



About the Director

Abstracts

Publications

Commentaries

Book Review Essays

Major Books

Synergism Hypothesis

Nature's Magic

Holistic Darwinism

<< Publications List

Holistic Darwinism

"Synergistic Selection" and the Evolutionary Process

Peter A. Corning, Ph.D.
Institute for the Study of Complex Systems
Email: pacorning@complexsystems.org

JOURNAL OF SOCIAL AND EVOLUTIONARY SYSTEMS, 20(4): 363-400.
Copyright © 1997, JAI Press

"Often the most important contribution a scientist can make is to discover a new way of seeing old theories or facts."

Richard Dawkins

"The power and majesty of nature in all its aspects is lost on one who contemplates it merely in the detail of its parts and now as a whole."

Pliny the Elder

"The whole is something over and above its parts, and not just the sum of them all..."

Aristotle

INTRODUCTION: THE PERILS OF GROUP SELECTION

The emotionally-charged group selection debate in biology -- which celebrated an unofficial 30th anniversary in 1996 -- provides a classic example of a controversy that arose from a misconception. To Darwin and many of his contemporaries, group selection was a perfectly respectable concept. Indeed, it was Darwin who first proposed, in *The Descent of Man* (1874/1871), the then unexceptional idea that differential group selection may have played an important role in human evolution, along with what he called "family" selection (now known as inclusive fitness or kin selection theory) and individual reciprocities (now called mutualism and reciprocal altruism). Darwin's "tripartite" explanation of human evolution was subtle, but his view of the role played by group selection is illuminated in this brief passage: "All that we know about savages, or may infer from their traditions and old monuments, the history of which is quite forgotten by the present inhabitants, show that from the remotest times successful tribes have supplanted other tribes" (p.147).¹ Herbert Spencer, one of the outstanding theorists of the 19th century, expressed a similar view in *The Principles of Sociology* (1897/1874-82), and many of the pioneer anthropologists of that period also seemed to agree.²

In the first half of this century, the founding fathers of modern genetics and population biology, notably including Haldane, Wright, Fisher, Morgan, Dobzhansky, and others (plus some non-geneticists like Huxley, Mayr, and Simpson) redefined evolutionary theory in quantitative genetic terms. However, the so-called "modern synthesis" was also deemed to be compatible with group selection of various kinds. For instance, Sewall Wright at the University of Chicago coined the term "interdemic selection" -- i.e., selection between discrete breeding groups, or "demes" -- and developed what he called a "shifting balance" model, which he believed was of the utmost importance in producing evolutionary changes (Wright 1968-78). Ernst Mayr, likewise, speaks of evolutionary change as a population-level phenomenon, meaning that populations and species are the ultimate units of evolutionary change, not individuals. Mayr also developed what he calls the "founder principle," which

envisions small, reproductively isolated groups as a significant source of evolutionary innovation (Mayr 1963; 1976). Meanwhile, various students of animal behavior, such as William Morton Wheeler and Warder C. Allee, stressed the co-operative aspect of animal behavior and social life. Wheeler (1927) also promoted the idea of "emergent evolution," and he borrowed from Spencer the idea that a socially-organized group can be likened to a "superorganism" (Wheeler 1928) (see below).

A theoretical "punctuated equilibrium" occurred in 1962. In his subsequently much-maligned book *Animal Dispersion in Relation to Social Behaviour*, V.C. Wynne-Edwards made himself a stalking horse, in Edward O. Wilson's characterization, by propounding a seriously overstated version of the group selection hypothesis. Wynne-Edwards asserted that group-living animals regularly display behaviors which involve the curtailment of their own personal fitness for the good of the group (for example, through "conventional" controls on personal reproduction that serve to limit population densities). "The great benefit of sociality," he claimed in a companion article in *Nature*, "arises from its capacity to override the advantage of individual members in the interest of the survival of the group as a whole" (1963). Some of Wynne-Edwards's critics, playing loose with the facts, accused him of a Pollyanna-like naivete that violated Darwinian theory, but in fact he clearly stated that altruistic, group-serving behaviors could arise only if natural selection were to operate between social groups "as evolutionary units." Notwithstanding, Wynne-Edwards became a pariah in evolutionary biology and has been routinely chastised for his heresy ever since -- rather like the treatment accorded to Lamarck.

Although the assault on group selection theory began with William D. Hamilton's now classic papers on "The Genetical Evolution of Social Behavior" (1964a,b), it was fully-elaborated in George C. Williams's *New Testament -- Adaptation and Natural Selection* (1966). Williams's near-legendary book was in many respects a therapeutic cold bath that served to purge evolutionary theory of some sloppy thinking. However, Williams also took an extreme position, from which he has since retreated, to the effect that selection at any higher level than that of an individual is essentially "impotent" and is "not an appreciable factor in evolution" (1966:8; cf., Williams 1992).

Although E.O. Wilson was more moderate by comparison in his discipline-defining volume, *Sociobiology* (1975), he also (inadvertently) propagated a conceptual muddle that has caused no end of confusion and mischief in evolutionary theory.³ Wilson launched his massive synthesis with the startling assertion that altruism is "the central theoretical problem of sociobiology" (p.3). The implication, which guided much subsequent work in this new interdiscipline, was that social life is founded on altruism. Therefore, co-operative behaviors are inherently a theoretical "problem" that can be overcome only under extraordinary circumstances -- i.e., via group selection, kin selection and maybe Robert Trivers's (1971) "reciprocal altruism". In opposition to Wynne-Edwards, Wilson considered "pure" group selection -- i.e., among non-kin -- to be highly improbable, a rare occurrence confined to humans and perhaps a few other species. (His detailed, chapter-length discussion of group selection included a review both of the available evidence and of various formal models, but his conclusion was preordained by the assumption that "pure" group selection necessarily implied genetic altruism (1975:106-129).

Another broadside against group selection theory occurred when Richard Dawkins published his ideologically-tinged popularization with the cunningly anthropomorphic title *The Selfish Gene* (1989/1976). "I think 'nature red in tooth and claw' sums up our modern understanding of natural selection admirably," Dawkins wrote with evident relish (1989/1976:2). Not surprisingly, *The Selfish Gene* became a controversial best-seller. In retrospect, the selfish gene

metaphor has proven to be a powerful heuristic tool. It has led to many new insights about the interactions within and among various functional units in nature and to much productive research. On the other hand, it also introduced a simplistic and seriously distorting perspective into evolutionary theory.

The short-term consequence of this rancorous theoretical debate was a wholesale rejection of the concept of group selection. Nevertheless, for the past 20 years David Sloan Wilson (lately with the collaboration of Elliott Sober and with parallel efforts from a growing number of other workers) has been attempting to resurrect group selection on a new foundation. What Wilson calls "trait group selection" (D.S. Wilson 1975, 1980; Wilson and Sober 1989, 1994) refers to a model in which there may be linkages (a "shared fate") between two or more individuals (genotypes) in a randomly breeding population, such that the linkage between the two becomes a unit of differential survival and reproduction. Initially, Wilson assumed that one of the two was an altruist, for he was then intent on accounting for the evolution of altruism without recourse to kin selection. John Maynard Smith (1982) developed a similar model, which he dubbed "synergistic selection," in recognition of the fact that it implies a functional interdependency. (See also Matessi and Jayakar 1976; Wade 1977, 1985; and the discussion in Dugatkin et al., 1992.)

The current revival of group selection theory may perhaps be attributed, in considerable measure, to the growing recognition that it can also entail "win-win" processes. Co-operating groups might provide mutual advantages for their members, so that the net benefits to all participants outweigh the costs. In other words, co-operation is not equivalent to altruism and does not by definition require sacrifices, or genes for altruism. (I refer to it as "egoistic co-operation," to distinguish it from altruism, and Maynard Smith has recently modified his usage of the term "synergistic selection" -- originally associated with altruism -- along the same lines.) This, in essence, is what game theory models of co-operation tacitly postulate (see Maynard Smith 1984, 1989; Axelrod and Hamilton 1981, inter alia.), which is why game theory formulations are largely indifferent to the degree of relatedness, if any, between the co-operators.

Moreover, game theory provides a window into a vastly larger galaxy of co-operative phenomena that, I submit, reduces the group selection controversy to a sideshow. This alternative formulation was originally developed in *The Synergism Hypothesis: A Theory of Progressive Evolution* (1983) and is summarized in Corning (1995, 1996a). It was also developed independently by Maynard Smith and Szathmary (1995), and it is supported by an accumulating body of research findings across many different specialized disciplines, from molecular biology and microbiology to behavioral ecology and sociobiology -- not to mention the social sciences. (See also Dugatkin and Reeve, 1994, and Dugatkin and Mesterton-Gibbons, 1996, on indirect "by-product mutualism" in evolution and Wilson and Dugatkin, 1997, on the role of "assortative interactions," or behavioral selection, a mechanism of group selection.) This alternative paradigm might be characterized as "Holistic Darwinism."

ON THE CONCEPT OF SYNERGY

Holistic Darwinism is not an oxymoron. The term was coined as a way of highlighting the paradox that selfish genes are, without exception, "selected" in the context of their functional consequences (if any) for various wholes.⁴ Holistic Darwinism is strictly Darwinian in its underlying assumptions about natural selection and the evolutionary process. It has no fundamental quarrel with the theoretical premise of "gene selfishness." Rather, it involves a

different perspective on the causal dynamics of evolution. In his preface to the second edition of *The Selfish Gene*, Dawkins uses the metaphor of a Necker cube -- a two-dimensional drawing of a three-dimensional object that can be perceived in different ways -- to characterize the intent behind his inspired metaphor: "My point was that there are two ways of looking at natural selection, the gene's angle and that of the individual...It is a different way of seeing, not a different theory" (1989/1976:x-xi).

Actually, there are more than two ways of looking at natural selection, and Holistic Darwinism focuses not on genes, or individuals, or even groups as units of selection but on the functional relationships among the "units" at various levels of biological organization, from genomes to ecosystems, and on their consequences for differential survival and reproduction. It involves refocusing the Necker cube on the "interactions" between genes, between cells, between organisms, and between organisms and their environment(s). Perforce, Holistic Darwinism is also about the role of synergy -- the combined effects produced by phenomena that "co-operate" (operate together) -- as a major cause of evolutionary continuity and change.

It should be stressed at the outset that the term co-operation will be used here in a strictly functional sense; it refers to functional interactions. In this conceptualization, co-operation may or may not also be considered selfish or altruistic, mutualistic or parasitic, positive or negative. Such attributes involve additional, post-hoc judgments about the consequences of a co-operative relationship with respect to some separately specified goal or value. (Of course, in Darwinian theory the "operative value" is survival and reproductive success.) By the same token, a co-operative relationship may or may not be voluntary. Slavery, in nature and in human societies alike, involves a form of involuntary co-operation, and so (presumably) does the host's role in a parasitic relationship.

Accordingly, a key point about co-operation as a functional concept is that it is found at every level of living systems. Beginning with the very origins of life, it is a common denominator in all of the various formal hypotheses about the earliest steps in the evolutionary process (reviewed in Corning 1996a). All share the common assumption that co-operative interactions among various component parts played a central role in catalyzing living systems.

Similarly, at the level of the genome, it goes without saying that genes do not act alone, even when major single-gene effects are involved. Indeed, the human genome sequencing project has so far established, among other things, that there are in fact 1,195 distinctive genes associated with the human heart, 2,164 with white blood cells and 3,195 with the human brain (see Little 1995). The functional (morphogenetic) implications behind those numbers are awesome to contemplate.⁵ As Richard Dawkins himself so eloquently put it in a more recent book, *The Blind Watchmaker* (1987/1986):

In a sense, the whole process of embryonic development can be looked upon as a cooperative venture, jointly run by thousands of genes together. Embryos are put together by all the working genes in the developing organism, in collaboration with one another.... We have a picture of teams of genes all evolving toward cooperative solutions to problems...It is the 'team' that evolves (pp., 170, 171).

The origin of chromosomes, likewise, may have involved a co-operative/symbiotic process (see Maynard Smith and Szathmáry 1993). Sexual reproduction, one of the major outstanding puzzles in evolutionary theory, is also a co-operative phenomenon, as the term is used here. Although there is still great uncertainty about the precise nature of the benefits, it is assumed

that sexual reproduction is, by and large, a mutually beneficial joint venture.

As we move up "the great chain of being" (to borrow that still-useful anachronism), we find further variations on the theme of functional co-operation. Once upon a time bacteria were considered to be mostly loners, but no longer. It is now recognized that large-scale, sophisticated co-operative efforts -- complete with a division of labor -- are commonplace among bacteria and can be traced back at least to the origin of the so-called stromatolites (rocky mineral deposits) that were constructed by bacterial colonies some 3.5 billion years ago (Shapiro 1988; Shapiro and Dworkin 1997; Margulis 1993; Bloom 1997). Shapiro suggests that bacterial colonies can be likened to multicellular organisms.

Eukaryotic cells can also be characterized as co-operative ventures -- obligate federations which may have originated as symbiotic unions (parasitic, predatory or perhaps mutualistic) between ancient prokaryote hosts and what have now become cytoplasmic organelles, particularly the mitochondria, the chloroplasts and, possibly, eukaryotic undulipodia (cilia) and certain internal structures that may have evolved from structurally-similar spirochete ancestors (Margulis 1993). The phenomenon of symbiosis, by definition a category of co-operative relationships in nature, provides yet another example. Not only has the darker side of symbiosis -- parasitism -- gained new prominence over the past decade or so but more benign commensalistic and mutualistic forms of symbiosis are also more widely appreciated (see below).

Sociobiology is also, by definition, concerned with co-operative relationships among conspecifics, interactions which can provide a variety of adaptive consequences for the participants. As shown by the many field studies and laboratory experiments that were inspired by inclusive fitness theory and game theory, the social interactions that occur in nature among members of the same species may be perturbed by free-riders, "defectors", exploiters, conspecific parasites, etc., yet the fact remains that within-species co-operative behaviors are fairly common and encompass a broad array of survival-related functions, including: (1) hunting and foraging collaboratively, which may serve to increase capture efficiency, the size of the prey that can be pursued, or the likelihood of finding food patches; (2) joint detection, avoidance of and defense against predators, the forms of which range from mobbing and other kinds of coordinated attacks to flocking, herding, communal nesting and synchronized reproduction; (3) shared protection of jointly acquired food caches, notably among many insects and some birds; (5) co-operative movement and migration, including the use of formations that increase aerodynamic or hydrodynamic efficiency and reduce individual energy costs and/or facilitate navigation; (6) co-operation in reproduction, which can include joint nest-building, joint feeding and joint protection of the young; and (7) shared environmental conditioning.

Neo-Darwinian theory -- as purified by the selfish gene perspective -- attributes evolutionary change to competition among the "replicators" -- the ultimate units of information transfer in evolution. In the classical neo-Darwinian model, co-operation plays a decidedly subsidiary role. But if we shift our perspective and view evolution as an ecological and economic process -- a "survival enterprise" in which living systems and their replicators are embedded -- then differential reproductive success may be viewed as the result of a complex interplay of competitive and co-operative interactions (along with a variety of other factors), both within and among functionally interdependent units of ecological interaction. Our focus shifts to the activities of the "vehicles" (in Dawkins's terminology) or the "interactors" (in the terminology of David Hull, 1980) -- and, more important, to the bioeconomic consequences of their functional interactions.

It has been a cardinal assumption of neo-Darwinism that co-operation in nature is a phenomenon that is at odds with the basic principle of gene competition, and that extraordinary conditions are required to overcome the inherent selective bias against the evolution of co-operation. This assumption is what accounts for the importance attached to inclusive fitness theory (or kin selection, in Maynard Smith's term) and to game theory. However, a functional/ bioeconomic perspective on the evolutionary process challenges that point of view. Not only is co-operation (broadly defined) fairly common in nature but synergistic effects (the functional consequences of co-operation), it is argued, have played an important causal role in evolution, especially in relation to the evolution of complexity. To put it baldly, functional synergy explains the evolution of co-operation in nature, not the other way around. In other words, functional groups (in the sense of functionally integrated "teams" of co-operators of various kinds) have been important units of evolutionary change at all levels of biological organization; "functional group selection" is thus a ubiquitous aspect of the evolutionary process.⁶ This is obviously a highly contentious assertion. Let me briefly summarize the evidence.

CONSIDER THE EVIDENCE

If co-operation in nature is not largely dependent on inclusive fitness, we would expect to find a significant degree of decoupling in the natural world between genetic relatedness and co-operation, and, in fact, there are at least four sources of evidence for this proposition. First, there is the entire domain of symbioses. Here we can observe a wide range of co-operative relationships that can only be accounted for in bioeconomic, cost-benefit terms. Kinship is largely irrelevant. Indeed, many types of symbioses, such as the estimated 20,000 species of lichen partnerships involving approximately 300 different genera of fungi, or the Rhizobium-like bacteria that form root nodules with some 17,500 species in 600 genera of plants, reflect a plethora of independent inventions. In other words, many different species may discover and utilize the same functionally-advantageous co-operative relationships. (As Maynard Smith, 1989, has noted, extreme non-specificity is the rule among mutualists, whereas parasitism is highly specific.) The case for "symbiogenesis" as a significant factor in evolution was documented by participants at a 1989 conference on the subject and in a subsequent volume edited by Margulis and Fester (1991). Among the extensive evidence that was presented:

- Mutualistic or commensalistic associations (not to mention parasitism) exist in all five "kingdoms" of organisms, as defined by Whittaker and modified by Margulis and Schwartz (1982). Most extant species may, in fact, be either a product of or currently involved in (or both) endo- or ecto-symbioses. Elsewhere, Bermudes and Margulis (1987) documented that 27 of 75 phyla in the four eukaryotic kingdoms (or 37%) exhibit symbiotic relationships.
- Silurian and Devonian plant fossils have been found to contain structures closely resembling the symbiotic "vesicles" produced by modern VAM (mycorrhizal) fungi (Smith and Douglas 1987), and over 90% of all modern land plants establish mycorrhizal associations (Lewis 1991).
- Land plants may have arisen through a merger between fungal and algal genomes, as sort of inside-out lichens. In any case, it is evident that modern land plants represent a joint venture between fungi and green algae (Pirozynski and Malloch 1975; Atsatt 1988, 1991).

- Approximately one-third of all known fungi are involved in mutualistic symbioses (e.g., lichens), many of which have conferred on their partnerships the ability to colonize environments that would not otherwise have been accessible to them (Kendrick 1991).
- Virtually all species of ruminants, including some 2,000 termites, 10,000 wood-boring beetles and 200 Artiodactyla (deer, camels, antelope, etc.) are dependent upon endoparasitic bacteria, protocists or fungi for the breakdown of plant cellulose into usable cellulases (Price 1991).
- Within the teeming communities of organisms that have recently been discovered in proximity to various sea floor hydrothermal vents, there are a number of symbiotic partnerships between chemoautotrophic (sulfur-oxidizing) bacteria and various invertebrates, which rely on the bacteria for their carbon and energy requirements (Vetter 1991).
- Most bacterial cells congregate and reproduce in large, mixed colonies with many endosymbionts (virus-like plasmids and prophages) and ectosymbionts (metabolically complementary bacterial strains). These congregations call into question the classical notion of a species, in the sense of competitive exclusion and reproductive isolation (Sonea 1991; also Shapiro 1988; Shapiro and Dworkin 1997).

A second body of supporting evidence can be found in the various game theoretic models of co-operation between unrelated individuals, along with the substantial research literature that these models have inspired. (These will be discussed further below.) Third, there is the entire category of outbreeding reproduction, a class of co-operative behaviors which, by definition, falls outside of the inclusive fitness model. Finally, over the past decade or so there have been many field and laboratory studies of co-operation among conspecifics that are inconsistent with inclusive fitness theory and/or suggest that the particular behaviors in question are more satisfactorily explained in bioeconomic terms, although co-operation remains more likely to occur in closely-related, or at least familiar, animals.

A detailed summary of this discordant evidence (including 28 recent field and laboratory studies and seven reviews of the older literature) can be found in Corning (1996a) (see also the careful analysis by Goodnight and Stevens 1997). One particularly well-documented illustration is the food-sharing behavior among vampire bats (*Desmodus rotundus*), which clearly demonstrates the power of functional/bioeconomic factors to transcend the influence of genetic relatedness in shaping co-operative behaviors (Wilkinson 1984,1988,1990). If gene competition were of overriding importance, the sharing of blood among vampire bats (their exclusive food-source) would be confined to close relatives. The reason is that blood sharing in this species has very high fitness value; an individual bat that fails to feed for two nights in a row will die. In field studies as well as controlled observations in captive groups over a ten-year period, Wilkinson found that blood-sharing both between relatives (matrilines) and non-relatives was extensive. Both relatedness and prior association proved to be important facilitators. Moreover, quantitative cost-benefit analyses showed that the cost to donors was relatively low (in effect, they were sharing their surpluses), while the fitness benefits to recipients was relatively high. When this was combined with the fact that the donors' generosity was usually reciprocated later (i.e., "reciprocal altruism" sensu Trivers, 1971,1985), there was a significant increase in the mutualists' joint fitness. Wilkinson concludes: "Reciprocity is likely to be more beneficial than kin selection -- provided that cheaters can be detected and excluded from the system" (1990:82).

Two themes stand out in the many other examples that are described in Corning (1996a): (1) the importance of bioeconomic cost-benefit considerations in co-operative relationships and (2) the presence of synergy -- combined functional effects (payoffs) which are jointly produced and provide benefits to the co-operators that are greater than would otherwise be possible. As Maynard Smith and Szathmáry put it in *The Major Transitions in Evolution* (1995), if an individual can produce two offspring on its own but by co-operating in a group consisting of "n" individuals can produce "3n" offspring, it pays to co-operate. (An application of this perspective to avian species can be found in Emlen 1996.)

GAME THEORY REVISITED

Game theory, viewed in the proper light, is also consistent with Holistic Darwinism. Game theory suggests that the evolution of co-operative behaviors depends on an appropriate set of strategic circumstances. Although the focus has always been on the behavioral context and the strategies of the "players," if one looks closely at the various game theory formalizations they tacitly depend on an interaction between the behavior of the players and the structure of the payoff matrix. And if one looks closely at the payoff matrices in some of the "classic" formulations, like Tit-For-Tat, the co-operative strategies in turn depend on synergy. In Axelrod and Hamilton's (1981) model, mutual defection yielded one point each; asymmetrical co-operation (parasitism?) yielded 5 points for the "defector" and none for the co-operator; and mutual co-operation yielded a total of six points, evenly divided. Furthermore, defectors would be penalized in subsequent "rounds" (it was conceived as an iterated game) so that mutual co-operation becomes an increasingly rewarding option over time. In effect, this amounts to a quantification of synergy; the implicit economics of the game are critically important.

But what about "cheating" or "defection" (the Prisoner's Dilemma)? Maynard Smith and Szathmáry (1995) have proposed a response in terms of game theory, as illustrated in the two diagrams below. (I have taken the liberty of revising the payoff values that were utilized by Maynard Smith and Szathmáry to accord with a more explicit assumption about the object of the game, namely, that the oarsmen are both seeking to cross a river.) The first diagram involves a "sculling" model in which two oarsmen each have a pair of oars and row in tandem. In this situation, it is easy for one oarsman to slack off and let the other one do the heavy work. This corresponds to the Prisoner's Dilemma game. However, in a two-person "rowing" model, each oarsman has only one opposing oar. Now their relationship to the performance of the boat is interdependent. If one oarsman slacks off, the boat will go in circles. In this case, mutual co-operation becomes an evolutionarily stable strategy and defection is totally unrewarding; in the absence of teamwork, the boat will not reach its goal.

Figure I: Sculling Versus Rowing Games

(Ed. note: for technical reasons, this figure could not be included online -- please contact Peter Corning (pacorning@complexsystems.org) for more information.)

Maynard Smith and Szathmáry conclude that the rowing model is a better representation of how co-operation evolves in nature: "The intellectual fascination of the Prisoner's Dilemma game may have led us to overestimate its evolutionary importance" (1995:261). Indeed, as Peck (1993:195) observed: "The position of [stable] equilibria (and hence the frequency of co-operators) depends on the size of the various payoffs that define the Prisoner's Dilemma

game." (See also Dugatkin et al., 1992; Brems 1996.)

AN EVOLUTIONARY THEORY OF GOVERNMENT

If many forms of co-operation are functionally interdependent and thus self-policing, many more are not. The problems of cheating, defection, and "free-riders" -- phenomena that the selfish gene metaphor has helped to illuminate -- are real. But, in retrospect the problem may have loomed much larger in theory than it does in fact; our models may have been too pessimistic about the constraints on errant behavior in co-operative relationships. In effect, the games may have been unintentionally "rigged." Consider some of the common assumptions in Prisoner's Dilemma games: The games are always voluntary and democratic; each player is free to choose his/her own preferred strategy, and the opposing player has no means available for coercing choices, or compliance. Also, the players are not allowed to communicate with one another in an effort to reduce the uncertainties in the interactions. Furthermore, defectors are usually rewarded handsomely for cheating while the co-operators are denied the power to prevent defectors from enjoying the rewards, much less punishing them for defection. Such "grade inflation" for defection biases the game in favor of cheating. Worse yet, in iterative games the players are forced to continue playing; they cannot exclude or ostracize a defector. They can only retaliate by themselves defecting and hoping thereby to penalize the other player.

A tacit rebuttal to this formulation was incorporated into a new kind of Prisoner's Dilemma model developed by Nowak and Sigmund (1993) called "Pavlov," which the authors suggest can outperform Tit-For-Tat. They call their strategy "win-stay, lose-shift," and the significance of this innovation is that, in contrast with an iterated game in which the players must continue playing regardless of the outcome, in Pavlov they have the choice of leaving the game if they don't like the results. In other words, a player may also have the power to exercise some control over the behavior of a defector by denying to that player future access to the game and its potential benefits. Punishments as well as rewards may be utilized as a means of keeping the game honest and, more important, as a means of restricting the game over time to mutual co-operators.

In addition to such suggestive formalizations, there is increasing evidence that a policing function does in fact exist in nature (see especially Boyd and Richerson 1992; Clutton-Brock and Parker 1995; also Frank 1995,1996; and the analysis in Michod 1996). As Clutton-Brock and Parker point out in the summary of their review article on the subject: "In social animals, retaliatory aggression is common. Individuals often punish other group members that infringe their interests, and punishments can cause subordinates to desist from behaviour likely to reduce the fitness of dominant animals. Punishing strategies are used to establish and maintain dominance relationships, to discourage parasites and cheats, to discipline offspring or prospective sexual partners and to maintain co-operative behaviour" (1995:209). Evidence of a policing function has also been documented in social insects (Ratnieks and Visscher 1989), naked mole-rats (Sherman et al., 1991), primates (de Waal 1996) and, needless to say, *Homo sapiens*.

From a functional (synergy) perspective, if co-operation offers sufficient benefits it may be in the interest of some individuals to invest in coercing the co-operation of others. Inclusive fitness provides one possible explanation for punishment as a successful strategy in social groups. Another might be the sort of individual fitness tradeoffs referred to above. But group selection may also provide a mechanism. The enforcement of co-operation in the "public

interest" might have significant fitness-enhancing value for groups that are in competition with other groups, or other species. (In effect, we are resurrecting Darwin's tripartite explanation of social evolution.) Maynard Smith's (1982, 1983, 1989) "synergistic selection" model is relevant here. The model suggests that, if co-operative interactions among two or more individuals -- related or unrelated -- produces selectively advantageous synergistic effects for all parties (on average), the co-operating "players" may become a unit of selection. A synergistic functional group might be favored in competition with other groups, or with ecological competitors from other species, or with the statistical probability of their survival and reproduction in the absence of co-operation. (More broadly, synergistic selection can be defined in terms of gene combinations that enable/induce synergistic functional effects at various levels of biological organization. For a model related to the multicellular level, see Michod 1996.)

SYNERGISTIC SELECTION

The concept of functional group selection, or synergistic selection, can be illustrated by returning to Maynard Smith and Szathmáry's sculling and rowing models, as described above. What if the object of the game were changed? Rather than merely crossing a river (say), now the two oarsmen in each boat share the objective of winning a race against the other boat. Now it has become a functional group selection game (see Figure II). In this situation, if either oarsman were to defect, their "team" might lose the race; only all-out co-operation would provide rewards for either player. (Note that the two payoff matrices are now identical.) Now the sculling and the rowing games are functionally equivalent in the sense that the performance of either boat depends upon both oarsmen; they have both become "functional groups"; there is "synergistic selection." Furthermore, whether the oarsmen are related or not is irrelevant.

Figure II: A Group Selection Game

(Ed. note: for technical reasons, this figure could not be included online -- please contact Peter Corning (pacorning@complexsystems.org) for more information.

Below are a few specific examples of synergistic selection:

- In insects, Page and Robinson (1991) conducted an analysis of their own and other researchers' data on the division of labor in honey bees, including a number of computer simulations, and concluded that natural selection operated on colony-level parameters. Oldroyd et al., (1992a,b) also studied the genetics of honey bee colonies and concluded that colony performance was also influenced by the interactions among subfamilies, a colony-level parameter. Fewell and Winston (1992) conducted a study that examined the relationship between pollen storage levels in honey bee colonies (a group-level parameter) and individual forager efforts; not only was the correlation strong, but the researchers detected evidence of a homeostatic "set point." And Guzmán-Novoa et al., (1994) reported on a study that was focussed on the relationship between colony-level natural selection and the level of effort associated with various components of the division of labor in honey bee colonies (see also Calderone and Page 1992).
- An older study by Hoogland and Sherman (1976) examined in detail the influence of six possible disadvantages and three potential advantages of colonial nesting in 54 colonies of the Bank Swallow (*Riparia*), ranging in size from 2 to 451 members.

Hoogland and Sherman concluded that the disadvantages were not very burdensome and, more important, that the maintenance of coloniality was most strongly associated with group-level defensive measures, which differentially benefitted the larger colonies. Although potential predators were not more frequent visitors to large groups, they were detected much more quickly and were mobbed by greater numbers of defenders; predators were also subject to more vocal commotion; and, bottom line, larger colonies were more effective overall in deterring predators.

- Scheel and Packer (1991), in a study of female African lions, found that the average degree of relatedness among the animals had no bearing on their propensity to engage in group hunting. The key variable was the potential for synergy; successful hunting of larger prey required group hunting. And in a separate study by Packer et al., (1990), it was concluded that the dynamics of female lion grouping were also strongly influenced by the need to defend their cubs (often a group-level function) and to compete against neighboring prides. In both situations, larger groups had an advantage.
- Finally, Maynard Smith illustrated his 1982 article on synergistic selection with, among others, the examples of orb-web spiders (*Metabus gravidus*), where groups of 15-20 females may co-operate in building a joint web to span a stream where prey are abundant; tropical wasps (*Metapolybia aztecoides*) that establish joint nests; and coalitions of lion males that co-operate in taking over and holding a pride. (It should also be noted that Wilson and Sober, 1994, in an in-depth target article on the subject, provide a compendium of over 200 references on group selection, of which 35 are identified as field or laboratory research efforts. See also the in-depth study of group selection in social bees in Moritz and Southwick 1992.)

DOWNWARD CAUSATION

Closely related to the notion of functional group selection, or synergistic selection, as an evolutionary phenomenon is the concept of "downward causation." The term was actually coined by psychobiologist Roger Sperry (1969, 1991, inter alia) in connection with the functional organization and operation of the human brain -- i.e., cybernetic control processes. (It may be that psychologist Donald Campbell, 1974, developed the concept independently.) Sperry was fond of using as an illustration the metaphor of a wheel rolling down hill; its rim, all of its spokes, indeed all of its atoms, are compelled to go along for the ride.

We will use the term here in a slightly different sense. Downward causation in this context refers to the selective influences that have shaped the evolution of co-operative phenomena generally and complexity in particular. Why do selfish genes co-operate in ways that produce teamwork which, in turn, leads to interdependency? What compels them to subordinate their interests to the interests of the "whole"? To be specific, how did morphological castes and a division of labor evolve in army ants? How do reproductive controls evolve in mutualistic symbioses where, as Margulis (1993) points out, there must of necessity be reproductive synchronization if the relationship is to remain stable? (See also the discussion of "sociogenesis" in E.O. Wilson 1985; also Buss 1987; Smith 1992; and the examples cited in Leigh 1991.) Equally important, how can the potential for cheating among selfish genes (or selfish individuals) be constrained?

Downward causation in an evolutionary context refers to the fact that the functional

(synergistic) properties of the whole become a selective "screen" -- a significant influence on the differential survival/reproduction of the parts. Sometimes the parts might be disadvantaged (e.g., non-reproductive workers), and kin selection may help us to understand how such sacrifices for the common good may occur. But, as the evidence cited above indicates, kinship is not a sine qua non. The whole may also be sustained by fitness tradeoffs; that is, the costs may be offset by commensurate benefits. For instance, an animal that is at risk from predators might suffer a reduction in its relative reproductive fitness in a social group setting, but it may also enjoy greatly enhanced odds of survival and absolute fitness. (This may help to explain why defeated contenders for breeding privileges sometimes stay on in the group and may even serve as helpers.) To quote Dawkins again: "In natural selection, genes are always selected for their capacity to flourish in the environment in which they find themselves...But from each gene's point of view, perhaps the most important part of its environment is all the other genes that it encounters [his emphasis]...Doing well in such environments will turn out to be equivalent to 'collaborating' with these other genes" (1987/1986: 170,171).

In some cases, the whole may represent an unalloyed benefit for the parts with little or no costs. Many cases of mutualistic symbioses seem to fit into this category. For instance, Margulis (1993) is adamant about the co-operativeness, promiscuity (and evolutionary significance) of bacterial colonies. (See also the parallel argument of Shapiro, 1988.) Thus, an isolated bacterium would be cut off from access both to the extensive gene swapping and the collective environmental "intelligence" (information) that commonly exists in bacterial colonies, not to mention the advantages of a division of labor and various collaborative efforts. Among mammals, some Cataceans may also fit the mutualistic category, although not enough is as yet known for certain about their breeding patterns (see Würsig 1988, 1989). Conversely, the power of a social group to isolate or ostracize a free-rider can be a significant deterrent and an agency of negative (downward) selection.

In any case, the synergies that result from co-operation may selectively "reinforce" co-operative behavior (to use the terminology of behaviorist psychology), and this may in turn differentially favor the evolution of relevant morphological/psychological characters over time. Thus, army ant sub-majors have acquired anatomical specializations that facilitate their role as "porters," and humans have evolved psychological predispositions that help us to orchestrate (and even enjoy) our participation in group activities.

In sum, the relevant "parameters" for explaining co-operative phenomena in nature (and in human societies) may include genetic relatedness, but kinship is neither necessary nor sufficient. The key lies in functional synergy and its bioeconomic consequences for differential survival and reproduction in a specific context; functional synergy is the frequently unappreciated common denominator in various models of co-operative behavior in sociobiology.

SUPERORGANISMS

Holistic Darwinism, and a multilevelled view of the evolutionary process, may also provide some additional insight into the venerable concept of a "superorganism". A well-known metaphor for social wholes that many theorists have found distasteful (e.g., George Williams and Richard Dawkins), the term superorganism was coined, in its modern incarnation, by Herbert Spencer (1897/1874-82). Spencer used it to connote the fact that societies exhibit a degree of functional interdependence that is analogous to the division of labor found in

complex organisms.⁷ Subsequent generations of theorists, both in biology and in the social sciences, have freely borrowed Spencer's term (often without attribution) and have generally used it either more loosely or more narrowly than Spencer intended. Sometimes the superorganism concept has even been endowed with mystical properties or an autonomous self-interest, making it a sort of metaphorical antipode of Dawkins's selfish gene. At the other extreme, Moritz and Southwick (1992), while arguing for a revival of the concept after a generation of being out of favor among biologists, nonetheless chose to use a very restrictive definition. Among other things, they require a segregation of sterile and reproductive castes, which pretty much confines their usage to eusocial insects. Not even a human society is a superorganism by that standard.

We prefer to define a superorganism, in the spirit of Spencer (and Plato before him), as: a behavioral system (social system) in which there are functional interdependencies and coordinated, joint actions with respect to one or more collective, goal-related activities. Thus, it can be said that the term superorganism refers only to a limited (and variable) aspect of any given social organization. Moreover, a particular group's superorganismic properties may change over the course of time. For example, while some of the coalitions and alliances that occur in various primate species are stable and long-lasting, many others are ephemeral, short-lived and situation-specific (de Waal 1982, 1996). Yet, regardless of the duration, each of these groupings can be characterized by an implicit collective goal and the coordination of individual behavior toward the realization of that goal, whether it be group defense, group hunting, dominance competition, rivalry over mating privileges, or the like.⁸

As Spencer suggested, the concept of a superorganism is also closely linked to what economists have traditionally called a "division of labor" -- though in many cases it could be termed, perhaps more felicitously, a combination of labor.⁹ Not only have various divisions/combinations of labor played a central role in the evolution of human societies, but they have also been prodigious generators of functional synergy in the overall evolutionary process. To cite a few, perhaps less familiar examples:

- Anabaena provides an unusual case of a primitive division of labor in a single-celled cyanobacterium. Anabaena engages in both nitrogen fixation and photosynthesis, a dual capability that gives it a functional advantage. However, these two processes are chemically incompatible. The oxygen produced by photosynthesis inactivates the nitrogenase required for nitrogen-fixing. Anabaena has solved this problem by complexifying. When nitrogen is abundantly available in the environment, the cells are uniform and in character. However, when ambient nitrogen levels are low, specialized heterocysts are developed that lack chlorophyll but are able to synthesize nitrogenase. The heterocysts are then connected to the primary photosynthesizing cells by filaments. Thus, a compartmentalization and specialization exists -- a sort of incipient multi-cellularity -- which benefits the "whole" (Shapiro 1988).
- Volvocales are a primitive order of algae that exhibit a great variety of somatic and reproductive patterns, and sizes. In a detailed study by Bell (1985), it was noted that the largest of the Volvox species, which are visible to the naked eye, also display a division of labor (and a combination of labor) between a multicellular soma and segregated, encapsulated germ cells. Comparative analyses have suggested some of the functional benefits. The division of labor appears to facilitate growth and results in a much larger overall size. It also results in more efficient reproductive machinery (namely, a larger number of smaller germ cells). Bell hypothesizes that in this case larger overall size also results in a greater survival rate. It happens that these aquatic, planktonic algae are subject to predation from filter feeders, but there is an upper

limit to the prey size that their predators can consume. Integrated, multicellular colonies are virtually immune from predation by filter feeders.

- Morphological specializations are often a reflection of a division of labor. Hasegawa (1993) concluded that early production of major workers in the dimorphic ant (*Colobopsis nipponicus*) plays a decisive role in differential colony survival. The reason is that the larger workers are able to ward off raiders by plugging up the colony entrances with their heads. Likewise, in colonies of army ants the so-called "sub-majors" (or porters), team up to carry sometimes very large prey which, if split up into pieces, would be more than each ant could carry alone (Franks 1989).
- A study of hunting behavior in lions by Stander (1992) speaks to the assertion (by Williams and others) that co-operative hunting behaviors may only be fortuitous effects. Stander's data for 486 group hunts by lions (*Panthera leo*) in Namibia displayed a clear pattern of coordinated roles among "wings" and "centres", or "drivers" and "catchers", with morphologically-differentiated individual animals commonly occupying the same role. Stander concluded: "Co-operative hunts were more successful than non-coordinated group hunts...and hunting success was further improved when lionesses hunted in their preferred stalk categories." (Some previous studies of group hunting had characterized as "cheating" behaviors what Stander interprets instead as, at least in some cases, an unrecognized role in a division of labor.) Similar coordinated hunting behaviors have also been observed in other species as well -- e.g., dolphins and whales (see Würsig 1989).

THE "SELFISH GENOME"

All of this holism begs a question, however. Do wholes have goals that transcend the goals of the parts? Can wholes come to exercise a degree of autonomous control as wholes? In other words, can we postulate a "selfish genome?" The neo-Darwinian response, it appears, is a somewhat equivocal "no". Richard Dawkins (1989/1976) became famous for the assertion that organisms are merely "robot vehicles" that have been blindly programmed to serve the interests of the genes, yet (as noted earlier) he also allowed that genes can be selected for their ability to serve the interests of the gene team. And George Williams (1966), while acknowledging the wholeness and unity of organisms, characterized many of the claims regarding superorganisms as figments of a "romantic imagination" (p.220). In truth, some of these superorganismic claims were inflated, but Williams's view of this issue was perhaps a bit too-jaundiced: "A wolf can live on elk only when it attacks its prey in the company of other wolves with similar dietary tendencies. I am not aware, however, of any evidence of functional organization of wolf packs" (pp. 217-218).

In contrast, Holistic Darwinism postulates that wholes at various levels of biological organization may evolve mechanisms that permit partially-autonomous control over the parts and their actions. Some insight into how superordinate controls can evolve in nature is provided in Egbert Leigh's various discussions of how groups might act to contain or override individual advantages for the good of the group -- what he calls the "parliament of the genes" (Leigh 1971, 1977, 1983, 1991; see also Michod 1996). Leigh's argument, in essence, is that, if the potential payoffs (synergies) for each of the participants in a co-operative relationship are high enough, this could also provide an incentive for the imposition of "government" in the "public interest." Leigh

even draws on Adam Smith's reasoning, not from *The Wealth of Nations* (1776) but from the less well-known *The Theory of Moral Sentiments* (1759). Although it is not widely appreciated, Smith argued for the necessity of a system of laws and appropriate means of enforcement in human societies to resist the dangers of unfettered self-interest. (pp., 86, 88-89, 340-341).

A key to understanding the evolution of "government" at various levels of biological organization may lie in what could be called the "paradox of dependency." Although co-operative interactions may produce individual fitness-enhancing synergies, a tradeoff may be that the more valuable the benefits the more likely it is that the parts will become dependent upon the whole. As the benefits of co-operation increase, so may the costs of not doing so. Wholes may then become obligatory survival units, one consequence of which may be that a decrement in the performance of the whole might result in the demise of the parts. An example can be found in a long-term study by Jeon (1972, 1983). A strain of *Amoeba proteus* were initially infected with bacterial parasites that were resistant to the hosts' digestive enzymes. After 200 generations, or 18 months, a mutualistic relationship had become established, and after 10 years the symbionts had developed complete interdependence. (Jeon, 1992, has also illuminated some of the biochemistry of these changes.) It should also be noted that Margulis (1993) makes a similar argument with respect to the integration of symbiotic organelles in the ancestral eukaryotic cells. An obvious implication is that the incentives (both proximate and ultimate) for imposing government over the parts are likely to increase in relation to the degree of interdependency among the parts, and the advantages of operating as a superorganism.¹⁰

In fact, in what may appear to be an utter contradiction of classical neo-Darwinism, it may often be the case that it is in the interest of a gene, or an individual, to promote the well-being of an interdependent "other", simply because functional interdependence means just that; it's "one for all, and all for one," to borrow a legendary slogan. Consider this hypothetical example. If one of the two oarsmen in the rowing game (above) should suffer from thirst and dehydration in the summer heat (he forgot his water bottle), his partner might decide to share his/her water supply, in the interest of reaching their joint goal. Or, to cite a concrete example from nature, consider the exquisitely complex energy-production services that the mitochondria provide for eukaryotic cells, in their own direct self-interest. Or, for that matter, consider the innumerable situations in human societies where our well-being depends, unequivocally, upon the performance of others -- airline pilots, railroad engineers, surgeons, and the other motorists that we encounter on the highways, to name a few. How do we explain these co-operative relationships? They have nothing to do with altruism, kin selection, reciprocal altruism or even (strictly speaking) tit-for-tat mutualism. They are sustained by "pure" self-interest.

One compelling example of a superorganism in nature involves the naked mole-rat (*Heterocephalus glaber*), a unique African rodent species that lives in large underground colonies (usually numbering 75-80 but sometimes over 200). Naked mole-rats represent a particularly significant illustration of an economic division of labor, because these odd-looking animals -- affectionately dubbed "sabre-toothed sausages" -- have morphologically-specialized castes and a pattern of breeding restrictions that is both unique among mammals and suggestive of eusocial insects. Typically (but not always), the breeding is done by a single "queen", with other reproductively suppressed females waiting in the wings. The smallest of the non-breeders, both males and females, engage co-operatively in tunnel-digging, tunnel-cleaning and nest-making, as well as in carrying pups, foraging and the

transportation of food (succulent tubers) within the colony's often extensive tunnel systems. (One investigator, Robert A. Brett, found a tunnel system in Kenya that was more than 3 kilometers long, altogether, and occupied an area equivalent to 20 football fields.) Sherman et al., (1992:75), who have studied these animals extensively, provide the following description of the mole-rats' co-operative tunnel-building efforts:

The animals line up head-to-tail behind an individual who is gnawing [with its oversized, powerful front teeth] on the earth at the end of a developing tunnel. Once a pile of soil has accumulated behind the digger, the next mole-rat in line begins transporting it through the tunnel system, often by sweeping it backward with its hind feet. Colony mates stand on tiptoe and allow the earthmover to pass underneath them; then, in turn, they each take their place at the head of the line. When the earthmover finally arrives at a surface opening, it sweeps its load to a large colony mate that has stationed itself there. This "volcanoer" [so-called because its actions appear to an observer outside to resemble miniature volcano eruptions] ejects the dirt in a fine spray with powerful kicks of its hind feet, while the smaller worker rejoins the living conveyor belt.

The vital and dangerous role of defense in a mole-rat colony is also allocated to the largest colony members, who respond to intruders, such as predatory snakes, by trying to kill or bury them and by sealing off the tunnel system to protect the colony. The mole-rats' "militia" will also mobilize for defense against intruders from other colonies.

Why do mole-rats utilize this highly co-operative survival strategy? Eusociality is relatively rare in nature, and the traditional view has been that a haplodiploid reproductive pattern provides a genetic facilitator. But this is obviously not the case with mole-rats, which are diploid. (Indeed, it seems that haplodiploidy is neither necessary nor sufficient; all species of Hymenoptera are haplodiploid, but most are not eusocial; on the other hand, all termites are eusocial and diploid.) Sherman et al., (1992) provide a bioeconomic (synergy) explanation for the mole-rat strategy: "We hypothesize that naked mole-rats live in groups because of several ecological factors. The harsh environment, patchy food distribution and the difficulty of burrowing when the soil is dry and hard, as well as intense predation, make dispersal and independent breeding almost impossible. By co-operating to build, maintain and defend a food-rich subterranean fortress, each mole-rat enhances its own survival" (p.78). (See also Sherman et al., 1991.) (Although it is not stressed in the mole-rat research literature, another critically important facilitator is a co-operative relationship -- and synergy -- between the mole-rats and an endosymbiotic bacterium which is able to break down the cellulose in succulent tubers.)

If the bioeconomics -- the functional synergies -- provide an important part of the explanation for the naked mole-rat survival strategy, the "political" aspects are equally important, and are also well-documented. As is the case with many other socially-organized species, naked mole-rats exhibit a combination of self-organized co-operation (pre-programmed individual "volunteerism") and orchestrated social controls that are policed by various coercive means. The control role of the breeding queen is of central importance. The queen is usually the largest animal in the colony (size usually determines the dominance hierarchy), and she aggressively patrols, prods, shoves and vocally harangues the other animals to perform their appointed tasks. Indeed, it has been observed that her level of aggressiveness varies with the relative urgency of the tasks at hand. In addition, the queen acts to suppress breeding

and reproduction on the part of non-queen females, who are always ready to take over that role. (Occasionally other females are allowed to share the breeding function with the queen; why this is so is not known.) The queen also intervenes frequently in the low-level competition that goes on among colony members over such things as nesting sites and the exploitation of food sources. And when the reigning queen dies, there is a sometimes bloody contest among the remaining females to determine her successor.

All of this control activity is facilitated by an elaborate communication system that includes 17 distinct categories of vocalizations -- alarms, recruitment calls, defensive alerts, aggressive threats, breeding signals, etc. In fact, the mole-rats' communication system rivals that of some primate species in its level of sophistication. Thus, a naked mole-rat colony may be characterized as a superorganism with a superordinate system of cybernetic control ("government"), along with clear evidence of downward causation in the mole-rats' morphological specializations and breeding restrictions.

One final point related to "downward causation," "government" and the "selfish genome." At the most basic level of biological organization (the genome itself), there is mounting evidence that the genes do not inhabit a "bean bag" (in Ernst Mayr's felicitous caricature), and that morphogenesis is not a "mindless" process. Rather, it is an organized, cybernetic process which entails the extensive use of superordinate feedback controls (the very essence of a "teleonomic" system). In other words, selfish genes are only citizens on good behavior in the selfish genome, and the outlaws, tax evaders and parasites among them do not have a license to pursue their anti-social interests ad libitum.

EVOLUTION AS A MULTILEVEL PROCESS

There is one other aspect of Holistic Darwinism that should be mentioned briefly. It relates to the traditional distinctions between parts and wholes, individuals and groups, even "self-interest" and the "public interest." During the past decade or so, there has been a growing appreciation of the fact that evolution is a multilevelled, hierarchical (some prefer "holarchical") process, just as survival and reproduction is a multifaceted problem (see especially Koestler 1967; Corning 1983; Brandon and Burian 1984; Eldredge and Salthe 1984; Salthe 1985; Eldredge 1985, 1995; Buss 1987; Grene 1987; Gould 1994; Wilson and Sober 1994; Maynard Smith and Szathmary 1995; Michod 1996). In essence, there is a recognition that natural selection operates at various levels of biological organization -- from genes to ecosystems -- often simultaneously. One implication of this more complex view of evolution is that both competition and co-operation may coexist at different levels of organization, or in relation to different aspects of the survival enterprise. There may be a delicately balanced interplay between these supposedly polar relationships. To illustrate:

- o Eusocial insect species can generally occupy a broader spectrum of habitats and are often able to dominate and even exclude potential competitors among solitary and primitively social species, as noted earlier (see Holldobler and Wilson 1990). Nevertheless, eusocial insect societies are not the harmonious communities that we once supposed. Among other things, there may be intense competition for breeding rights among potential queens and there is evidence of nepotism among the patrines in polyandrous

species.

- A number of ant species establish pleometrotic colonies; multiple foundresses co-operate in initial nest construction and brood production. In at least one case, the desert seed-harvester ant *Messor pergandei*, a study by Rissing and Pollack (1991) has shown that pleometrotic colonies are able to prevail in direct ecological competition with single-foundress colonies; multiple-foundress colonies are able to produce a larger brood raiding force more quickly, and this apparently provides a decisive competitive advantage (group selection). However, other studies of these colonies suggest that one tradeoff may be internal competition among co-foundresses and their offspring -- all very suggestive of human societies.
- Members of African lion prides co-operate and compete with one another in a variety of ways: Females typically hunt large prey in groups, share food and may even share in guarding cubs and defending the pride. As Packer and Rutten (1988) observe, there is evidence of synergy. For instance, a group of females can more effectively defend a kill against scavengers, including other groups. Likewise, a group of males can successfully defend access to a group of females, whereas single males cannot. However, there is also much intra-coalition competition among the males for mating privileges.
- One of the more dramatic examples of the interplay between competition and co-operation concerns the Northern Elephant Seals (*Mirounga angustirostris*). Males of this species, which can weigh up to 4500kg., are legendary for their prolonged and bloody battles for dominance and mating privileges when they come ashore to breed in the winter and early spring. However, the males will only fight when estrous females have formed "harems" of 50 or more. And when the fighting is over, the "alpha" males commonly form coalitions with a half-dozen or more "beta" males, who will defend the perimeter of the harem against other marauding males (in return for which the beta males get limited mating privileges for themselves). Elephant seals generally feed at sea alone, and at great depths, but whenever they are ashore they congregate peacefully in tightly packed "rookeries" that facilitate defense and heat-sharing (a critically-important function in these animals). Males collaborate in this way during their summer moulting season; non-breeding males also aggregate into "loser groups" during the breeding season; females huddle closely together to share heat and defend their pups during the breeding season, and "pods" of weanling pups huddle for warmth and mutual self-defense before setting off on their initial feeding expeditions (Le Boeuf 1985; Le Boeuf and Laws 1994).

EMERGENT EVOLUTION

Closely associated with this multi-levelled paradigm is the venerable concept of "emergent evolution." The concept traces back at least to the 1920s, when C. Lloyd Morgan (1923), Jan Smuts (1926), William Morton Wheeler (1927) and others mounted a theoretical counterattack against the reductionist evolutionary theories of August Weismann (1891, 1902), Hugo de Vries (1901) and others of the so-called "mutationist" school, which many people at that time viewed as an alternative to Darwin's theory.

The underlying theme of emergent evolutionism is familiar to us. The central idea is that evolved "wholes" (organisms, groups and species) are significant units of evolutionary change and are not reducible to the sum of their parts. Some of these early holists, like Smuts, asserted that whole organisms were the "only" unit of evolutionary change. Citing Charles Darwin's flirtation with Lamarckism as a precedent for his own views, Smuts also suggested that "holistic selection," or the actions and choices of organisms, often precede and precipitate evolutionary changes. ("Organic selectionism," as it was more commonly called, has had a checkered history, which goes back to the end of the 19th century -- see Corning 1983, 1995, 1996a and below.)

Although the term "emergent evolution" fell into disuse in the middle years of the century, it reemerged (so to speak) in, of all places, E.O. Wilson's *Sociobiology: The New Synthesis* (1975). In the very opening line of his second, foundation-building chapter, entitled "Elementary Concepts of Sociobiology," Wilson wrote: "The higher properties of life are emergent" (p.7). Wholes cannot be comprehended as a mere sum of their parts, he said. He also asserted that the "new holism," as he called it, is rigorous and testable, not a vague, mystical abstraction. What is the key? (Here I am augmenting Wilson's words.) The difference is that the "new holism" is based on the testable premise that natural selection also acts directly on wholes -- combinations of parts with synergistic functional properties which may be differentially selected, along with their genes, as emergent wholes (i.e., synergistic selection). So far as I know, Wilson's bold challenge to the monolithic reductionism of some of his colleagues was totally overlooked in the ensuing bitter controversy over sociobiology. Ironically, Wilson was portrayed as a genetic determinist (reductionist) and was accused of having "genitis" (the genetic disease), in Sherwood Washburn's pejorative term.

The concept of emergent evolution has had a vigorous revival in the 1980s and 1990s, particularly in paleontology where it is often treated under the heading of "species selection." Although the theoretical roots of the contemporary debate trace back to the early days of population genetics and especially the work of Sewall Wright (1968-78) on what he called "interdemic selection," the term "species selection" was actually coined by Steven Stanley (1975, 1979), who was particularly concerned about how to explain the widely varying patterns of phenotype distributions among species. Needless to say, species selection was quickly challenged (e.g., Bock 1979, Vrba 1980, 1983). Bock characterized it an illusion; the so-called emergent properties of a species can be reduced to the interactions between individual organisms and their environments; any aggregate consequences are epiphenomenal. In a similar vein, Elizabeth Vrba advanced what she called "the effect hypothesis" -- the idea that speciation events could be the incidental consequences of a variety of non-adaptive factors and random accidents. Likewise, Gould (1982), Vrba and Eldredge (1984) and others proposed that the term species selection be narrowed in scope so as to apply, not to statistical patterns or the "aggregate properties" of populations but only to "emergent" higher-level functional properties that have a direct causal influence at the population/species level -- what Kawata (1995) calls "effective properties." An unambiguous case in point would be a bacterial colony, where the individual members reproduce independently and yet each bacterium benefits from various collaborative efforts -- from the food quest to environmental conditioning.

I would argue that the distinction between "aggregate" properties and "emergent" properties is not so clear cut as it may appear. The key criterion for "higher-level" selection is that there are functional interdependencies among the "units". As Michael

Ghiselin (1997) puts it, the aggregate must have some of the properties of an "individual". That is, if the differential survival and reproduction of a given "unit", or all of the units in combination, is materially affected by their relationships with one another (there is a "shared fate"), then it can properly be called emergent selection (synergistic selection). Obvious examples include the many cases in nature where the fitness of any given individual is density- or frequency-dependent -- some function of the size and spatial distribution of a population. Thus, if you are a member of a very small school of dwarf herring, your odds of getting eaten by a predatory barracuda may be considerably greater than if you are in a very large school; your fitness is a function of the "aggregate" size of your group. Likewise, the literature in ecology includes many instances of population "crashes"; for various reasons, a population may fall below some minimum threshold for successfully reproducing itself and may go extinct (as some of our commercial fishermen have been learning to their regret).

A more subtle example of how "aggregate properties" may be irreducible involves the "gene pool" in a sexually reproducing population. One way to illustrate this point is by means of a thought experiment based on H.B.D. Kettlewell's (1955, 1973) classic studies of "industrial melanism." Kettlewell documented that the relative frequencies of two strains of moths found in the English countryside near its industrial cities had changed dramatically over the years. A mottled, "cryptic" strain (*Biston betularia*), originally the dominant form, had gradually been replaced by a darker, melanic form (*Biston carbonaria*). The reason, it was determined, was that the relative visibility of the two strains had markedly changed over time as industrial soot progressively blackened the trees that were the moths' favored resting places. Originally, the cryptic form had been less visible to avian predators, but now they stood out and the darker form blended in much better against the soot-blackened tree-trunks.

Now consider a hypothetical variation on that real-world example of natural selection. Suppose there are two distinct, non-interbreeding species of moths. One species is totally cryptic in coloration (monomorphic), while the other has (initially) a 50-50 mixture of the melanic and cryptic forms (it is polymorphic). Selection from airborne predators commences suddenly (not an unusual occurrence in nature) and operates equally in both species. In the monomorphic species, the population soon goes extinct and all of its genes are history. However, in the polymorphic species, the melanic and cryptic forms continue to interbreed and to maintain the population as a whole, including most of the genes of the melanic form as well. Over time, the frequency of the gene or genes associated with cryptic coloration declines and may disappear from that species' "gene pool" (as the textbook selection equations predict), but all of the other genes that were not subject to negative selection survive and prosper. There has been a form of "group selection," or "interdemic selection," or "species selection" (take your choice) between the two species, involving a species-level genetic "resource". (For a more extensive analysis of this paradigm, to which I am indebted, see Smillie 1995. Also, see Stidd and Wade 1995).

TESTING HOLISTIC DARWINISM

Can Holistic Darwinism be tested? Specifically, can we demonstrate the causal role of synergistic phenomena and functional group selection (synergistic selection) in evolution? There are at least three different ways of doing so. Game theory provides one possible means for formulating testable hypotheses of synergistic selection.

Another method involves either experiments or "thought experiments" (like the one above) in which a major part is removed from the whole and the consequences are then observed (an idea originally suggested by Aristotle in *The Metaphysics*, 1041b11-31, to my astonishment). Thus, for example, it is not hard to imagine what would happen if a major gene were to be removed from the homeobox gene complex, or if the mitochondria were removed from a eukaryotic cell, or the gut bacteria from a termite, or the sub-majors from an army ant colony, or the water supply from a human settlement. A third means of testing for synergistic selection involves comparative analyses of various kinds. Lichens provide a ready-made example. Many of these symbiotic partnerships are facultative, and their constituent alga and fungi can exist independently. However, they do not go it alone in the barren environments which they are legendary for pioneering; their ability to survive in these more rigorous settings is dependent upon their joint capabilities. In short, if synergistic effects are real and measurable, an absence of synergy should also provide measurable comparisons.

Human evolution may provide a singular illustration of the synergistic, functional group selection hypothesis. In effect, the principles which were elucidated above can also be observed in the evolution of the human species, and in cultural evolution as well. For various reasons, the evolution of humankind has often been portrayed as a process that is *sui generis*. Of course, this overlooks the fact that all of evolution can be said to be *sui generis*, given its historical and situation-specific causal dynamics. As Darwin himself put it in *The Descent of Man* (1874/1871), any evolutionary innovation depends upon many "concurrent favorable developments" that are always "tentative" (p. 150). Nevertheless, the evolution of humankind is undeniably one of the more remarkable episodes in evolutionary history.

A number of suggestive and thoughtfully argued theories of human evolution have been advanced over the years. These theories were reviewed and critiqued in depth in Corning (1983), and a "synthetic" explanation was offered there that, in effect, combined Darwin's "tripartite" selection theory of human evolution -- family (kin) selection, mutualism (including reciprocity) and group selection -- with the concept of functional synergism. As Darwin pointed out, and this is a crucial point, the three modes of selection need not be opposed to one another; they can be complementary and mutually reinforcing. In addition, the synergism hypothesis asserts, in essence, that it was the bioeconomic payoffs (the synergies) associated with various forms of social co-operation that produced -- in combination -- the ultimate directional trend over a period of several million years, from the earliest bipedal hominids to modern *Homo sapiens*. That is, the synergies produced by various collaborative behavioral innovations provided "proximate" rewards or reinforcements (as the behaviorists would say) that were substantial enough to create a behavioral "pacemaker" (sensu Ernst Mayr, 1960) for the "progressive" evolution over time of our distinctive wardrobe of biological characteristics. In other words, we invented ourselves in response to various ecological pressures and opportunities -- a paradigm that may be more widely applicable to evolutionary change than is generally appreciated (see Corning 1996a). Here I can only summarize the argument.¹¹

THE SYNERGISM HYPOTHESIS

The traditional approach to explaining human evolution has been to propose a "prime

mover" theory, which is typically portrayed as the "engine" that has powered the course of human evolution. Darwin, in *The Descent of Man* (1874[1871]), singled out the role of tool-making. E.O. Wilson (1975) stressed our primate "preadaptations" and speculated about the possible role of an unspecified "autocatalysis". Bipedalism, which we now know preceded the development of the "big brain," is currently viewed by many theorists as the "breakthrough" development (e.g., Johanson, Leakey, White, etc.). Major climate changes during the Miocene and Pliocene have also been suggested as important precipitating factors (e.g., Coppens, Vrba). Then there are the various competing "group theories": group hunting (Dart, Washburn, Ardrey, Thompson and others), group scavenging (Potts, Blumenshine, Shipman, etc.), female gathering (Zihlman and Tanner), the nuclear family and male provisioning (Lovejoy), collective defense against predation (Kruuk, Kortlandt, Alexander, etc.) and the ever-popular group conflict hypothesis, which traces back to Darwin and Spencer and which has been championed in this century by Dart, Keith, Ardrey, Lorenz, Bigelow, Otterbein, and Alexander, among others. In the latter stages of human evolution, climate change, population growth, food surpluses, the adoption of fire, language development, increased intelligence and warfare have also been singled out as prime movers by various theorists at various times.

Holistic Darwinism suggests the contrarian view that all of these factors were important but that none was sufficient -- the engine is nothing without the car -- and that the answer lies in the unique combination of factors that produced, over time, many compatible and mutually supportive co-operative effects (functional synergies). Indeed, objections can be mounted against every one of the factors cited above, taken individually. For example, bipedalism is not unique to humans; birds are bipedal, after all, and kangaroo forelimbs have atrophied rather than becoming instruments for the skilled manipulation of tools. In fact, hominid bipedalism existed for some millions of years before the "big brain" emerged. Tool-making is also an insufficient explanation; we now know that many species make and use tools, especially our closest relatives the chimpanzees. And, again, crude stone tools were used by our hominid ancestors for perhaps a million years before the more refined and standardized Acheulean tool-kit appeared (Leakey 1994; Tattersall 1995). Group hunting and scavenging are also inadequate explanations, for the same reasons; our ancestors were hardly unique in this regard. The primeval gathering scenario and the nuclear family scenario are appealing, though difficult to support empirically, yet they are in any case insufficient because they overlook other factors -- namely, the often serious threat from potential predators and the premium associated with meat-getting (via scavenging, hunting or both) in the more open savanna-like environment in which some of the later hominid developments most likely occurred. Even the conflict hypothesis -- which Alexander (1979) asserts is both necessary and sufficient -- begs the question: why are there no nation-states composed of chimpanzees, which we now know can be quite warlike? The very absurdity of that idea highlights the fact that there had to be many other factors that "worked together" to propel the process. Indeed, the extensive hominid migrations out of Africa over time suggest that conflict avoidance might well have been a common adaptive strategy.

In a major critique of cultural evolution theories many years ago, anthropologist Elman Service came to this emphatic conclusion: "down with prime movers!" (1971:25) The same can be said, equally emphatically, of the larger process of human evolution. Prime mover arguments invariably take for granted some, or all, of the other requisites for survival and reproduction. Very often they reflect a kind of ecological naivete; they discount the many life-and-death challenges associated with living (and evolving) in a demanding and changeable environment over a period of

several million years. But if no one factor alone can provide a sufficient explanation for the evolution of humankind, then what is sufficient? The answer is that all of the important human traits were necessary and none were sufficient. In effect, there was a mutually-reinforcing synergy among the key innovations -- combined effects that would not otherwise have been possible. Consider a few of the relevant points (here in outline form):

- Bipedalism in a relatively slow-moving primate makes no sense as a primary means of propulsion unless it frees up the hands to (co-operatively) do other things -- namely to grasp, manipulate and carry things (perhaps including our ancestors' progressively more helpless infants) and to fashion and use tools. Bipedalism, manual dexterity and the intelligence needed to exploit these adaptations were synergistic morphological changes that must have supported one another and reinforced a trend.
- Defense against predators and scavenging behaviors, not to mention systematic hunting activities, would have been relatively perilous (and most likely unrewarding) for hominid loners, especially when their competitors were socially organized. Group defense and group food procurement are common strategies in various primates and social carnivores, with suitably rewarding payoffs for the participants; many studies have documented the potential synergies associated with such group behaviors (although the benefits are also context-dependent, and there are frequently significant costs).
- Group anti-predation, group scavenging, group hunting and inter-group conflict are not four competing theories of human evolution but four complementary, mutually-reinforcing forms of co-operative behavior (and synergy), all of which would have favored kin-group selection (at least) and possibly "pure" group selection as well.
- Gathering, scavenging and/or hunting collectively are also hypotheses that are not mutually exclusive. Indeed, a group-living species that could engage flexibly in all of these diverse forms of behavior would most likely enjoy a significant ecological/selective advantage. Not coincidentally, humans have done so routinely in historical times. (Of course, fine-grained questions concerning the evolutionary precedence and relative importance of various human traits remain unresolved, and may perhaps prove to be unresolvable in any definitive sense. However, paleoanthropologist Ralph Holloway has built a strong case, based on a detailed analysis of the neuroanatomical evidence, for his thesis that a major functional reorganization of the hominid brain occurred relatively early in the process, and that these changes reflected significant developments in behavior, social organization and verbal communications. See especially Holloway 1995, 1996.)
- Flexible serial monogamy, nuclear families, female gathering, male provisioning and a division of labor are not separate, conflicting theories of human evolution but, again, complementary pieces in the larger puzzle; they can also help to account for a reduction of within-group conflict and increased ability to support a lengthening of childhood dependency (what Kortlandt calls "the virtuous circle") in an already "K-selected" species. In short, these developments were additional reinforcers for a multifaceted

pattern of synergistic co-operative relationships.

- Finally, major cognitive improvements and fully-developed language capabilities (a highly interdependent, synergistic set of adaptations) were manifestly not the prime movers of human evolution but evolved in the context of their ability to enhance already existing forms of co-operation, along with their attendant functional synergies. It is also highly likely that our proto-linguistic hominid predecessors benefitted greatly from the advantages of jointly-produced and shared information -- just as other social species do, from army ants (Franks 1989, Franks et al., 1991) to chimpanzees (de Waal 1996). (See also Moritz and Southwick 1992; Quiatt and Reynolds 1993; Wilson and Sober 1994.) More elaborate "political" organization and information sharing based on more sophisticated language capabilities can be viewed as secondary, supportive developments that enhanced the synergies (the payoffs) that were responsible for the evolution of group living in the first place.

"MAN MAKES HIMSELF"

In sum, the dominant theme of human evolution may have been the expansion of various modes of social co-operation (including co-operative modes of competition), which have been rewarded with commensurate bioeconomic benefits. To reiterate, competition and co-operation are not mutually exclusive explanations for human evolution; both played an important role in shaping our evolution. Nevertheless, the thesis here is that increasingly potent (and selectively advantageous) forms of social co-operation may have given our ancestors the competitive edge.

As Edward O. Wilson (1975; 1985) has noted, a multifaceted group-living ecological strategy is a relatively rare occurrence in nature. We rightly admire the complex social organization of honeybees, naked mole-rats, army ants and a small number of other highly social species, including some of our close primate relatives. The synergies that have made such collective survival strategies rewarding for various social species are increasingly well documented. We are among that select company, and it has been the key to our evolutionary success. A human society can be characterized as a "collective survival enterprise." We meet our basic survival needs through elaborate networks of social co-operation. We do not know, and likely never will know, the full story of our evolution as a species, although we are gradually adding more details to the outline and making better-informed guesses. However, there is reason to believe that behavioral changes in the direction of greater social co-operation for specific functional purposes were the "pacemakers" that precipitated supportive morphological changes. In a very real sense, as anthropologist V. Gordon Childe (1951[1936]) put it in the title of his famous book on the rise of civilization, the human species may have "invented" itself. The real key to human evolution, accordingly, was not any single prime mover but the entire suite of co-operative behavioral, cultural and morphological inventions -- a synergy of synergies.¹²

An oft-used (and important) illustration of this dynamic is the adoption by evolving hominids of the controlled use of fire (or, more broadly, various exogenous forms of energy). This is a uniquely human cultural invention and is still a major factor in our ongoing evolution -- a point that various energy-oriented theorists have thoroughly

documented (e.g., White 1943, 1949; Cottrell 1953; Odum 1971; Adams 1975, 1988). The earliest strong evidence for the use of fire by our hominid ancestors is identified with the Middle Pleistocene, perhaps 200-400,000 years B.P. However, some theorists argue on plausibility grounds, albeit with more fragmentary evidence, for a much earlier date (see especially the cautious review by James 1989 and the offsetting commentary by Lewis). The controlled use of fire by hominids (in effect, a co-operative animal-tool symbiosis) had enormous long-term benefits. Over the course of time, fire was most likely used as an effective means of defense against predators; it was a source of warmth that facilitated migration into colder climates; it might well have served as an insect repellent and as a means for obtaining honey from bee hives (as a bee suppressant); it probably became a weapon for driving and capturing prey animals; it was a means for shaping and hardening tools; it could be used for conditioning the environment (as in slash and burn horticulture); and, not least, it enabled our ancestors to add to their diets many foods that would otherwise have been toxic, indigestible, or possibly even infectious if eaten raw (Leopold and Ardrey 1972; Stahl 1984 and commentaries).

Fire represented the functional equivalent of a major morphological development. With the acquisition of fire, our ancestors were able to expand their niche over time, which in turn changed the selective forces to which our ancestors were subject. Furthermore, fire most likely became another focal point of social co-operation. Fire-keeping was a "collective good" that required a division of labor -- for gathering fire wood, fire tending, fire transport and, eventually, fire-making. In other words, this primordial hominid technology, like most human technologies, was at once a source of bioeconomic benefits and a generator of social co-operation and social organization.

How can this synergistic theory of human evolution be tested? Let us try out a few thought experiments: Take away fire (along with other energy sources in modern societies); we are utterly dependent upon exogenous forms of energy. Or, take away language; or bipedalism; or tools and technology. In short, there is no major adaptive modality that we could do without; they are all necessary parts of an interdependent, synergistic system.

CONCLUSION: A POST-NEO-DARWINIAN PARADIGM?

I believe that Holistic Darwinism can plausibly be viewed as a candidate for a post-neo-Darwinian synthesis. It involves a paradigm that refocuses evolutionary theory on the "vessels" (to borrow a metaphor from our rowing examples) and their functional properties as the vanguard of evolutionary change. In fact, that is where natural selection as a causal dynamic actually occurs; to use an older turn of phrase, it is the vessels that are "tested" in the environment. Holistic Darwinism shifts our focus from the anthropomorphic purposes of selfish genes in theoretical isolation to the evolved, emergent purposiveness of the living systems as wholes, and to the functional interactions and relationships (adaptations in specific environments) that result in differential survival and reproduction.

Equally important, Holistic Darwinism de-emphasizes (without denying) the role of genetic mutations, recombinations, transpositions, etc., as sources of creativity in evolution and emphasizes purposeful innovations which may occur at the behavioral,

cognitive, even social levels (inclusive of symbiogenesis). In this model, proximate "teleonomic selections" by wholes (i.e., adapting organisms and, in some cases, adapting groups) assume a much more important role in evolutionary change than is acknowledged in neo-Darwinism.

Finally, and perhaps most contentious of all, I maintain that Holistic Darwinism also encompasses human evolution and, indeed, the ongoing bio-cultural evolution of our species. It is a seamless theoretical framework that does not require any additional causal principle or "mechanism" to account for humankind.¹³ We must recognize human culture, human economies, even human political systems for what they truly are -- an augmentation of adaptive modalities that can be found in rudimentary form in many other species. (In this paradigm, the activities of humankind virtually everywhere on earth are viewed as an integral part of the evolutionary process, not something that is separate from it.) But, having recognized that, we must also acknowledge our uniqueness as a species. Complex human societies are as different from those of honeybees or naked mole-rats or even chimpanzees as complex multicellular organisms are from single-celled protists. The cumulative, synergistic effects of many differences in degree have produced a difference in kind -- and a dynamic of rapid change at the behavioral/cultural level that is obviously unique. This is an evolutionary development that Holistic Darwinism can fully comprehend. It is not even conceivable in a theoretical world that barely recognizes the existence of wholes.

I believe that it is time to refocus the Necker cube on the problem of explaining the evolution of complex wholes in a way that is fully consistent with Darwin's vision. In the long run, I believe that the Darwinian, functional explanation of complexity will prevail over various orthogenetic theories of "self-organization" (in reality a teleological "black box" that begs the question), or theories that postulate a random "drunkard's walk" (Gould 1996) -- a formulation which tacitly ignores the functional costs and benefits related to the evolution of biological complexity; complexity is not a free lunch but a cumulation of adaptive changes over the eons. (This is a surprising argument, coming from such a sophisticated and articulate student of evolution.)¹⁴ I can only second the conclusion of George Williams in the peroration of his famous book (1966:273): "It may not, in any absolute or permanent sense, represent the truth, but I am convinced that it is the light and the way."

FOOTNOTES

11. More sanguinary versions of this hypothesis, stripped of the subtlety of Darwin's tripartite approach, have proliferated since Darwin's day. A popular variation is the "warfare hypothesis" (see especially Keith 1947; Ardrey 1966; Lorenz 1966; Bigelow 1969; Alexander 1979). Herbert Spencer has often been associated with this school, but in fact his mature views were dualistic and "interactional" in character (see the review in Corning 1982). ([^ click back to text](#))
12. Subsequently, a number of modern theorists, beginning with W.D. Hamilton (1964a), have asserted that Darwin did not solve the key problem associated with group selection, namely, how does a gene (or genes) for altruism spread within a group? How can it/they avoid being supplanted by selfish genes? The answer, quite simply, is that group selection need not be associated exclusively with altruism (self-sacrifice). Genes can be both selfish and co-operative. But this is getting ahead of our story. ([^ click back to text](#))
13. Actually, it was W. D. Hamilton who started it. Hamilton had previously asserted that there were only three forms of social interaction -- (1) altruism, (2) exploitative ("zero-sum") selfishness, and

(3) spite (E.O. Wilson 1975). ([^ click back to text](#))

14. At least, this is so for the functional DNA strands commonly referred to as "exons". Presumably, the many non-functional "introns" that have been found in the genomes of complex organisms are invisible to natural selection. ([^ click back to text](#))
15. Indeed, it is one of the unsolved mysteries of the biological sciences that the concept of synergy has been used (and documented) extensively in biochemistry and functional biology but relatively little in other disciplines, to date. For instance, a literature search in a biological sciences data-base for a recent two-year period using the keyword "synerg" produced over 10,000 citations, of which only an estimated 5 percent (based on a small sample) were associated with behavioral biology, ecology or evolutionary biology. It may be another case of only seeing what you are looking for. ([^ click back to text](#))
16. Douglas H. Boucher (1985), in an edited volume on mutualism, pointed out that there is a long-standing debate among ecologists over the relative importance of competition and co-operation in nature, which can be traced back at least to the 1920s. He noted the remarkable fact that, despite a general bias over the years in favor of competition as the basic organizing principle of nature and a concomitant preference among theoretical ecologists for using the famed Lotka-Volterra competition model in their analyses, in fact a co-operative version of the model (involving a simple sign change) has been reinvented (evidently independently) at least 29 times since 1935. Boucher's volume reflected yet another of the periodic renewals of interest in the co-operative aspect of ecology. Similarly, in an overview and analysis of co-operative behaviors, Jerram Brown (1983:29) noted: "Natural selection is an ecological process and cannot be understood solely from genetic considerations. Relatedness to non-descendants does not determine the direction or product of natural selection; it only supplies an additional cost or benefit." Also, Jon Seger (1991), echoing Darwin's proposed explanation for human evolution in *The Descent of Man*, points out that the various hypothesized explanations for social life are not mutually exclusive and in many cases might reinforce one another. ([^ click back to text](#))
17. As the product of a classical English education, the wide-ranging Spencer surely knew of the "organismic analogy" that has graced political theory ever since Plato's *The Republic*. In any event, Spencer was quite clear about where his formulation began and ended. He never equated his term with the totality of culture (as Durkheim did), nor did he confuse a limited analogy with an homology. As Spencer wrote in *The Principles of Sociology* (1897[1874-82]): "Here let it once more be distinctly asserted that there exists no analogies between the body politic and a living body, save those necessitated by that mutual dependence of parts which they display in common...structures and functions in the human body furnish familiar illustrations of structures and functions in general...These, then, are the analogies alleged: community in the fundamental principles of organization is the only community asserted" (I, p.592). See also the more extended discussion of the superorganism concept in Corning 1983; also, Seeley 1989; D.S. Wilson and Sober 1989; Hölldobler and Wilson 1990; Moritz and Southwick 1992. ([^ click back to text](#))
18. What about ecosystems? Can they also be viewed as superorganisms? This is a particularly contentious issue. Although ecosystems certainly display complex patterns of interdependency, as Darwin insisted, many theorists hold the view that they cannot be treated as superorganisms because they do not represent units of differential survival and reproduction. To be sure, there are many complex coevolutionary processes that occur among the various inhabitants of an ecosystem. However, it has been argued that ecosystems do not evolve as wholes. To treat an ecosystem as a whole, then, is an inappropriate reification. A counterargument is that the concept of a superorganism need not be confined only to vehicles of selection and the dynamics of evolutionary change. From a bioeconomic perspective, the term could also be applied to units of functional interdependency, to functional wholes. Moreover, viewing an ecosystem as a whole is not a mystical abstraction. We need only apply the same test to an ecosystem that was suggested above for other kinds of synergistic phenomena. If we were to take away a major part - - say the photosynthesizers at the bottom of the food chain or the decomposers that facilitate nutrient recycling -- what would be the consequences for the rest of the ecosystem? ([^ click back to text](#))
19. To some extent, this distinction may involve no more than a different perspective on the same phenomenon (a refocussing of the Necker cube). Thus, it could be said that the individuals, or parts, in a division of labor are contributing their specialized skills and efforts to the production of a combined result. However, the terminological distinction may also be useful in drawing attention to some important functional differences. For instance, many collective efforts, in nature and human societies alike, do not entail any task specialization. The joint efforts of various honey bee workers that serve to warm or cool the interior of the hive, or the combined efforts of the players in a classic tug-of-war game, do not entail a breakdown of the task at hand into specialized roles. Nevertheless, individual efforts are combined to produce collective results. A categorical distinction between a division and a combination of labor may also be useful in drawing attention to how a particular collaborative activity arose, or evolved. The eukaryotic cell, it is now generally agreed, provides an example of both. Some of its major organelles are most likely the product of a symbiotic union -- a joint venture among specialists -- whereas other organelles are believed to have resulted from an internal differentiation process over the course of time (Margulis 1993). In human societies, various combinations of labor go under such headings as partnerships, strategic alliances, joint ventures, even cooperatives. ([^ click back to](#)

text)

20. Another implication of this insight is that political theory can now be connected directly to evolutionary theory; insofar as politics and government are related to the problem of survival and reproduction, in any species, there is a common functional basis. Human political systems may thus be viewed as variations on an evolutionary theme. For an extended treatment of this paradigm, see Corning 1983, 1996b. Also, see the offerings in Somit 1976; Willhoite 1976; Wiegele 1979; Somit et al., 1980; de Waal 1982; Schubert 1989; Masters 1989; Schubert and Masters 1991; Vanhannen 1992; Johnson 1995. ([^ click back to text](#))
21. Among the many recent publications that are relevant to this complex issue -- including items in virtually every issue of the *American Anthropologist* and *Current Anthropology* -- see especially Johnson and Earle 1987; Byrne and Whiten 1988; Mellars 1989; Mithen 1990; Durham 1991; Jones et al., 1992; Maryanski and Turner 1992; Smith and Winterhalder 1992; Gibson and Ingold 1993; Quiatt and Reynolds 1993; Soltis et al., 1995; Holloway 1996; Boehm 1996; Feldman and Laland 1996; Flynn 1997. Particular note should be made of anthropologist William Durham's (1991) dualistic gene-culture "coevolution" paradigm, which directs our attention to the partially independent nature of human cultural evolution, even as it recognizes its interdependency with biological constraints and influences, and the interactions between the two evolutionary modes. See also Cavalli-Sforza and Feldman 1981; Corning 1983; and Boyd and Richerson (1985). Ghiselin (1993), on the other hand, sharply criticizes Durham for using "information" as the basis for his definition of culture, an obvious analogy with the informational properties of genes. Ghiselin rightly observes that this confuses a means, or an instrumentality of transmission and replication, with the functional product: "The recipe is not the cake." It should also be noted that Flynn, an evolutionary psychologist, stresses the influence of evolved, biologically-based psychological mechanisms in cultural selection and evolution, but this is not incompatible with the notion that there are multiple, interacting levels of causation involved in cultural processes. ([^ click back to text](#))
22. In support of this scenario, anthropologist Christopher Boehm (1996) has proposed that a suite of behavioral/cultural "factors" which are widely observed in contemporary egalitarian foraging bands might also have enhanced the influence of group selection among prehistoric human groups (whose life-styles are presumed to have been similar). These factors are (1) internal social "levelling" pressures, (2) moralistic policing of cheats and shirkers, (3) consensual decision-making and shared within-group adaptive strategies, and (4) marked differences between groups in adaptive strategies. Together, these behaviors could have had the effect of dampening within-group variation and selection pressures while augmenting between-group variation and selection. Once again, this implies a behavioral "pacemaker" for natural selection. Also consistent is the novel proposal of Wilson and Dugatkin (1997) that "assortative interactions" among individual organisms at the cognitive/ behavioral level may also play a role in determining differential reproductive success. (It could serve as an alternative mechanism of group selection.) As Wilson and Dugatkin note, this scenario is particularly relevant to human evolution. On the other hand, Soltis, Boyd and Richerson, 1995, have questioned what they call "cultural group selection" (the differential survival of different cultural traits) as a significant factor in human evolution. Utilizing data from New Guinea, they conclude that it would take 500-1000 years for a cultural trait to spread by a process of differential group "extinction". However, as various commentators on their paper pointed out, much depends upon the assumptions used, how groups are defined, which data set is used, and, indeed, which trait is involved. A food taboo is one thing, but a weapon -- say thrown spears or horse cavalry, or wheeled chariots, or Greek Fire, or the phalanx, or the cross-bow, or siege cannons, or tanks -- can be used by one group to gain a military advantage that results in a rapid process of differential group selection. History is replete with examples of such military "breakthroughs". Conversely, many cultural traits "diffuse" between groups without discernable (biological) selective consequences. ([^ click back to text](#))
23. This is not to deny either the partial autonomy of cultural processes/systems or our unique (evolved) biological needs and psychological capabilities -- "human nature" (see Footnote 11). The "mechanism" of cultural evolution, which I refer to elsewhere as "teleonomic selection," involves an "interaction" between these two sets of causal factors (and much more besides). Teleonomic selection obviously plays a unique role in shaping the course of humankind. But the rudiments of this "mechanism" can be found elsewhere in nature as well. (For a full discussion of this issue, see Corning 1983; also see Barkow et al., 1992; Flynn 1997.) ([^ click back to text](#))
24. In his recent book, *Full House*, Gould finds "almost chilling" E.O. Wilson's testimonial about the functional improvements that have been associated with the evolution of complexity in nature. "We grasp at the straw of progress (a desiccated ideological twig) because we are still not ready for the Darwinian revolution" (p.29). As in some of his other recent writings, Gould wishes to deny the relevance of any notion of general "improvement" as a significant aspect of the evolutionary process. He seeks to undermine the traditional paleontological conceit that there has been "progress" (culminating of course in humankind), or that the so-called "trends" in evolution imply that something has gotten (normatively) better. Gould has a point, of course, but objections to the notion of any "driven" trend toward betterment or progress (orthogenesis) go back to Darwin himself. Perhaps Gould is speaking to the "structuralists" -- the proponents of evolution as a self-organized, self-propelled process. This is a view that currently appeals particularly to various biophysicists, for obvious reasons. What is new -- Gould's conceit if you will -- is the assertion that the evolutionary process is essentially random in its overall course

and that the simplest forms of life -- bacteria -- represent the modal trend. For instance, Gould attacks Cope's Rule (after the 19th century paleontologist Edward Drinker Cope), which holds that most lineages tend to increase in size over time. This is an artifact, he says, of the circumstance that life began at the extreme "left wall" (or tail) in the distribution of biological size and complexity. Therefore, any subsequent directional change could only be toward the "right wall." (greater complexity). Furthermore, complexity in living systems is not a product of natural selection; organisms merely "wander" into complexity (like a "drunkard's walk"). There is a kind of "just-so" quality to this notion (to borrow a metaphor from Gould). It implies that systematic size/complexity increases in nature could occur without being "tested" and winnowed by natural selection. On the contrary, such changes always entail bioeconomic "costs" (energy, for instance) that have to be offset by at least equivalent "benefits." So intent is Gould on making his anti-progressive case that he even allows himself to fall into a logical trap -- a rare event for such a stellar thinker. In light of some recent, suggestive work by various colleagues, Gould claims that "a small overall tendency toward decreasing complexity may characterize the history of most lineages" (p.200). This is absurd on the face of it. If life began in extreme simplicity, it had to get more complex before it could become less complex. So, if there is any residue of complexity left in nature, the overall trend at the margin had to be in that direction (unless there is some statistical sleight of hand going on). Indeed, in the process of unpacking his most important (and eccentric) example -- the disappearance of .400 hitters in baseball -- Gould inadvertently undermines his own argument. Gould's key point is that, despite appearances, baseball hitters have not gotten worse over the years. This trend is a result (in his words) of an "improvement in general play" -- i.e., pitching and fielding. What's that? Did he say "improvement" -- a "progressive" advance in functional performance rather than a "drunkard's walk"? So it seems there is a role for functionally-based changes after all, at least in the evolution of baseball. (^ [click back to text](#))

REFERENCES / BIBLIOGRAPHY

- Adams, R. (1975). *Energy and Structure*. Austin: University of Texas Press.
- Adams, R. (1988). *The Eighth Day: Social Evolution as the Self-Organization of Energy*. Austin: University of Texas Press.
- Alexander, R.D. (1979). *Darwinism and Human Affairs*. Seattle and London:University of Washington Press.
- Ardrey, R. (1966). *The Territorial Imperative*. New York:Atheneum.
- Atsatt, P.R. (1988). "Are Vascular Plants Inside-Out Lichens?" *Ecology*, 69, 17-23.
- Atsatt, P.R. (1991). "Fungi and the Origin of Land Plants." In *Symbiosis as a Source of Evolutionary Innovation*, eds. L. Margulis and R. Fester, pp. 301-305. Cambridge, MA:The MIT Press.
- Axelrod, R., and W. Hamilton. (1981). "The Evolution of Cooperation." *Science*, 211, 1390.
- Barkow, J., et al. (1992). *The Adapted Mind*. Oxford:Oxford University Press.
- Bell, G. (1985). "Origin and Early Evolution of Germ Cells as Illustrated by the Volvocales." In *Origin and Evolution of Sex*, eds. H.O. Halvorson and A. Monroy, pp. 221-256. New York:Alan R. Liss, Inc.
- Bermudes, D., and L. Margulis. (1987). "Symbiont Acquisition as Neoseme: Origin of Species and Higher Taxa." *Symbiosis*, 4, 185-98.
- Bigelow, R. (1969). *The Dawn Warriors: Man's Evolution Towards Peace*. Boston:Little Brown.
- Bloom, H. (1997). "A History of the Global Brain: Creative Nets in the Pre-Cambrian Age." *ASCAP (Across Species Comparisons and Psychopathology Society)* 10(3), 7-11.
- Bock, W.J. (1979). "The Synthetic Explanation of Macroevolutionary Change -- A Reductionistic Approach." *Bulletin of the Carnegie Museum of Natural History*, 13, 20-69.
- Boehm, C. (1996). "Emergency Decisions, Cultural-Selection Mechanics, and Group Selection." *Current Anthropology*, 37, 763-793.
- Boucher, D.H., ed. (1985). *The Biology of Mutualism: Ecology and Evolution*. New York:Oxford University Press.
- Boyd, R., and P.J. Richerson. (1985). *Culture and the Evolutionary Process*. Chicago:University of Chicago Press.
- Boyd, R., and P.J. Richerson. (1992). "Punishment Allows the Evolution of Cooperation (or Anything Else) in Sizable Groups." *Ethology and Sociobiology*, 13, 171-195.
- Brandon, R.N., and R.M. Burian, eds. (1984). *Genes, Organisms, Populations: Controversies Over the Units of Selection*. Cambridge, MA:The MIT Press.

- Brembs, B. (1996). "Chaos, Cheating and Cooperation: Potential Solutions to the Prisoner's Dilemma." *Oikos*, 76, 14-24.
- Brown, J.L. (1983). "Cooperation--A Biologists' Dilemma." *Advances in the Study of Behavior*, 13, 1-37.
- Buss, L.W. (1987). *The Evolution of Individuality*. Princeton, NJ:Princeton University Press.
- Byrne, R.W. and A. Whiten, eds. (1988). *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes and Humans*. Oxford: Clarendon Press.
- Calderone, N.W., and R.E. Page. (1992). "Effects of Interactions Among Genotypically Diverse Nestmates on Task Specialization by Foraging Honey Bees (*Apis mellifera*)." *Behavioral Ecology and Sociobiology*, 30, 219-226.
- Campbell, D.T. (1974). "Downward Causation in Hierarchically Organized Biological Systems." In *Studies in the Philosophy of Biology*, eds. T. Dobzhansky and F.J. Ayala, pp. 85-90. Macmillan.
- Cavalli-Sforza, L.L., and M.W. Feldman. (1981). *Cultural Transmission And Evolution*. Princeton, NJ:Princeton University Press.
- Childe, V.G. (1951[1936]). *Man Makes Himself*. New York:New American Library.
- Clutton-Brock, T.H., and G.A. Parker. (1995). "Punishment in Animal Societies." *Nature*, 373, 209-216.
- Comins, P.A. (1982). "Durkheim and Spencer." *The British Journal of Sociology*, 33, 359-382.
- Comins, P.A. (1983). *The Synergism Hypothesis: A Theory of Progressive Evolution*. New York:McGraw-Hill.
- Comins, P.A. (1995). "Synergy and Self-Organization in the Evolution of Complex Systems." *Systems Research*, 12, 89-121.
- Comins, P.A. (1996a). "The Co-operative Gene: On the Role of Synergy in Evolution." *Evolutionary Theory*, 11, 183-207.
- Comins, P.A. (1996b). "Synergy, Cybernetics and the Evolution of Politics." *International Political Science Review*, 17, 91-119.
- Cottrell, F. (1953). *Energy and Society*. New York:McGraw Hill.
- Darwin, C.R. (1874/1871). *The Descent of Man, and Selection in Relation to Sex*. New York:A.L. Burt.
- Dawkins, R. (1987/1986). *The Blind Watchmaker*. New York:W.W. Norton.
- Dawkins, R. (1989/1976). *The Selfish Gene*, 2nd ed. Oxford:Oxford University Press.
- Dugatkin, L.A., and M. Mesterton-Gibbons. (1996). "Cooperation Among Unrelated Individuals: Reciprocal Altruism, By-product Mutualism and Group Selection in Fishes." *BioSystems* 37, 19-30.
- Dugatkin, L.A., and H.K. Reeve. (1994). "Behavioral Ecology and Levels of Selection: Dissolving the Group Selection Controversy." *Advances in the Study of Behavior*, 23, 101-133.
- Dugatkin, L.A., et al. (1992). "Beyond the Prisoner's Dilemma: Towards Models to Discriminate Among Mechanisms of Cooperation in Nature." *Trends in Ecology and Evolution*, 7, 202-205.
- Durham, W.H. (1991). *Coevolution: Genes, Culture and Human Diversity*. Stanford, CA:Stanford University Press.
- Eldredge, N. (1985). *Unfinished Synthesis: Biological Hierarchies and Modern Evolutionary Thought*. Oxford University Press.
- Eldredge, N. (1995). *Reinventing Darwin*. New York:John Wiley & Sons.
- Eldredge, N., and S.N. Salthe. (1984). "Hierarchy and Evolution." In *Oxford Surveys in Evolutionary Biology*, Volume 1, eds. R. Dawkins and M. Ridley, pp. 184-208. Oxford:Oxford University Press.
- Emlen, S.T. (1996). "Living With Relatives: Lessons from Avian Family Systems." *IBIS*, 138, 87-100.
- Feldman, M.W., and K.N. Laland. (1996). "Gene-Culture Coevolutionary Theory." *Trends in Ecology and Evolution*, 11, 453-457.
- Fewell, J.H., and M.L. Winston. (1992). "Colony State and Regulation of Pollen Foraging in the Honey Bee, *Apis Mellifera* L." *Behavioral Ecology and Sociobiology*, 30, 387-393.
- Flynn, M.V. (1997). "Culture and the Evolution of Social Learning." *Evolution and Human Behavior*, 18, 23-67.
- Frank, S.A. (1995). "Mutual Policing and Repression of Competition in the Evolution of Cooperative Groups." *Nature (London)*, 377, 520-522.
- Frank, S.A. (1996). "Policing and Group Cohesion When Resources Vary." *Animal Behaviour*, 52, 1163-1169.

- Franks, N.R. (1989). "Army Ants: A Collective Intelligence." *American Scientist*, 77, 139-45.
- Franks, N.R., et al. (1991). "The Blind Leading the Blind in Army Ant Raid Patterns: Testing a Model of Self-organization (Hymenoptera: Formicidae)." *Journal of Insect Behavior*, 4(5), 583-607.
- Ghiselin, M.T. (1993). "Book Review: Coevolution: Genes, Culture, Human Diversity." *Politics and the Life Sciences*, 12, 123-124.
- Ghiselin, M. (1997). *Metaphysics and the Origin of Species*. Albany, NY:SONY Press.
- Gibson, R., and T. Ingold, eds. (1993). *Tools, Language, and Cognition in Human Evolution*. Cambridge, MA:Cambridge University Press.
- Goodnight, C., and L. Stevens. (1997). "Experimental Studies of Group Selection: What They Tell Us About Group Selection in Nature." *Bulletin of the Ecological Society of America*, 77 (3 Suppl. Part 2), 168.
- Gould, S.J. (1996). *Full House: The Spread of Excellence from Plato to Darwin*. New York, NY:Harmony Books.
- Gould, S.J. (1982). "The Meaning of Punctualional Evolution and Its Role in Validating a Hierarchical Approach to Macroevolution." In *Perspectives on Evolution*, ed. R. Milkman. Sunderland, MA:Sinauer Associates.
- Gould, S.J. (1994). "Tempo and Mode in the Macroevolutionary Reconstruction of Darwinism." *Proceedings of the National Academy of Sciences (USA)*, 91, 6764-6771.
- Grene, M. (1987). "Hierarchies in Biology." *American Scientist*, 75, 504-610.
- Guzmán-Novoa, E., et al. (1994). "Behavioral and Life-History Components of Division of Labor in Honey Bees, (*Apis mellifera* L.)" *Behavioral Ecology and Sociobiology*, 34, 409-417.
- Hamilton, W.D. (1964a). "The Genetical Evolution of Social Behavior, I." *Journal of Theoretical Biology*, 7, 1-16.
- Hamilton, W.D. (1964b). "The Genetical Evolution of Social Behavior, II." *Journal of Theoretical Biology*, 7, 17-52.
- Hasegawa, E. (1993). "Nest Defense and Early Production of the Major Workers in the Dimorphic Ant *Colobopsis nipponicus* (Wheeler) (Hymenoptera: Formicidae)." *Behavioral Ecology and Sociobiology*, 33, 73-77.
- Hölldobler, B., and E.O. Wilson. (1990). *The Ants*. Cambridge, MA:Harvard University Press.
- Holloway, R.L. (1995). "Toward a Synthetic Theory of Brain Evolution." In *Origins of the Human Brain*, eds. J.P. Changeux and J. Chavaillon. Oxford:Clarendon Press.
- Holloway, R.L. (1996). "Evolution of the Human Brain." In *Handbook of Human Symbolic Evolution*, eds. A. Lock and C.R. Peters. Oxford:Oxford Science Publications.
- Hoogland, J.L., and P.W. Sherman. (1976). "Advantages and Disadvantages of Bank Swallow (*Riparia riparia*) Coloniality." *Ecological Monographs*, 46, 33-58.
- Hull, D.L. (1980). "Individuality and Selection." *Annual Review of Ecology and Systematics*, 11, 311-332.
- James, S.R. (1989). "Hominid Use of Fire in the Lower and Middle Pleistocene." *Current Anthropology*, 30, 1-26.
- Jeon, K.W. (1972). "Development of Cellular Dependence in Infective Organisms: Micurgical Studies in Amoebas." *Science*, 176, 1122-23.
- Jeon, K.W. (1983). "Integration of Bacterial Endosymbionts in Amoebae." *International Review of Cytology*, Supplement 14, 29-47.
- Jeon, K.W. (1992). "Macromolecules Involved in the Amoeba-Bacteria Symbiosis." *Journal of Protozoology*, 39, 199-204.
- Johnson, A.W., and T. Earle. (1987). *The Evolution of Human Societies: From Foraging Group to Agrarian State*. Stanford, CA:Stanford University Press.
- Johnson, G.R. (1995). "The Evolutionary Origins of Government and Politics." In *Human Nature and Politics*, eds. A. Smot and J. Losco, pp. 243-305. Greenwich, CT:JAI Press.
- Jones, S., et al. (1992). *The Cambridge Encyclopedia of Human Evolution*. Cambridge, MA:Cambridge University Press.
- Kawata, M. (1995). "Emergent and Effective Properties in Ecology and Evolution." *Researches on Population Ecology*, 37, 93-96.
- Keith, A. (1947). *A New Theory of Human Evolution*. Gloucester, MA:Peter Smith.
- Kendrick, B. (1991). "Fungal Symbioses and Evolutionary Innovations." In *Symbiosis as a Source of Evolutionary Innovation*, eds. L. Margulis and R. Fester, pp. 249-261. Cambridge, MA:MIT Press.
- Kettlewell, H.B.D. (1955). "Selection Experiments on Industrial Melanism in the Lepidoptera." *Heredity*, 9, 323-42.

- Kettlewell, H.B.D. (1973). *The Evolution of Melanism: The Study of a Recurring Necessity*. Oxford:Clarendon Press.
- Koestler, A. (1967). *The Ghost in the Machine*. New York:Macmillan.
- Le Boeuf, B.J. (1985). "Elephant Seals." In *The Natural History of Año Nuevo*, eds. B.J. Le Boeuf and S. Kaza. Pacific Grove, CA:Boxwood Press.
- Le Boeuf, B.J., and R.M. Laws. (1994). *Elephant Seals: Population Ecology, Behavior and Physiology*. Berkeley, CA:University of California Press.
- Leakey, R. (1994). *The Origin of Human Kind*. New York, NY:Basic Books.
- Leigh, E. (1971). *Adaptation and Diversity*. San Francisco, CA:Freeman, Cooper & Co.
- Leigh, E. (1977). "How Does Selection Reconcile Individual Advantage with the Good of the Group." *Proceedings of the National Academy of Sciences (USA)*, 74, 4542-4546.
- Leigh, E. (1983). "When Does the Good of the Group Override the Advantage of the Individual?" *Proceedings of the National Academy of Sciences (USA)*, 80, 2985-2989.
- Leigh, E. (1991). "Genes, Bees and Ecosystems: The Evolution of a Common Interest Among Individuals." *Tree*, 6, 257-262.
- Leopold, C.A., and R. Ardrey. (1972). "Toxic Substances in Plants and the Food Habits of Early Man." *Science*, 176, 512-14.
- Lewis, D.H. (1991). "Mutualistic Symbioses in the Origin and Evolution of Land Plants." In *Symbiosis as a Source of Evolutionary Innovation*, eds. L. Margulis and R. Fester, pp. 288-300. Cambridge, MA:MIT Press.
- Little, P. (1995). "The Genome Directory: Navigational Progress." *Nature*, 377, 288.
- Lorenz, L. (1966). *On Aggression*. (M.K. Wilson, trans.) New York:Harcourt, Brace, World.
- Margulis, L. (1993). *Symbiosis in Cell Evolution*. 2nd ed. New York:W.H. Freeman.
- Margulis, L., and K.V. Schwartz. (1982). *Five Kingdoms: An Illustrated Guide to the Phyla of Life on Earth*. San Francisco:W.H. Freeman.
- Margulis, L., and R. Fester, eds. (1991). *Symbiosis as a Source of Evolutionary Innovation: Speciation and Morphogenesis*. Cambridge, MA:MIT Press.
- Maryanski, A., and J.H. Turner. (1992). *The Social Cage: Human Nature and the Evolution of Society*. Stanford,CA:Stanford University Press.
- Masters, R.D. (1989). *The Nature of Politics*. New Haven:Yale University Press.
- Matessi, C., and S.D. Jayakar. (1976). "Conditions for the Evolution of Altruism Under Darwinian Selection." *Theoretical Population Biology*, 9, 360-387.
- Maynard Smith, J. (1982). "The Evolution of Social Behavior - A Classification of Models." In *Current Problems in Sociobiology*, ed. King's College Sociobiology Group, pp. 28-44. Cambridge, MA:Cambridge University Press.
- Maynard Smith, J. (1983). "Models of Evolution." *Proceedings of the Royal Society of London (B)*, 219, 315-325.
- Maynard Smith, J. (1984). "Game Theory and the Evolution of Behaviour." *The Behavioral and Brain Sciences*, 7, 95-125.
- Maynard Smith, J. (1989). *Evolutionary Genetics*. Oxford:Oxford University Press.
- Maynard Smith, J., and E. Szathmáry. (1993). "The Origin of Chromosomes I. Selection for Linkage." *Journal of Theoretical Biology*, 164, 437-446.
- Maynard Smith, J., and E. Szathmáry. (1995). *The Major Transitions in Evolution*. Oxford:Freeman Press.
- Mayr, E. (1960). "The Emergence of Evolutionary Novelities." In *Evolution After Darwin*, Vol. I ed. S. Tax. Chicago: University of Chicago Press.
- Mayr, E. (1963). *Animal Species and Evolution*. Cambridge, MA:Harvard University Press.
- Mayr, E. (1976). *Evolution and the Diversity of Life: Selected Essays*. Cambridge, MA:Harvard University Press.
- Mellars, P. (1989). "Major Issues in the Emergence of Modern Humans." *Current Anthropology*, 30, 349-385.
- Michod, R.E. (1996). "Cooperation and Conflict in the Evolution of Individuality. II. Conflict Mediation." *Proceedings of the Royal Society of London (B)*, 263, 813-822.
- Mithen, S.J. (1990). *Thoughtful Foragers: A Study of Prehistoric Decision Making*. Cambridge, MA:Cambridge

University Press.

Morgan, C.L. (1923). *Emergent Evolution*. New York:Henry Holt.

Moritz, R.F.A., and E.E. Southwick. (1992). *Bees as Superorganisms: An Evolution and Reality*. New York, NY:Springer-Verlag.

Nowak, M., and K. Sigmund. (1993). "A Strategy of Win-Stay, Lose-Shift that Outperforms Tit-for-Tat in the Prisoner's Dilemma Game." *Nature*, 364, 56-58.

Odum, H.T. (1971). *Environment, Power and Society*. London:Wiley.

Oldroyd, B.P., et al. (1992a). "Intra-Colonial Foraging Specialism by Honey Bees (*Apis mellifera*) (Hymenoptera: Apidae)." *Behavioral Ecology and Sociobiology*, 30, 291-295.

Oldroyd, B.P., et al. (1992b). "Effects of Intra-colonial Genetic Diversity on Honey Bee (Hymenoptera: Apidae) Colony Performance." *Annals of the Entomological Society of America*, 85(3), 335-343.

Packer, C., and L. Rutan. (1988). "The Evolution of Cooperative Hunting." *The American Naturalist*, 132(2), 159-198.

Packer, C., et al. (1990). "Reproductive Success of Lions." In *Reproductive Success*, ed. T.H. Clutton-Brock. Chicago:University of Chicago Press.

Page, R.E., and G.E. Robinson. (1991). "The Genetics of Division of Labour in Honey Bee Colonies." *Advances in Insect Physiology*, 23, 118-169.

Peck, J.R. (1993). "Friendship and the Evolution of Co-operation in Honey Bee Colonies." *Journal of Theoretical Biology*, 162, 195-228.

Pirozynski, K.A., and D.W. Malloch. (1975). "The Origins of Land Plants: A Matter of Mycotrophism." *Biosystems*, 6, 153-64.

Price, P.W. (1991). "The Web of Life: Development Over 3.8 Billion Years of Trophic Relationships." In *Symbiosis as a Source of Evolutionary Innovation*, eds. L. Margulis and R. Fester, pp. 262-272. Cambridge, MA: The MIT Press.

Quiatt, D.D., and V. Reynolds. (1993). *Primate Behaviour: Information, Social Knowledge, and the Evolution of Culture*. Cambridge, MA:Cambridge University Press.

Ratnieks, F.L.W., and P.K. Visscher. (1989). "Worker Policing in the Honey Bee." *Nature*, 342, 796-797.

Rissing, S.W., and G.B. Pollack. (1991). "An Experimental Analysis of Pleometrotic Advantage in the Desert Seed-Harvester Ant *Messor pergandei* (Hymenoptera: Formicidae)." *Ins. Soc.*, 38, 205-211.

Salthe, S.N. (1985). *Evolving Hierarchical Systems*. Columbia University Press.

Scheel, D., and C. Packer. (1991). "Group Hunting Behaviour of Lions: A Search for Cooperation." *Animal Behaviour*, 41, 697-710.

Schubert, G. (1989). *Evolutionary Politics*. Carbondale, IL:Southern Illinois University Press.

Schubert, G., and R. Masters, eds. (1991). *Primate Politics*. Carbondale, IL:Southern Illinois University Press.

Seeley, T.D. (1989). "The Honey Bee Colony as a Super-Organism." *American Scientist*, 77, 546-553.

Seeger, J. (1991). "Cooperation and Conflict in Social Insects." In *Behavioural Ecology: An Evolutionary Approach* (2nd ed.), eds. J.R. Krebs and N.B. Davis, pp. 338-373. Oxford:Blackwell Scientific Publications.

Service, E.R. (1971). *Cultural Evolutionism: Theory in Practice*. New York:Holt, Rinehart, & Winston.

Shapiro, J.A. (1988). "Bacteria as Multicellular Organisms." *Scientific American*, 258(6), 82-89.

Shapiro, J.A., and M. Dworkin, eds. (1997). *Bacteria as Multicellular Organisms*. New York, NY:Oxford University Press.

Sherman, P.W., et al., eds. (1991). *The Biology of the Naked Mole-Rat*. Princeton, NJ: Princeton University Press.

Sherman, P.W., et al. (1992). "Naked Mole Rats." *Scientific American*, 267(2), 72-78.

Smillie, D. (1995). "Darwin's Two Paradigms: An Opportunistic Approach to Natural Selection Theory." *Journal of Social and Evolutionary Systems*, 18, 231-255.

Smith, A. (1964/1776). *The Wealth of Nations*. 2 vols. London:Dent.

Smith, A. (1976/1759). *The Theory of Moral Sentiments*. Oxford:Clarendon Press.

Smith, D.C., and A.E. Douglas. (1987). *The Biology of Symbiosis*. Baltimore, MD:Edward Arnold.

- Smith, D.C. (1992). "The Symbiotic Condition." *Symbiosis*, 14, 3-15.
- Smith, E.A., and B. Winterhalder, eds. (1992). *Evolutionary Ecology and Human Behavior*. New York, NY:Aldine Gruyter.
- Smuts, J.C. (1926). *Holism and Evolution*. New York:Macmillan Co.
- Soltis, J., et al. (1995). "Can Group-Functional Behaviors Evolve by Cultural Group Selection?" *Current Anthropology*, 36, 473-494.
- Somit, A., ed. (1976). *Biology and Politics: Recent Explorations*. The Hague/Paris:Mouton.
- Somit, A., et al. (1980). *The Literature of Biopolitics*. (Revised) Dekalb, IL:The Center for Biopolitical Research.
- Sonea, S. (1991). "Bacterial Evolution Without Speciation." In *Symbiosis as a Source of Evolutionary Innovation*, eds. L. Margulis and R. Fester, pp. 95-105. Cambridge, MA:The MIT Press.
- Spencer, H. (1897/1874-1882). *The Principles of Sociology*, 3 vols., 3rd ed. New York:D. Appleton.
- Sperry, R.W. (1969). "Modified Concept of Consciousness." *Psychological Review*, 76, 532-36.
- Sperry, R.W. (1991). "In Defense of Mentalism and Emergent Interaction." *The Journal of Mind and Behavior*, 12(2), 221-46.
- Stahl, A.B. (1984). "Hominid Dietary Selection Before Fire." *Current Anthropology*, 25, 151-168.
- Stander, P.E. (1992). "Cooperative Hunting in Lions: The Role of the Individual." *Behavioral Ecology and Sociobiology*, 29, 45-454.
- Stanley, S.M. (1975). "A Theory of Evolution Above the Species Level." *Proceedings of the National Academy of Sciences, USA*, 72, 646-650.
- Stanley, S.M. (1979). *Macroevolution: Pattern and Process*. San Francisco:Freeman.
- Stidd, B.M., and D.L. Wade. (1995). "Is Species Selection Dependent Upon Emergent Characters?" *Biology and Philosophy*, 10, 55-76.
- Tattersall, I. (1995). *The Fossil Trail: How We Know What We Think We Know About Human Evolution*. Oxford:Oxford University Press.
- Trivers, R.L. (1971). "The Evolution of Reciprocal Altruism." *Quarterly Review of Biology*, 46, 35-57.
- Trivers, R.L. (1985). *Social Evolution*. Menlo Park, CA:Benjamin/Cummings.
- Vanhanen, T. (1992). *On the Evolutionary Roots of Politics*. New Delhi:Sterling.
- Vetter, R.D. (1991). "Symbiosis and the Evolution of Novel Trophic Strategies: Thiotrophic Organisms at Hydrothermal Vents." In *Symbiosis as a Source of Evolutionary Innovation*, eds. L. Margulis and R. Fester, pp. 219-245. Cambridge, MA:MIT Press.
- Vrba, E.S. (1980). "Evolution, Species and Fossils: How Does Life Evolve?" *South African Journal of Science*, 76, 61-84.
- Vrba, E.S. (1983). "Macroevolutionary Trends: A New Perspective on the Roles of Adaptation and Incidental Effect." *Science*, 221, 387-389.
- Vrba, E.S., and N. Eldredge. (1984). "Individuals, Hierarchies and Process: Towards a More Complete Evolutionary Theory." *Paleobiology*, 10, 146-171.
- de Vries, H. (1901). *Die Mutations Theorie*. Leipzig:Veit.
- de Waal, F.B.M. (1982). *Chimpanzee Politics: Power and Sex Among Apes*. New York:Harper & Row.
- de Waal, F.B.M. (1996). *Good Natured: The Origins of Right and Wrong in Humans and Other Animals*. Cambridge, MA:Harvard University Press.
- Wade, M.J. (1977). "An Experimental Study of Group Selection." *Evolution*, 31, 134-153.
- Wade, M.J. (1985). "Soft Selection, Hard Selection, Kin Selection, and Group Selection." *The American Naturalist*, 125(1), 61-73.
- Weismann, A. (1891). *Essays Upon Heredity and Kindred Biological Problems* (2nd ed.). Oxford:Clarendon Press.
- Weismann, A. (1902). *Vorträge über Descendenz Theorie*. Jena:Gustav Fischer.
- Wheeler, W.M. (1927). *Emergent Evolution and the Social*. London:Kegan Paul, Trench, Trubner.
- Wheeler, W.M. (1928). *The Social Insects: Their Origin and Evolution*. London:Kegan, Paul, Trench, Trubner & Co.

- White, L.A. (1943). "Energy and the Evolution of Culture." *American Anthropologist*, 45, 335-356.
- White, L.A. (1949). *The Science of Culture: A Study of Man and Civilization*. New York:Grove Press.
- Wiegele, T.C. (1979). *Biopolitics: Search for a More Human Political Science*. Boulder, CO:Westview Press.
- Wilkinson, G.S. (1984). "Reciprocal Food Sharing in the Vampire Bat." *Nature*, 308, 181-184.
- Wilkinson, G.S. (1988). "Reciprocal Altruism in Bats and Other Mammals." *Ethology and Sociobiology*, 9, 85-100.
- Wilkinson, G.S. (1990). "Food Sharing in Vampire Bats." *Scientific American*, 262(2), 76-82.
- Willhoite, F.H., Sr. (1976). "Primates and Political Authority: A Biobehavioral Perspective." *The American Political Science Review*, 70, 1110-1126.
- Williams, G.C. (1966). *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought*. Princeton, NJ:Princeton University Press.
- Williams, G.C. (1992). *Natural Selection: Domains, Levels, and Challenges*. New York:Oxford University Press.
- Wilson, D.S. (1975). "A General Theory of Group Selection." *Proceedings of the National Academy of Sciences (USA)*, 72, 143-146.
- Wilson, D.S. (1980). *The Natural Selection of Populations and Communities*. Menlo Park, CA:Benjamin/Cummings.
- Wilson, D.S., and L.A. Dugatkin. (1997). "Group Selection and Assortative Interactions." *The American Naturalist*, 149, 336-351.
- Wilson, D.S., and E. Sober. (1989). "Reviving the Superorganism." *Journal of Theoretical Biology*, 136, 337-56.
- Wilson, D.S., and E. Sober. (1994). "Reintroducing Group Selection to the Human Behavioral Sciences." *Behavioral and Brain Sciences*, 17, 585-608.
- Wilson, E.O. (1975). *Sociobiology: The New Synthesis*. Cambridge, MA:Harvard University Press.
- Wilson, E.O. (1985). "The Sociogenesis of Insect Colonies." *Science*, 228, 1489-1495.
- Wright, S. (1968-1978). *Evolution and the Genetics of Populations: A Treatise*. 4 vols. Chicago:University of Chicago Press.
- Würsig, B. (1988). "The Behavior of Baleen Whales." *Scientific American*, 258(4), 102-107.
- Würsig, B. (1989). "Cetaceans." *Science*, 244, 1550-1557.
- Wynne-Edwards, V.C. (1962). *Animal Dispersion in Relation to Social Behaviour*. New York:Hafner.
- Wynne-Edwards, V.C. (1963). "Intergroup Selection in the Evolution of Social Systems." *Nature*, 200, 623.

ACKNOWLEDGEMENTS

The author wishes to thank the following for encouragement and helpful suggestions on an earlier version of this paper: Howard Bloom, Michael Ghiselin, Lynn Margulis, Peter Meyer, John Maynard Smith, Ernst Mayr, Anatol Rapoport, John Paul Scott, David Smillie, Eörs Szathmáry, and David Sloan Wilson. I also benefitted from an on-line discussion of some of these issues among the members of Howard Bloom's International Paleopsychology Project group. Particularly helpful were the comments of David Smillie, Timothy Perper and Peter Frost. The diligent and resourceful research efforts of Patrick Tower are also greatly appreciated, along with the indispensable bibliographic assistance of Kitty Chiu.

<< [Publications List](#)

Copyright © 2007 ISCS. All rights reserved.