone expecting reproduce and reproduction restricted to a few units in the group), juvenile life (protracted specialized growth and development), adult (reproductive) life, senescence (shorter life. . .?)

How might a 3+ parent ideal come into these questions? Or does this happen only after queens become hyper-fertile?

If monogamy is imposed by the reproductive value of having two parents for each set of siblings, it's not an aspect of group selection (group in which the monogamous individuals reside). If inheritance patterns are imposed by relatives and in-laws it's not a product of group selection. Why are there marriage rules in societies? To serve powerful individuals? To serve majorities or powerful groups? To serve men? If monogamy is imposed by group rules it could be a result of group selection to equalize reproduction and unify the group. Are both monogamy and inheritance rules levelers?

Can mere rejection of immigrants be a sign of group selection? Trends toward equality of reproduction? Intergroup hostility? If so, ever, are they always?

Can long-lasting inter-hostile groups that divide by fission be stable? If so, what would cause such groups to evolve into a eusocial or genomic organism-like state; or do such have different origins? Of course these groups can exist -- they do. So that must mean that group selection is extremely rare because organisms probably haven't evolved often.