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Kin Selection as the Key to Altruism: Its Rise and Fall

ONE OF THE ENDURING UNSETTLED ISSUES OF EVOLUTIONARY BIOLOGY is the paradox of collateral altruistic behavior—that is, when some individuals subordinate their own interests and those of their immediate offspring in order to serve the interests of a larger group beyond offspring (Wilson, 1975). How might such behavior evolve if the genes promoting it are at such a disadvantage in competition with genes that oppose it?

Charles Darwin saw that the paradox was dangerous to his theory of evolution by natural selection. He was particularly concerned by the social behavior of ants. Not only do flagrantly selfless individuals exist, but they form distinct worker castes, which in some species are subdivided further into specialized subcastes—for example, large, aggressive (but sterile) soldiers and small nurses and foragers. How could such creatures come into existence if they never reproduce? Darwin solved the dilemma to his own satisfaction and that of other biologists for nearly a hundred years by noting that if the combined offspring of the queen ant formed a colony that allowed her to produce more offspring than could an otherwise comparable solitary female, sterile castes would evolve as part of the variation of a single hereditary type. That hereditary type, not the plastic forms it produces, is therefore the unit of selection. The altruistic castes, he said, are like the well-flavored vegetable part in a single crop strain produced by selective breeding (Darwin, 1859).

In 1932 and again in 1955 J. B. S. Haldane, one of the founders of the modern genetic theory of evolution, put a new twist on the altru-

ism problem (Haldane, 1932; 1955). He pointed out how selflessness could evolve even if individuals are not organized into societies. His solution later came to be known as kin selection. Your genes, Haldane said, can be multiplied in a population even if you never reproduce, providing your actions favor the differential survival and reproduction of collateral relatives, such as siblings, nieces, and cousins, to sufficient degree. Suppose, he argued, you see a relative drowning, and if in rescuing him you have a one-tenth chance of drowning yourself. Your genes, including those predisposing you to perform this act of altruism, will nevertheless be increased in the population if such actions increase the number of offspring of the relative by more than the reciprocal of the fraction of genes you share by common descent with the person saved. Thus, if the drowning person is a brother (one-half genes shared) you need only increase the number of his children by more than twice, if a nephew (one-fourth genes shared) the payoff needs only to be more than fourfold, and so on.

In 1964 and in subsequent publications, William D. Hamilton expanded this perception into a general theory (Hamilton, 1964). He defined the property of inclusive fitness, which totals the result of all interactions, whether altruistic, neutral, or negative, throughout a group of relatives and nonrelatives. Turning to ants and other social insects, Hamilton then proposed a theory of the origin of colonies separate from (but not contrary to) the competition among colonies and solitaires conceived by Darwin. By brilliant insight, he connected the following two facts. First, the haplodiploid mechanism practiced by the Hymenoptera (ants, bees, and wasps), in which fertilized eggs become females and unfertilized eggs become males, causes full sisters to be more closely related to one another (by three-fourths) than are mothers and daughters (one-half). Second, almost all of the known 11 independent origins of such colonial life in nature have occurred in the Hymenoptera. Only one such phylad (branch of an evolutionary tree), the termites, was known in the 1960s that practice ordinary, diplodiploid sex determination. In diplodiploidy, sisters are no more closely related than are mothers and daughters. Hamilton concluded, quite

reasonably, that kin selection is a decisive driving or at least strongly biasing force in the origin of the advanced insect colonies. In such colonial phylads, sterile workers put more of their genes into the next generation by sacrificing their personal reproduction, and even their lives, to produce sisters as opposed to daughters.

Hamilton's perception, later called the haplodiploid hypothesis, and intensively promoted (not least by myself, while synthesizing the new discipline of sociobiology in the 1970s [Trivers and Hare, 1976]), became firmly entrenched as an explanatory idea in studies of the evolution of animal colonies. It became further influential in the study of human societies under the aegis of the branch of sociobiology usually called evolutionary psychology.

The core conception by Haldane and Hamilton is expressed in what has come to be called Hamilton's rule:

$$rb > c$$

That is, altruistic behavior will evolve if the benefit b in offspring to the recipient discounted (multiplied by) the fraction of genes shared by common descent between recipient and altruist exceeds the cost in offspring to the altruist. Hamilton's rule, until very recently, has been the textbook encapsulation of the binding force in the origin of colonies that contain altruistic workers.

It turns out, however, that this is wrong. Hamilton made three mistakes, which have led to the vitiation of his main thesis concerning altruism and the origin of sociality.

The first mistake, a simple error in arithmetic, is the conclusion that the production of each sister by individuals in haplodiploid societies passes more of their genes to the next generation than does the production of each daughter. As pointed out by Robert L. Trivers in 1976 (Bourke and Franks, 1995), workers also have to raise brothers, and because the gender of these females are determined by haplodiploidy, they are related by only one-fourth of their genes by common descent. In the case of the typical 1:1 gender ratio for the colony as a whole, one-half of males with one-fourth genes in common with their sisters

plus one-half of females with three-fourths genes in common with their sisters equals one-half genes in common, so that being altruistic and deferring to the mother queen for reproduction yields the same as having sons and daughters.

In short, the need of a colony to produce males as well as females, or at least the need to adjust the production so as to benefit from a population-of-colonies sex ratio of 1:1, cancels out the gain from raising sisters as opposed to daughters. Yet, as Trivers also pointed out, altruism can still confer an advantage if the workers (all ant workers are female and all males are nonparticipating drones) have control of the colony and invest more in sisters than in brothers in the rearing of the next generation of reproductive females (virgin queens) and males. This choice puts them in conflict with the mother queen, who is equally related to her sons and daughters; hence, in order to maximize the multiplication of her own genes, the queen should opt for a 1:1 sex ratio.

It has come to pass, from abundant field and laboratory studies, that Trivers' predictions have been proved correct. In circumstances where other evidence indicates that workers are in control, the production of reproductives is tilted toward females. When the mother queen is in charge, the ratio of investment centers on 1:1. And when the queen is absent and a worker takes over, the ratio tilts toward males—another inference from the corrected arithmetic.

What Trivers had stumbled across was evidence that queens and their worker daughters are in a situation that promotes internal conflict. In other words, kin selection is dissolutive, at least in part, as opposed to binding, in the social evolution of insects.

The haplodiploid hypothesis, and the seemingly strong evidence that supported it in the 1970s and 1980s, still favored the binding effect of kin selection. But that too has now collapsed. So many phylads have been discovered that contain colonies with altruistic workers—among ambrosia beetles (Kent and Simpson, 1992), for example, snapping shrimps (Duffy, 1996), and even in one species of rodents (Sherman, Jarvis, and Alexander, 1991)—that the association between haplodip-

loidy and the presence of worker castes is no longer statistically viable. Further, in the gall-making thrips, which like hymenopterans are haplodiploid, males and not just females serve as nonreproductive castes, contrary to the haplodiploid hypothesis of the origins of sterile castes in colonies (Crespi, 1992).

If there is as yet no evidence that collateral kin selection drives or biases the origin of colonies with nonreproductive workers, there is abundant evidence that the driving force is natural selection by pressures and opportunities in the environment. Such colonies are favored by their superior ability to create and defend nest sites that are stable over extended periods of time, allowing them refuges from which to forage for food. These communal nest sites include chambers in soil and leaf litter for ants, similar chambers in decaying wood for termites, cavities in sponges for snapping shrimps, plant galls for aphids and thrips, and the soil burrow systems of naked mole rats.

Moreover, a growing body of research has disclosed that colonies of social ants and wasps are often founded by unrelated queens; that workers do not show preference for their own mothers in multiple-queen colonies, only occasionally for their sisters; and that colonies remain well organized and stable even in the extreme cases when the workers composing them are only very distantly related or not at all (Choe and Crespi, 1997; Hölldobler and Wilson, in preparation).

In short, the critical binding force of colony evolution appears to be ecological natural selection operating at the level of the colony, a level that comprises both colonies versus individuals, and colonies versus other colonies. It is theoretically possible, and may well occur in nature, that colonies evolve by the selective favoring of genes that prescribe group formation with altruistic workers in a manner that has little or nothing to do with kinship. It is often remarked, and much made of the fact, that colonies of most social insect species are composed of closely related individuals. Writers have jumped to the conclusion that kinship must therefore have been a driving or at least biasing force in the origins of colonies. But this step in logic is a non sequitur. The reverse increasingly appears to be the case: once colonies have evolved,

members of the worker caste tend to be closely related to one another simply because they have common parentage.

Put another way, individuals do not form colonies because they are closely related. They are closely related because they form colonies (Hölldobler and Wilson, in preparation).

This brings us to the third error by Hamilton and most subsequent researchers, including the present author. The rule " $rb > c$ leads to altruism" is logically correct, but, given that altruism can also evolve when $r = 0$, it is also incomplete. A more accurate expression is " $(rb_k + b_e) > c$ leads to altruism," with b_k the benefit from collateral kin selection and b_e being the benefit accruing from colony-level selection independent of kinship. If b_e is overwhelmingly larger than rb_k , then the latter will be too small to measure, which in fact is the apparent condition in nature. Hence, in practical terms, the inequality reduces to $b_e > c$.

To date the only conclusive effects demonstrated for collateral kin selection are dissolutive. The sex investment ratios of reproductive castes by colonies are perturbed in some (but not all) species as predicted. Also, policing, the harassing by nestmates of workers who try to reproduce, is biased in some species by kinship. But again, not in all species. Policing occurs even in colonies that are clonal, and hence whose workers are genetically identical. Because workers who reduce their labor and try to reproduce reduce colony efficiency, policing, even when biased by kinship, can be subsumed under colony-level selection.

So, in the explanation of the origin of colonies with altruistic worker castes, the empirical evidence appears to be moving us back to Darwin's well-flavored vegetable, and to the primacy in social insects of colony-level selection. The gene is still the primary unit of selection, but the target of selection in the origin of colonial behavior is the higher of the two adjacent levels of biological organization—of superorganisms over organisms, much as is the case for organisms over cells and tissues.

The research on collateral kin selection was a thriving industry for three decades. Thanks to the detour given it by Trivers' correction of Hamilton's arithmetical error, kin selection theory opened a new realm of research on conflict in societies, fruitful not only in the study

of social insects (Wilson, 1971; 1975) but also in parent-offspring studies (Trivers, 2002), genomic imprinting in developmental biology (Haig, 2002), and in evolutionary psychology, the human-oriented discipline spinoff from sociobiology (Betzig, 1997). The collapse of the haplodiploid hypothesis, reducing collateral kin selection to a weak dissolutive role, gives reason to place more emphasis on the ecological forces of colony-level selection, and hence the complex ergonomic devices of caste and communication that adapt colonies to those forces.

All of these developments in sociobiology are in full progress, and surprises no doubt lie ahead. The interpretation I have presented here may itself in time be swept aside. New evidence might be found that reinstates collateral kin selection as a primary binding force. For the present, however, the ongoing shift to group-level selection forced by empirical evidence suggests that it might be profitable to undertake a similar new look at the wellsprings of social evolution in human beings and nonhuman vertebrates where, I believe, surprises also await us.

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