A new theory of cooperation

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The function of laws is to regulate . . . the reproductive strivings of individuals and subgroups within societies, in the interest of preserving unity in the larger group. . . . Presumably, unity in the larger group feeds back beneficial effects to those . . . that propose, maintain, adjust, and enforce the laws. (Alexander 1979, p. 240)

A corollary to reproductive opportunity leveling in humans may occur through mitosis and meiosis in sexual organisms. . . . The leveling of reproductive opportunity for intragenomic components . . . is a prerequisite for the remarkable unity of genomes. (Alexander 1987, p. 69)

When I first read Alexander's (1987) *The Biology of Moral Systems*, I was stunned to find a truly new theory of biological cooperation. I had thought of the theory of social evolution as an already mature subject, fully developed with regard to fundamental concepts. Yet, in Alexander's book, I could see a completely new way to think about social evolution. In this essay, I explain that new theory and where it came from.

Dick Alexander, Bill Hamilton, and Bob Axelrod taught me the classical theory of social evolution at the University of Michigan in the late 1970s and early 1980s. That classical theory provided two explanations for cooperation: kin selection and reciprocity. At that time, the theory seemed mature and complete with regard to setting the foundation for the field. I hardly expected to come across a totally new way of thinking about the evolution of cooperation.

Yet the main weakness of the theory was also apparent. Extensive cooperation occurs between nonrelatives. Different genes in genomes are functionally integrated but not related. Larger human societies often have many highly cooperative but distantly related individuals. Some of this cooperation between nonkin can be explained by extensions of reciprocity to a general notion of mutual benefit for interacting partners (West Eberhard 1975). In the early 1980s, kin selection plus these extended notions of reciprocity were the main conceptual tools.

Those limited conceptual tools led to blind spots about unsolved problems. Only rather forced theories of mutualism could work for the nearly complete integration of genes into cooperative genomes. Only a very enthusiastic belief in the scope of reciprocity could explain the broad social integration in larger groups of weakly related humans.

In the 1970s, Alexander had already seen the problem. Primitive human groups were perhaps something like chimpanzee troops, in which kin selection and reciprocity could be at least roughly matched to the level of cooperation and social integration. But human history has been characterized by a great expansion in group size. How could one account for the transitions from chimpanzee troop to village to nation-state? Group against group competition potentially explains the

benefit of larger group size. But what prevented internal conflict in larger groups, which could no longer be bound by close relatedness or tight reciprocity?

Without some mechanism to control those internal conflicts, larger groups could not be sustained. Stating the puzzle in that way, the solution is clear. There must be some mechanism that suppresses internal conflict. If individuals cannot compete against members of their own group, then they can only increase their success by increasing the success of the group as whole. Suppression of internal competition unites all group members into a cohesive and cooperative unit.

That idea of internal suppression and group cohesion is the new theory of cooperation that I took away from *The Biology of Moral Systems*. I was truly surprised that so simple and so powerful an explanation could appear as a new idea in 1987. For Alexander, human moral systems were systems for regulating internal competition within groups to promote group cohesion and success in competition against other groups. The broader generality of regulating internal competition in biological evolution was clear to Alexander, and he had in fact reasoned about human evolution by extension of his understanding of the evolutionary history of life.

Of course, no truly deep and general idea appears out of nothing. The first clear description often coincides with others who soon express similar notions arising out of independent lines of study. In the early 1990s, I become increasingly interested in Alexander's theory internal suppression as a way to achieve group integration. My own interest developed because I was trying to understand the principles by which early genomes arose near the origin of life. How did different replicating molecules come together to form larger, cohesive genetic systems? I felt that was an important question, because it seemed that we could not say we understood any aspect of sociality if we could not at least give a plausible theory for the origin of genomes.

The more I thought about it, the more I realized that, at that time in the early 1990s, we really did not have the conceptual tools to give a plausible theory of the origin of genomes. So I was brought back to Alexander's vision of how biological systems could achieve broader group integration in spite of limited relatedness and limited opportunities for reciprocity and synergism. Specifically, I had to understand how a theory of suppression of internal competition could work broadly in evolutionary theory.

In effect, I needed to work out the step-by-step aspects of Alexander's theory applied to the origin of genomes, in the absence of any advanced behavioral or cognitive abilities. My own work appeared in Frank (1995), but is not the key point here. What matters is that I also had to understand the historical genesis of Alexander's thinking and the different parallel lines by which similar ideas developed through the 1980s and 1990s (Frank 2003).

Alexander cited two clear precedents to his own ideas. First, John Rawls's (1971) famous theory of justice from moral philosophy developed the notion of the "veil of ignorance." A just society establishes rules that individuals regard as fair from behind a veil of ignorance about their position within society. An individual may, in practice, end up on one end or the other of any particular social interaction. (Harsanyi [1953] developed a similar idea; see Skyrms [1996] for discussion of these ideas in an evolutionary context.)

It does not pay to argue the fine details of how precisely these humanistic thoughts presage current evolutionary understanding. These thoughts from moral philosophy do contain the following kernels: group cohesion returns benefits to individuals, and randomization of position levels individual opportunity and promotes group cohesion. In other words, given randomization of individual success within the group, an individual increases success only by increasing the success of the group as a whole.

The second precedent came from Leigh's (1971, 1977) work on Mendelian segregation in meiosis. In standard diploid genetics, each genetic locus has one allele from the mother and one from the father. Each gamete made by an individual has either the maternal or paternal allele. Mendelian segregation, or fair meiosis, gives an equal chance to maternal and paternal alleles of being in a successful gamete. Meiotic drive subverts fairness by giving one allele a greater chance of transmission. The pieces of chromosomes that can drive against their partners gain a reproductive advantage by increasing their chance for transmission to offspring. As driving chromosomes spread because of their transmission advantage, they often carry along deleterious effects that are partly protected from selection by being associated with transmission advantage (Zimmering et al. 1970).

Other parts of the genome lose when a driving chromosome carries with it deleterious effects into the majority of gametes. Suppression of drive has the immediate effect of reducing association with the deleterious effects of driving chromosomes; it has the long-term consequence of taking away the transmission advantage that protects the deleterious effects. Drive suppression thus helps to purge the genome of the deleterious effects carried by driving chromosomes. The many genes of the genome repress the drive ''as if we had to do with a parliament of genes, which so regulated itself as to prevent 'cabals of a few' conspiring for their own 'selfish profit' at the expense of the 'commonwealth''' (Leigh 1977, p. 4543).

When meiosis is fair, randomization puts each allele behind a veil of ignorance with regard to its direct transmission (interests) in each progeny. Behind the veil, each part of the genome can increase its own success only by enhancing the total number of progeny and thus increasing the success of the group. However, discussing ''interests'' in arguments about how natural selection operates can be misleading. In this case, natural selection directly favors the immediate advantage of

drive suppression, which reduces association with the deleterious effects that often hitchhike along with drive. The long-term advantage of purging the hitchhiked deleterious effects also contributes to favoring drive suppression when groups compete against groups, for example, species against species (Leigh 1977).

Leigh (1977) noted that alignment of individual and group interests shifts selection to the group level. However, meiosis was the only compelling case known at that time. Without further examples, there was no reason to emphasize repression of internal competition as an important force in social evolution and the formation of evolutionary units. From the conceptual point of view, it may have been clear that repression of internal competition could be important, but not clear how natural selection would favor such internal repression.

Alexander and Borgia (1978) joined Leigh in promoting the possible great potency of internal repression in shaping interests and conflicts in the hierarchy of life. From this, Alexander (1979, 1987) developed his theories of human social structure (see introductory quotes). In this theory, intense group-against-group competition shaped societies according to their group efficiencies in conflicts. Efficiency, best achieved by aligning the interests of the individual with the group, favored in the most successful groups laws that partially restricted the opportunities for reproductive dominance within groups. For example, Alexander (1987) argued that socially imposed monogamy levels reproductive opportunities, particularly among young men at the age of maximal sexual competition. These young men are the most competitive and divisive individuals within societies and are the pool of warriors on which the group depends for its protection and expansion. If these young men cannot compete against their neighbors within their groups, then they can increase their success only by cooperating with their neighbors in competition against other groups.

Rawls and Leigh directly influenced Alexander. With regard to biology, Leigh (1971, 1977) may have been the first to emphasize how repression of internal competition aligns individual and group interests. However, meiosis provided the only good example at that time, so the idea did not lead immediately to new insight. Alexander (1979, 1987) used Leigh's interpretation of meiosis as the foundation for his novel theories about human social evolution. I was aware of the discussion about meiosis in the 1970s, but I only realized the general implications for repression of competition as a powerful evolutionary force after reading Alexander (1987). With two examples—meiosis and the structuring of social groups—I could see how a simple idea could be applied to different contexts.

Around the same time, Buss (1987) was independently analyzing cellular competition in metazoans. Many multicellular animals are differentiated into tissues that predominantly contribute to gametes and tissues that are primarily nonreproductive. This germ-soma distinction creates the potential for reproductive

conflict when cells are not genetically identical. Genetically distinct cellular lineages can raise their fitness by gaining preferential access to the germline. This biasing can increase in frequency even if it partly reduces the overall success of the group.

One way to control renegade cell lineages is to enforce a germ-soma split early in development (Buss 1987). This split prevents reproductive bias between lineages during subsequent development. Once the potential for bias has been restricted, a cell lineage can improve its own fitness only by increasing the fitness of the individual. This is another example of how reproductive fairness acts as an integrating force in the formation of units.

Buss stimulated Maynard Smith (1988) to consider how social groups became integrated over evolutionary history. Maynard Smith disagreed with Buss's particular argument about the importance of the germ-soma separation in metazoans. But in considering the general issues, Maynard Smith had in hand several possible examples of group integration, including meiosis and genomic integration and perhaps repression of cellular competition in metazoans. From these examples, Maynard Smith (1988, pp. 229-230) restated the essential concept in a concise and very general way:

> *One can recognize in the evolution of life several revolutions in the way in which genetic information is organized. In each of these revolutions, there has been a conflict between selection at several levels. The achievement of individuality at the higher level has required that the disruptive effects of selection at the lower level be suppressed.*

This view led to Maynard Smith and Szathmary's (1995) book *The Major Transitions in Evolution*, a popular account of the history of life based on the key events in which competition within groups became suppressed. Maynard Smith and Szathmary's synthesis arose independently from Alexander's work. But Alexander was the first to take Leigh's insight about meiosis and apply that view in a general and powerful way to propose a solution to the puzzle of progressive social integration of complex groups. Buss (1987) came soon after. In this light, *The Major Transitions in Evolution* (Maynard Smith and Szathmary 1995) can be seen as the great development and synthesis of Alexander's insight about suppression of competition in the evolution of cooperation.

Since 1995, suppression of competition has developed into a broad research topic applied to many puzzles of cooperative evolution. I list just three of the most recent applications taken from articles published during the past few years. These applications give a sense of the research that has grown out of Alexander's original insights. Frank (2003) reviews several additional examples.

Higginson and Pitnick (2011) summarize aspects of competition between sperm within the ejaculate of a single male. They conclude by noting the potential importance of mechanisms that repress such intra-ejaculate competition:

> *Competition between sibling sperm may reduce male reproductive fitness, even in monogamous systems, by reducing the number of fertilization-competent sperm per ejaculate (e.g. killing of Y-chromosome-bearing sperm in the case of sex chromosome meiotic drive) or by displacing sibling sperm from the site of storage or fertilization. Male-level selection for adaptations that reduce intra-ejaculate competition in favour of improved whole-ejaculate success aligns the interests of males and the sperm they produce. When competition between sibling sperm is restricted or prevented, individual sperm fitness can only be maximized by enhancing inter-ejaculate competitive success (Frank 2003). We refer interested readers to two recent reviews for a more detailed discussion of sperm-level selection and male-sperm conflict (Immler 2008; Pizzari and Foster 2008).*

Hoffmann and Korb (2011) studied replacement of reproductives in termite colonies. They emphasized the potential importance of mechanisms that repress competition during the replacement phase of the colony life cycle. They noted "Strong conflicts were predicted as all colony members (except soldiers) have the capability to become neotenic replacement reproductives. Our behavioural observations first implied that there was no overt conflict during replacement, but the killing of some neotenics suggested that conflict was not completely suppressed. Various mechanisms were found that may regulate conflict." Among possible mechanisms that may repress competition in the colony, they emphasize a possible form of randomization analogous to fair meiosis:

> *One proximate mechanism that can reduce overt conflict is the sensitive period: a short period during the moulting interval when the developmental fate of an organism at the next moult is determined … During this period, individuals are sensitive to environmental stimuli, such as the absence of reproductive … Among the workers, only individuals in the sensitive period are able to respond to orphaning and become neotenic replacement reproductives. As all workers regularly pass through this period, they all have a fair chance of becoming neotenic, while at the same time the number of actually competing individuals is reduced. Thus, the sensitive period functions as a 'fair lottery' mechanism similar to, for example, Mendelian segregation during gamete formation (Frank 2003).*

The evidence remains ambiguous with respect to this argument for a fair lottery mechanism to repress competition. The point here is that Alexander's conceptual framing of cooperative evolution plays a key role in Hoffman and Korb's (2011) thinking about termite biology.

Many other aspects of social insect cooperation have been interpreted with respect to repression of competition within colonies (Ratnieks et al. 2006). Smith et

al.'s (2009) recent study continues the development of this topic. They summarize their conclusions:

> *Cheaters are a threat to every society and therefore societies have established rules to punish these individuals in order to stabilize their social system ... Recent models and observations suggest that enforcement of reproductive altruism (policing) in hymenopteran insect societies is a major force in maintaining high levels of cooperation ... In order to be able to enforce altruism, reproductive cheaters need to be reliably identified ...[Our data provide] the first direct evidence that cuticular hydrocarbons are the informational basis of policing behaviors, serving a major function in the regulation of reproduction in social insects. We suggest that even though cheaters would gain from suppressing these profiles, they are prevented from doing so through the mechanisms of hydrocarbon biosynthesis and its relation to reproductive physiology. Cheaters are identified through information that is inherently reliable.*

The current literature contains many additional applications of Alexander's theory of cooperative evolution. Repression of competition has indeed joined kin selection as the second key process in the major evolutionarily transitions throughout the history of life.

Acknowledgments

References

Alexander, R. D. 1979. Darwinism and human affairs. Univ. of Washington Press, Seattle, WA.

Alexander, R. D.. 1987. The biology of moral systems. Aldine de Gruyter, New York.

Alexander, R. D., and G. Borgia. 1978. Group selection, altruism, and the levels of organization of life. Annu. Rev. Ecol. Syst. 9: 449–474.

Buss, L. W.. 1987. The evolution of individuality. Princeton Univ. Press, Princeton, NJ.

Frank, S. A. 1995. Mutual policing and repression of competition in the evolution of cooperative groups. Nature 377:520–522.

Frank, S. A. 2003. Repression of competition and the evolution of cooperation. Evolution 57:693-705.

Harsanyi, J. 1953. Cardinal utility in welfare economics and the theory of risk taking. J. Pol. Econ. 61:434–435.

Higginson, D. M. and Pitnick, S. 2011. Evolution of intra-ejaculate sperm interactions: do sperm cooperate? Biological Reviews 86:249-270.

Immler, S. 2008. Sperm competition and sperm cooperation: the potential role of diploid and haploid expression. Reproduction 135, 275–283.

Leigh, E. G., Jr. 1971. Adaptation and diversity. Freeman, Cooper, San Francisco, CA.

Leigh, E. G., Jr. 1977. How does selection reconcile individual advantage with the good of the group? Proc. Natl. Acad. Sci. USA 74: 4542–4546.

Maynard Smith, J. 1988. Evolutionary progress and levels of selection. Pp.219–230 *in* M. H. Nitecki, ed. Evolutionary progress. Univ. of Chicago Press, Chicago, IL.

Maynard Smith, J., and E. Szathmary. 1995. The major transitions in evolution. Freeman, San Francisco, CA.

Pizzari, T. and Foster, K. R. 2008. Sperm sociality: Cooperation, altruism, and spite. PLoS Biology 6, e130.

Ratnieks, F. L. W., Foster, K. R., and Wenseleers, T. 2006. Conflict resolution in insect societies, Annu. Rev. Entomol. 51:581–608.

Rawls, J. 1971. A theory of justice. Harvard Univ. Press, Cam- bridge, MA.

Skyrms, B. 1996. Evolution of the social contract. Cambridge Univ. Press, Cambridge, U.K.

Smith, A. A., Holldobler, B., and Liebig, J. 2009. Cuticular hydrocarbons reliably identify cheaters and allow enforcement of altruism in a social insect. Current Biology 19:78-81.

West Eberhard, M. J. 1975. The evolution of social behavior by kin selection. Q. Rev. Biol. 50:1-32.

Zimmering, S., L. Sandler, and B. Nicoletti. 1970. Mechanisms of meiotic drive. Annu. Rev. Genet. 4:409–436.