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Call Number: QP360 B425
Location: IQUS Periodicals

Journal Title: BEHAVIORAL AND BRAIN SCIENCES
Volume: 17
Issue: 4
Date: 1994
Pages: 630-631

Article Author: MILLER, GF
Article Title: BEYOND SHARED FATE - GROUP-SELECTED
MECHANISMS FOR COOPERATION AND COMPETITION IN
FUZZY, FLUID VEHICLES

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Beyond shared fate: Group-selected mechanisms for cooperation and competition in fuzzy, fluid vehicles

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Abstract: This commentary makes two points about group selection. First, selection can certainly act on vehicles of various kinds, but applying this idea to human groups is tricky, because a human group is such a fluid, fuzzy sort of vehicle. Nevertheless, even without shared fate, human groups can use “resource levellers” and “resource lotteries” to foster cooperation. Second, vehicles can exploit internal competition as well as internal cooperation to promote their efficient survival and reproduction, so adaptations for meritocratic sexual competition within human groups, as well as adaptations for egalitarian cooperation, may have been favored by group selection.

1. Resource levellers and resource lotteries as group-selected mechanisms for human cooperation. Classic examples of evolutionary vehicles, such as multicellular bodies and multi-insect colonies, share several features: (1) high genetic relatedness among constituent individuals; (2) a physically integrated vehicle structure (a body or hive) that imposes a shared fate on the constituent individuals; and (3) an obligate division of labor between germ-line individuals (e.g., sperm and egg cells or hive queens) and somatic individuals (e.g., somatic cells or sterile workers). Human tribal groups make unusual vehicles because they lack these three features: human group selection differs from kin selection by definition because of the low genetic relatedness of individuals in the group; humans probably did not construct group vehicles (e.g., village stockades) until recently, and no human group, not even the Hutterites, has a happy, consensual division of labor between a reproductive caste and a sterile caste. Rather, human tribal groups have genetic, social, cultural, linguistic, and spatial boundaries that are fuzzy and fluid. Theories of human group selection must therefore explain how selection can favor cooperation in fuzzy, fluid, facultative vehicles that do not have a genetic identity, a vehicle phenotype, or a separate germ-line. In groups composed of individuals who can survive, reproduce, and migrate separately, shared fate can erode and selfishness can win out.

Shared fate really means shared fitness: the vehicle's structure in relation to its environment ensures that fitness is highly correlated across individuals within the vehicle. Sometimes,

pack-hunting predators or genocidal group warfare may have imposed true shared fate on ancestral human groups. Most shared fate in modern human groups, however, depends on fairly recent technology, such as ropes to tie mountain-climbers together, or real "vehicles" to navigate land, air, and water (such that "we're all in the same boat"). The fluidity of tribal groups and the autonomy of individuals suggest that human groups created moderately correlated fitnesses among their members, rather than truly shared fate.

Without obligate shared fate, there seem to be two main ways to promote cooperation in human groups: (1) "resource levellers" that distribute resources obtained by group cooperation fairly equally across individuals, and (2) "resource lotteries" that make the distribution of fitness benefits resulting from group cooperation unpredictable at the moment that individuals commit to cooperate. Resource levellers probably work best for cooperative tasks that impose low risks and low costs on individuals, whereas resource lotteries work best for those that impose high risks and high costs. Because Wilson & Sober (W & S) discuss resource levellers such as egalitarian ideology and food sharing at some length, I will focus on resource lotteries, as introduced and analyzed by Tooby and Cosmides (1988; 1993).

Resource lotteries work best when cooperation produces individual payoffs with a positive mean value and a high variance, with positive and negative outcomes that are fast, final, unpredictable, and unshareable (such as successful fertilization or death). These conditions make it foolish to defect before the lottery and impossible to defect afterward. The main resource lotteries in human evolution were probably cooperative hunting, cooperative warfare, and cooperative sexual coercion. For example, Tooby and Cosmides (1993) suggested that the development of projectile weapons may have facilitated the evolution of human cooperative warfare, by making the outcome of warfare more unpredictable to the individual but more beneficial to the winning group. A fast hail of projectiles imposes a less predictable survival lottery than an afternoon of hand-to-hand combat, so individual defection is less likely. Likewise, prey animals that have evolved "protean" abilities to flee and counter-attack unpredictably (Driver & Humphries 1988; Miller & Freyd 1993) impose a survival lottery on cooperative hunters. Moreover, warriors or hunters may draw lots at random to decide who will lead a dangerous raid. Cooperative sexual coercion by males can also function as a reproductive lottery, because the outcome of sperm competition among multiple males is not predictable (see Bellis & Baker 1990).

W & S do recognize the analogy between meiosis at the genetic level and randomization mechanisms for ensuring cooperation at the group level, and mention the Hutterite lottery method for assigning the original home site to one of two groups after splitting. Even John Rawls (1971) used a resource lottery argument to support his resource-levelling theory of political justice, when he asked how one would want society to be structured if one's birth position (family, sex, class, and race) were to be determined at random. Because the importance of adaptive unpredictability in biology and psychology has been long overlooked (Driver & Humphries 1988), the study of unpredictable resource lotteries to promote group cooperation may be a fruitful area for further research. Rapoport and Budescu (1992) have already demonstrated that individual humans are rather good randomizers under ecologically valid conditions; perhaps human groups are too.

2. Cultural courtship systems as group-selected mechanisms for efficient sexual selection. My second main point is that efficient vehicles use internal competition as well as internal cooperation to organize and maintain functional adaptations. Multicellular bodies exploit competition in many ways: brain development depends on competition between neurons for neurotrophic signals, learning depends on competition between synapses for reinforcement, and immune system functioning depends on differential reproduction between antibodies in favor of superior antigen-matches (see Gazzaniga 1993). At the

level of human groups, then, group selection itself may favor a subtle balance between egalitarian collectivism and eugenic meritocracy. Some apparently selfish behaviors such as role differentiation, status seeking, and sexual competition may have been favored by group selection, just as certain modes of competition between neurons and between anti-bodies were favored by individual selection.

In particular, group selection between human tribes may have favored ritualized modes of sexual competition and courtship that promote efficient mate choice, thus amplifying differences in reproductive success and maintaining the tribe's gene-pool quality across generations. Whereas resource levelling and resource lotteries promote group cooperation within a generation, amplifying reproductive differences through meritocratic sexual competition promotes group eugenics across generations. Consider two hypothetical tribes of equal size, cooperativeness, and technology: the Random Mates enforce random mating and equal numbers of offspring among all its surviving men and women, whereas the Selective Breeders encourage selective and assortative mating, meritocratic polygamy, and higher numbers of offspring for higher-viability men and women. Across generations, we would expect group selection itself to favor the Selective Breeders, who coevolve against pathogens, propagate heritable innovations, and guard against recurrent deleterious mutations much more efficiently than the Random Mates do. The idea that group selection can favor group-level eugenics has bad historical connotations, but eugenics is what selective mate choice is all about, and any group mechanisms that promote efficient mate choice, such as parties, feasts, dances, sporting contests, religious rituals, political rallies, and scientific conferences, may serve a eugenic function for the group. Individual selection and group selection can sometimes reinforce one another, creating powerful evolutionary pressures on organisms (and difficult methodological problems for biologists.)

Of course, the Random Mates might gain an advantage if egalitarian mating fostered better group cooperation and if technological and economic innovations made this short-term cooperation much more important than long-term sexual-selective efficiency. This may help to explain the otherwise mysterious historical shift from polygynous, hierarchical medieval cultures to more monogamous, egalitarian capitalist cultures in Europe (Betzig 1986). More often, though, we might expect group selection to push toward egalitarian collectivism in survival domains but eugenic meritocracy in reproductive domains. Indeed, many human groups have developed cultural distinctions between collective rituals to promote group cooperation in survival domains and ritualized courtship competitions to promote meritocratic selective mating in reproductive domains. The classical liberal principle of "equality of opportunity, inequality of outcome" also strikes a balance between cooperation-promoting egalitarianism and competition-promoting meritocracy. This balance may have been favored by group selection: whereas economic individualists probably starved to death, reproductive communists were probably mutated into collective oblivion. Our ancestors may have prospered, as individuals and groups, by combining tender economic socialism with tough reproductive libertarianism. This hybrid system may reflect a conflict between different group-selection pressures over different time scales, not just a conflict between levels of selection. If so, group selection may have favored group cooperation that buffered individuals from natural selection by the external environment, but it may have increased the intensity of sexual selection through mate choice, thereby setting the stage for runaway sexual selection in human mental evolution (see Miller 1993; Ridley 1993).