

THE CO-OPERATIVE GENE: ON THE ROLE OF SYNERGY IN EVOLUTION

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**"In civilized society [man] stands at all times in need of
the co-operation of and assistance of great multitudes....
man has almost constant occasion for the help of his brethren."**

-- Adam Smith
The Wealth of Nations

*ABSTRACT: Although the heuristic value of Richard Dawkins's "selfish gene" metaphor has been considerable, there has been an increasing emphasis in recent years on the role of co-operative phenomena in nature, along with a renewed interest in the evolution of complexity. Various theorists have also advocated a multi-leveled model of evolution, one which focusses on the "vehicles" of selection at various levels rather than on the "replicators". To borrow Dawkins's Necker cube image, it is suggested here that it might be useful to view the evolutionary process from the perspective of the functional effects that are produced by co-operative interactions among various "units" of selection -- genes, genic "interaction systems" (after Sewall Wright), organisms, symbionts, and "superorganisms". This approach is concerned with the "bioeconomics" of co-operation, and it highlights the role of synergy -- combined effects produced by two or more elements, parts or individuals. It is noted that synergy is a multi-levelled phenomenon that can take many different forms. But more important, it is proposed that synergy has played a significant causal role in the evolution of complexity. The interdependent synergistic effects produced by co-operative interactions of various kinds have often provided the proximate causal mechanisms (the functional "payoffs") associated with the differential selection of more complex forms and more inclusive "levels" of organization; underlying the many specific "transitions" in the complexification process, a common functional principle has been operative. Some implications of this perspective are also briefly discussed. **Keywords: Synergy, co-operation, symbiosis, bioeconomics, complexity, group selection.***

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INTRODUCTION

It should be stated at the outset that there can be no gainsaying the heuristic value of Richard Dawkins's "selfish gene" metaphor. A gene-centered approach has led to many new insights about what Cosmides and Tooby (1981) called "intragenomic conflict," including particularly the significance of meiotic drive (Hamilton 1967), transposable elements and non-functional DNA sequences (Doolittle and Sapienza 1980; Orgel and Crick 1980), uniparental inheritance of cytoplasmic organelles in eukaryotes (Grun 1976) and the biasing of sex ratios in reproduction (reviewed in Hurst 1993), among other things. The gene's-eye view of evolution also inspired

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Peter A. Corning

George Williams's landmark treatise, *Adaptation and Natural Selection* (1966) -- a therapeutic cold bath that served to purge evolutionary biology of some fuzzy thinking about group selection and the "good of the species."

Gene selfishness also provided the core assumption for inclusive fitness theory (Hamilton 1964a,b), as well as various game theoretic approaches to social life (Maynard Smith 1982, 1984a; Axelrod and Hamilton, 1981), which have spawned many testable and successfully tested hypotheses. As a result, it is now appreciated that "harmony" within and among various functional units in nature -- from DNA sequences to honey bee colonies -- is not a given. It must be "engineered" by natural selection, with an eye to the costs and benefits for the parts.

On the other hand, the gene-centered approach has also inspired a radical reductionism in some quarters that, in its most extreme form, denies the relevance or evolutionary significance of "higher levels" of biological organization. As Anatol Rapoport warned in an essay on the "Ideological Commitments in Evolutionary Theories" (1991), metaphors can exert a powerful influence over our perceptions, for better or worse. The imagery we use to characterize nature, or human societies, may also become a distorting lens that can bias our interpretation of a more complex reality; we oversimplify at our peril. John Maynard Smith, whose credentials as a neo-Darwinian are impeccable, launches his new volume (coauthored with Eörs Szathmáry) on *The Major Transitions in Evolution* (1995:3) with the assertion that: "Living organisms are highly complex, and are composed of parts that function to ensure the survival and reproduction of the whole." Wholes are real; they are not epiphenomena. But more important, it will be argued here that wholes have played a major causal role in the evolution of complexity. The question can be framed as follows: Why are selfish genes so often co-operative? Why have selfish genes combined with one another over time to produce complex, interdependent systems? (Even a simple virus, like the much studied SV40 in monkeys, has five genes and 5,243 base pairs of DNA.)

In a new preface accompanying the revised edition of *The Selfish Gene*, Dawkins acknowledged that his famous metaphor is, after all, a heuristic device. Responding to critics who had accused him of extremism, Dawkins deployed another metaphor, the Necker cube (a two dimensional drawing that can be perceived in different ways), to illustrate the intent behind his inspired bit of anthropomorphism. "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-ix). In that spirit, what I propose to do here is to rotate the Necker cube in such a way that our focus shifts to the functional interactions that occur within and among various "units" of selection -- genes, genic "interaction systems" (after Sewall Wright), organisms, symbionts and "superorganisms". To borrow Dawkins's terminology, we will focus on the role played by the "vehicles" rather than the "replicators".

In recent years, various theorists have advocated a multi-leveled, hierarchical (some prefer "holarchical") model of the evolutionary process (reviewed in Grene 1987; also, see especially Brandon and Burian 1984; Eldredge and Salthe 1984; Salthe 1985; Eldredge 1985, 1995; Buss 1987; Vrba 1989). Meanwhile, a number of other theorists have been seeking to reestablish group selection on a firmer theoretical foundation. For instance, David Sloan Wilson and Elliott Sober (1994) stress the importance of a "shared fate" among the genes in "higher-level" entities (see also D.S. Wilson 1975, 1980; Wilson and Sober 1989; Wade 1977; Wade and McCauley 1980). Here the focus will be on the "economics" of co-operation at various levels of biological organization, with particular emphasis on the role of synergy (the combined effects produced by two or more elements, parts or individuals). It will be suggested that the vehicles of selection at various levels not only exhibit a "shared fate" but they also produce synergies -- interdependent functional effects that have served as the proximate causal mechanisms (the "payoffs") underlying the emergence and persistence of more complex forms and more inclusive levels of organization.

It is only possible to provide an abbreviated discussion of this paradigm here. Of necessity, a number of points that should be treated at length will be mentioned only briefly, while some contentious issues can be dealt with only summarily.

THE CO-OPERATIVE GENE

It is important to begin with a definition of co-operation. As the term will be utilized here, co-operation refers to a relationship -- a condition in which two or more parts "operate together." Co-operation thus connotes a functional interaction. In this sense, 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. By the same

The Co-operative Gene

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.

A second 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 the common denominator in all of the various formal hypotheses about the earliest steps in the evolutionary process -- from Eigen and Schuster's (1977, 1979) "hypercycle", to King's (1986) "chemical symbiosis" model, to Szathmáry and Demeter's (1987) "stochastic corrector" to Wächtershäuser's (1988, 1990) "surface metabolism" model, to Kauffman's (1993) "collective phase transitions." All share the common assumption that co-operative interactions among various component "parts" played a central role in catalyzing living systems.

At the level of the genome, it goes without saying that genes do not act alone, even when major single-gene effects are involved. As Dawkins observed in one of the less frequently quoted but more important passages of *The Selfish Gene*, the genes are not really free and independent agents: "They collaborate and interact in inextricably complex ways, both with each other and with their external environment...Building a leg is a multi-gene co-operative enterprise" (1989[1976]:37). To underscore this point, Dawkins employed a metaphor from rowing: "One oarsman on his own cannot win the Oxford and Cambridge boat race. He needs eight colleagues...Rowing the boat is a co-operative venture" (p.38). Furthermore, Dawkins noted: "One of the qualities of a good oarsman is teamwork, the ability to fit in and co-operate with the rest of the crew" (p.39). (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.)

By the same token, the evidence that "intragenomic conflicts" do in fact exist does not negate the overall conclusion that, by and large, such conflicts are exceptions rather than the rule. Cosmides and Tooby (1981:86,88), in their original paper on the subject (which was focussed particularly on potential conflicts between cytoplasmic and nuclear genes), pointed out that: "There can be little doubt that the great proportion of cytoplasmic gene expression does act symbiotically with nuclear genes....No part of the genome can act to any great extent against the interests of the rest, or it will be rendered inert by the rest of the genome through balancing selective processes, constituting a sort of 'parliament of the genes' [after Egbert Leigh, 1971]."

The origin of chromosomes, likewise, may have involved a co-operative/symbiotic process. This hypothesis, suggested by Margulis and Sagan (1986) and Maynard Smith (1991), has recently been developed as a formal model by Maynard Smith and Szathmáry (1993). The model indicates that, if two (theoretically separate) genes interact co-operatively, so that the two in combination are "synergistic" (functionally superior to each one alone), then there is clearly an advantage to becoming linked so that they will replicate and segregate together.

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. Among the various hypotheses about what the benefits of sexual reproduction may be, there is Weissmann's (1889) proposal that it is a source of increased genetic variation, and thus a generator of raw material for natural selection. There is also Muller's (1964) "ratchet", the idea that sexual reproduction serves to brake the otherwise relentless buildup of deleterious mutations in the genome. Bernstein et al., (1981, 1985; and Margulis and Sagan 1986) have proposed that sexual reproduction contributed a critically-important DNA damage-repair function to evolving organisms. Kondrashov (1982, 1988) has argued that sexual reproduction can act to reduce the genetic load, especially when there are linkages between mutations that, synergistically, augment their effects. Hamilton et al., (1990) see sexual reproduction as an anti-parasite strategy, a way of keeping ahead of coevolving parasites in a Red Queen's race (*sensu* Van Valen 1973). And Howard and Lively (1994) developed a model that combines the mutation-accumulation and parasite coevolution hypotheses. Their conclusion was that, given moderate rates of mutation and anti-parasite coevolution, sexual reproduction could be evolutionarily stable. (See also the more extensive examinations of sex in Maynard Smith 1988, and Michod and Levin 1988.)

Eukaryotic cells can also be characterized as a co-operative venture -- an obligate federation which may have originated as a symbiotic union (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) that may have evolved from structurally-similar spirochete ancestors (Margulis 1970, 1981, 1993; but see also the alternative scenario of Cavalier-Smith 1981, 1987, 1991). The broad theoretical implication of this important evolutionary development is that a co-operative relationship (as defined

Peter A. Corning

above) between previously distinct genomes precipitated, or at least augmented, one of the major breakthroughs in the process of biological complexification. The functional consequence, which we will discuss in greater depth below, was a union of specialists and a melding of complementary functions -- both a "division of labor" and a co-operative "combination of labor."

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 increased recognition over the past decade or so as a source of evolutionary change, but more benign commensalistic and mutualistic forms of symbiosis are also more widely appreciated. 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). (See also the commentary by Maynard Smith 1989 and the volume edited by Boucher 1985.) Among the supporting evidence:

- 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, protoctists 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).

Sociobiology is also, by definition, concerned with co-operative relationships among conspecifics, which may 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 in nature among members of the same species may be perturbed by free-riders, "defectors", exploiters, conspecific "parasites", etc., and 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; (4) 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; (5) co-operation in reproduction, which can include joint nest-building, joint feeding and joint protection of the young; and (6) shared environmental conditioning and thermo-regulation. (Among the many references, see for example Allee et al., 1949; Tinbergen 1965; Mech 1970; Kummer 1971; Kruuk 1972; Schaller 1972; E.O. Wilson 1975; Oster and Wilson 1978; Trivers 1985; Goodall 1986; Smuts et al., 1987; Brown 1987; Sherman et al., 1991.)

One caveat should be mentioned at this point about where the boundary line should be drawn in using the

The Co-operative Gene

term "co-operation". Although the definition proposed above could be stretched to include all of the nearly infinite number of functional interactions that occur in nature, including interactions with the physical environment, our usage is confined to those relationships and interactions which involve biological (and biosocial) processes -- the interactions that occur within and between organisms. (One borderline category includes the "tools" and other artifacts -- nests, hives, dams, galleries, spider webs, etc., -- that are the products of biological processes.)

CO-OPERATION VERSUS COMPETITION

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 (see also May 1982).

Charles Darwin was also well aware of the importance of co-operation in nature. In the final recapitulation of his epochal work, he penned the following, oft-quoted passage:

It is interesting to contemplate an entangled bank, clothed in many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have been produced by laws acting around us (1968[1859] p. 459).

Indeed, suffused throughout *The Origin of Species* are many expressions about "the web of complex relationships" in nature, the "infinitely complex relations" among species, and the "marked interdependence" of living forms. Darwin also made reference to the "economy of nature" (a term that apparently can be traced to Linnaeus), which suggests that the problem of earning a living and reproducing, not competition per se, is what defines the overall character of an organism's relationship to its environment, as well as to other members of its own species and to other species. In this conceptualization, natural selection refers to any functionally-relevant factors (adaptations) -- as distinct from the operation of physical laws, historical contingencies, stochastic factors and teleological influences -- that significantly affect differential survival and reproductive success. Natural selection is a way of characterizing a causal dynamic that involves relationships -- the effects produced by the functional interactions that occur between an organism and its environment, inclusive of other organisms.

In this light, the so-called "neo-Darwinian" focus on gene competition contrasts with the more balanced "Darwinian" perspective. Accordingly, there have been various calls of late for a refocussing of the theoretical Necker cube. For instance, Edward O. Wilson asserts that: "The key remaining questions of evolutionary biology are more ecological than genetic in nature" (1987:1). R.I.M. Dunbar points out that: "The societies of advanced vertebrates are designed to allow animals to solve a diverse range of biological problems, with mating often being one of the least important of these" (1989:131). David Sloan Wilson (with his co-author Elliott Sober) argue that: "We must restructure the entire edifice [of evolutionary theory] around the concept of vehicles, not replicators" (1994:591). And paleontologist Niles Eldredge, in a combative new volume, writes that: "Most adaptations are concerned with issues of matter-energy transfer...Most adaptations, in other words, are *economic* in nature...The connection [between ecological and genealogical realms] is most immediately apparent if we paraphrase Darwin's original conception of natural selection; natural selection is the biasing effect that differential economic success has on an organism's reproductive success...It is the fate that organisms, with their heritable features -- their economic adaptations -- face in the economic arena that acts as the filter determining what proportions of genetic information are passed along to the next generation" (1995:177,195; see also Eldredge 1986).

A shift of focus away from a preoccupation with the differential reproductive success of genes to the process of adaptation -- the causal dynamics of natural selection in the "economy of nature" -- has a number of implications. One implication that should be mentioned at this point is that co-operative interactions of various kinds (including those that are parasitical as well as those that are commensalistic or mutualistic) assume greater significance relative to direct ecological and reproductive competition. It may not be an exaggeration to say that

competition and co-operation are co-equal phenomena in terms of the lifetime process of earning a living and reproducing. Indeed, there is very often in nature a complex interplay between competition and co-operation; many animals use co-operation as a means for more effective competition. Also, there are many cases where the two modes of interaction coexist in a multi-faceted relationship that combines competitive costs and offsetting co-operative benefits, as was pointed out many years ago by Alexander (1974). (For additional perspective, see Addicott 1985; Brown 1987; Walters and Seyfarth 1987; Clutton-Brock 1988; Pianka 1988; and Krebs and Davies 1993). Below are a few specific examples of this interplay:

- 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 (Hölldobler 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 patriline in polyandrous species (see also Seger 1989, 1991).
- A number of ant species establish pleometrotic colonies; multiple foundresses co-operate in initial nest construction and brood production (Rissing and Pollack 1988). 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; multi-foundress colonies are able to produce a larger brood raiding force more quickly and this apparently provides a decisive competitive advantage (group selection). Yet, other studies of these colonies suggest that one tradeoff may be internal competition among co-foundresses and their offspring.
- The possible costs and benefits of prairie dog coloniality were studied over a six-year period by Hoogland (1979a,b, 1981) in colonies of two species (*Cynomys leucurus* and *C. ludovicianus*). His tentative conclusion (because some of his evidence was circumstantial) was that prairie dog colonies do experience greater interpersonal aggression and a higher incidence of parasite infestations but that these disadvantages are more than offset by the joint increase in fitness due to greater protection from predators.
- 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 Rutan (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 for mating privileges among males, as shown in an earlier study by Packer and Pusey (1982) (see also Packer et al., 1988).
- 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 congregate in this way during their summer moulting season; non-breeding males also congregate in "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).

Neo-Darwinian theory -- as purified by the selfish gene perspective -- attributes evolutionary change to competition among the "replicators" -- the ultimate units of selection. In the Neo-Darwinian model, co-operation plays a decidedly subsidiary role. But if we rotate the Necker cube and view evolution as an ecological/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 (see Clutton-Brock 1988). 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.

The Co-operative Gene

THE GENETICS OF CO-OPERATION

It has been a cardinal assumption of neo-Darwinism that co-operation in nature is a theoretical "problem" -- 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. Thus the importance attached to inclusive fitness theory (or kin selection, in Maynard Smith's term) and to game theory. However, a "bioeconomic" perspective on the evolutionary process challenges that point of view. 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 nondescendants does not determine the direction or product of natural selection; it only supplies an additional cost or benefit." Moreover, 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 (what Darwin called "family selection", parental manipulation, group selection and mutualism) are not mutually exclusive and in many cases might reinforce one another.

One implication of these statements is that we should expect to find a significant degree of decoupling between genetic relatedness and co-operation in nature, 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 which 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.)

Second, 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 is still more likely to occur in closely-related animals). A sampler of this discordant evidence includes the following:

In birds, Ligon and Ligon (1982) analyzed the communal nesting and extensive helping behaviors among green woodhoopoes (*Phoeniculus purpureus*), both among closely related and unrelated birds. They found that this behavior pattern markedly increased the woodhoopoes' likelihood of survival and reproductive success in an East African environment characterized by a severe shortage of suitable nest sites. A similar pattern was identified by Clarke (1989) in the bell miner (*Manorina melanophrys*). (But note also the more strongly kin-oriented pattern observed in other woodhoopoe populations by Du Plessis, 1993.) Parker et al., (1994) used DNA fingerprinting to document that food sharing in feeding aggregations of common ravens (*Corvus corax*) in the forests of western Maine was not primarily kin-directed. Møller (1987) analyzed various trade-offs (costs and benefits) of colonial nesting in swallows (*Hirundo rustica*) and concluded that the costs and benefits of coloniality varied markedly with such factors as group size, the frequency of predation, exposure to parasites, etc.

In the same vein, Mumme and his co-workers (1988) were able to conduct a comparative cost-benefit analysis of a 15-year data set comparing joint-nesting and solitary acorn woodpeckers (*Melanerpes formicivorus*). The data indicated that communally-nesting females experienced a fitness trade off: lower average annual reproduction in exchange for higher year-to-year survival rates. In a later study of the Florida scrub jay (*Aphelocoma c. coerulescens*), Mumme (1992) showed that the presence of non-breeding helpers in experimental groups correlated with lower predation and higher nestling survival rates than was the case with control groups that were denied helpers. And Haig et al., (1994), utilizing a DNA analysis with 224 red-cockaded woodpeckers (*Picoides borealis*), found that helping behaviors involved a variety of related and unrelated birds and that there was no direct benefit to the helpers from "extra matings." (Brown, 1987, in a book-length synthesis on communal breeding and helping behaviors in birds, provided additional evidence, although he also observed that, as a rule, unrelated helpers do not seem to work as hard as close kin.)

Peter A. Corning

Recent discoveries that many insect colonies consist of multiple queens or multiple patriline have presented a challenge to the long-standing inclusive fitness explanation for social insects (the rudiments of which can be traced all the way back to Darwin). For instance, Queller et al., (1988) observed that swarm-founding neotropical wasp colonies (*Parachartergus colobopterus*) may have multiple queens, sometimes numbering in the hundreds, and yet the level of relatedness and inbreeding is low. Similarly, Strassmann et al., (1994) compared allozyme polymorphisms in "incipient" social wasps of the subfamily Stenogastrinae and estimated that the average relatedness among colony members in one of the best studied species (*Liostenogaster flavolineata*) was .22, the lowest so far reported for any primitively eusocial insect. And Scott (1994) found that, in the burying beetle (*Nicrophorus tomentosus*), competition with flies (as well as conspecific groups) promotes communal breeding among unrelated males and females. As Breed (1988) points out, genetic models predict that reduced relatedness among colony members should have a divisive, if not fatal, effect on colony functioning. Nevertheless, eusocial species do exist and are obviously successful -- if less than perfectly integrated.

Indeed, Sherman et al., (1988) hypothesized that genetic diversity within social hymenoptera may have a previously unrecognized group-level advantage as a buffer against parasites and pathogens. This hypothesis was subsequently supported in a study of the bumblebee (*Bombus terrestris*) (Shykoff and Schmid-Hempel 1991). In addition, a series of reports by Robinson and Page (1988), Page et al., (1989) and Page and Robinson (1991), have supported the hypothesis that the genetic differences observed within honey bee colonies (*Apis mellifera*) can be correlated with performance differences among workers with respect to the division of labor and to ecological variations. In other words, the genetic composition of the colony may reflect "downward" causation in relation to colony-level functional (bioeconomic) needs; natural selection in this domain may operate on the parameters of the colony as a dynamic system (group selection). Supporting evidence for this hypothesis was also found in both honey bees (*Apis mellifera*) and dwarf honey bees (*Apis florea*) by Oldroyd and his co-workers (1992a,b, 1994). (See also Woyciechowski 1990.) Likewise, Rissing et al., (1989) discovered in a field study of the colonial leaf-cutting ant (*Acromyrmex versicolor*) that co-foundresses were unrelated and yet the colonies exhibited specialization without apparent conflict. These researchers concluded that intense between-colony competition and brood raiding provided a group-level selection pressure in favor of such behaviors. (See also the analysis by Mesterton-Gibbons and Dugatkin, 1992.)

In social carnivores, Packer and Pusey (1982) observed that breeding coalitions of African male lions included non-relatives much more commonly than kin selection theory would predict. And Scheel and Packer (1990) found a similar pattern in the hunting and cub-guarding behaviors of female lions. In primates, Moore (1984) reviewed and reanalyzed the earlier studies of Goodall, Teleki, McGrew and others on meat sharing in chimpanzees, a pattern whose potential costs and benefits turned out to be surprisingly complex and were not unambiguously associated with inclusive fitness. Stanford (1992) studied allomothering in capped langurs (*Presbytis pileata*) and found that it could best be interpreted as a low-cost behavior that benefits both related and non-related recipients. And, in the evening bat (*Nycticeius humeralis*), Wilkinson (1992) documented an extensive pattern of communal nursing of pups that was not preferentially directed to kin.

Co-operative hunting is a survival strategy that exists in a diverse range of species, from canids to felids, birds, and even some spiders. In a systematic reanalysis of the data from 28 studies encompassing 60 species, Packer and Ruttan (1988) concluded that co-operative hunting is a behavioral pattern that is likely to occur only when there are "synergies" -- per capita food acquisition that is greater than each participant could obtain alone. For example, they cite Kruuk's descriptions of how a solitary hyena would be unable to separate a wildebeest calf from its mother. But when hyenas hunt in pairs, there is a division of labor; one engages the mother while the other catches the calf. Packer and Ruttan also found that the propensity to hunt collaboratively varies greatly across species. The critical factor is not relatedness, they noted, but the size, abundance and character of the prey and the degree of preexisting gregariousness among the hunters, which might be due to other ecological benefits, particularly protection against predation.

Quantitative cost-benefit analyses of co-operative behaviors have also been conducted with increasing frequency in recent years. Some were cited above. In addition, there are many studies of energetic costs and benefits in relation to the associations between nectar-producing plants and their pollinators, and between plants and seed dispersers (reviewed in May 1982; also Brown 1983, 1987). There are also a growing number of time-budget studies that assess the time/energy trade-offs among behavioral strategies, including sociality. For instance, Hogendoorn and Velthuis (1993) examined the impact of ecological factors on the costs and benefits associated

The Co-operative Gene

with helping behaviors by "defeated" (non-reproductive) females in facultatively social carpenter bees (*Xylocopa pubescens*) and concluded that the cost-benefit calculus was greatly affected by ecological constraints, particularly the foraging times required and the likelihood of pollen robbery by conspecifics. Isbell and Young (1993) examined the potential costs and benefits of social organization in six groups of vervet monkeys (*Cercopithecus aethiops*) at Amboseli National Park in Kenya and found that the results varied significantly with group size. The percentage of time each animal spent scanning for predators decreased markedly as the group size increased (although the total amount of scanning time increased, along with the amount of allogrooming). However, group size did not strongly correlate with intra-group competition and conflict. Bertram (1980) observed a similar relationship between group size and individual vigilance in wild ostriches (*Struthio camelus*). In contrast, a time-budget analysis by Dunbar (1992) of data for 18 populations of baboons (genus *Papio*) throughout sub-Saharan Africa suggested that the cost-benefit ratio might become unfavorable as groups increase in size beyond a "tolerable" level, at which point various "stresses" might occur. Dunbar noted that very large groups spent less time in resting and social activity, there was more group fragmentation during foraging and travel and faster travel between various sites. (See also the reviews in Krebs and Davies 1993.)

The extensive cost-benefit studies in vampire bats (*Desmodus rotundus*) by Wilkinson (1984, 1988, 1990), provide a particularly well-documented example of the capacity of functional/bioeconomic factors to transcend the influence of genetic relatedness in shaping co-operative behaviors. If gene competition were of overriding importance, blood sharing among vampire bats would be confined to close relatives. (Blood sharing in this species has very high fitness value, because 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 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 (ie., "reciprocal altruism" sensu Trivers, 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).

SYNERGY AND THE BIOECONOMICS OF CO-OPERATION

A common factor in all of these diverse examples of co-operation is functional synergy -- combined effects produced by two or more elements, parts, or individuals which cannot otherwise be achieved. Derived from the Greek word *synergos* (to "work together"), the term synergy is used here with reference to the bioeconomic effects that are produced by things that "operate together" (co-operation). Although the term is frequently associated with the slogan "the whole is greater than the sum of its parts" or " $1+1=3$ ", actually this is a caricature of a much more subtle and multi-faceted concept. It would be more accurate to say that the effects produced by wholes are different from what the parts can produce alone. In any case, a key to understanding synergy is that it involves effects that are jointly produced and interdependent. Take away a major part and the synergy will attenuate or dissolve. Below are a few examples:

- The observed error rate in normal cellular DNA replication is remarkably low (about 10^{-10} to 10^{-8} per base pair) compared with the theoretical potential, given the ambient sources of decay, damage and copying errors of about 10^{-2} . The reason for this discrepancy is that it is the combined result of a complex set of mechanisms that "work together," including proofreading by DNA polymerases, methylation-instructed mismatch correction, enzymatic systems that repair or bypass potentially lethal or mutagenic DNA damage, processes that neutralize or detoxify mutagenic molecules, the regulation of nucleotide precursor pools and, of course, the redundancy achieved by double-stranded genetic material (Haynes 1991).
- Hemoglobin is a tetrameric protein, and each of its four monomers bind oxygen. However, hemoglobin also displays the remarkable property of positive co-operativity; binding activity by one monomer increases the binding affinity of the others.
- Many species of beetles in the family Scolytidae have adopted the strategy of tunnelling under the bark or into the heartwood of various trees to create "galleries" for laying their eggs and protecting their larvae. The beetles are able to overcome the trees' natural defenses with the assistance of a pathogenic fungus that kills the wood in the vicinity of the gallery. In addition, the beetles deposit non-pathogenic fungi and yeast bacteria which produce a thick lining

Peter A. Corning

for the gallery and, more important, provide a food supply for the beetle larvae. Not only are these organisms interdependent, but the beetles have also developed specialized structures to aid in carrying their symbionts with them when they leave their natal trees (Wilson and Sober 1989).

- Strassmann and Queller (1989) describe an experiment with the primitively eusocial paper wasp (*Polistes bellicosus*) to test the hypothesis that one important advantage of sociality is the capacity to quickly rebuild a nest or build a new one when the original nest is destroyed, often by a predator. The findings were clear-cut; groups that were larger than four had a strong advantage in terms of ultimate reproductive success. The researchers also noted that the period of dependency in some wasp species is longer than the life span of a single adult. "Most individuals, if they nested alone, would fail completely." Finally, Strassmann and Queller pointed to the advantage of "redundancy". In any species where there are both dependant offspring and a significant risk of parental mortality, that risk can be protected against with helpers.
- Emperor penguins (*Aptenodytes forsteri*) are able to buffer themselves against the intense cold of the Antarctic winter by huddling together in dense heat-sharing colonies numbering in the tens of thousands. Experiments have shown that, in so doing, the penguins are able to reduce their energy expenditures by 20-50% (Le Maho 1977). Similarly, honey bees, through joint heat production or fanning activities, as the need arises, are able to maintain the "core" temperature of their hives within a narrow range (Gould and Gould 1995).
- The African honeyguide (*Indicator indicator*) is an unusual bird species that utilizes beeswax as a food source. However, in order to obtain beeswax, these birds must rely on a coordinated search-and-destroy effort with a symbiont, such as the African badger (*Mellivora capensis*), which has the capacity to dismember the hive and to consume only the honey, leaving the beeswax behind. However, this unusual example of symbiotic predation depends on a third symbiont, a gut bacterium associated with the honeyguide that produces an enzyme which can break down wax molecules (Bonner 1988).
- In addition to Dawkins's tacit example of synergy in the Oxford-Cambridge boat race, Maynard Smith and Szathmáry (1995) use as a metaphor specifically for synergy the image of two men in a rowboat, each with one oar. If only one oarsman is rowing, the boat will go in circles (see below). A quantitative example can also be added to these nautical metaphors: A world class "varsity eight" (plus a coxswain) can cover 2000 meters over the water in about 5.5 minutes. However, a single sculler can at best row the same distance in about 7 minutes. The difference is a synergistic effect.

As this sampler suggests, there are many different kinds of synergy. Some involve threshold effects, "phase transitions," or density-dependent phenomena. Although each of the parts in such cases may have an additive relationship to any other part, the parts in combination may produce non-linear effects. For instance, the players in a classic tug-of-war might be evenly divided, so that there is a stalemate. But if you add one more player to either side, the war may soon be over.

The dynamics and functional consequences of density-dependence have been studied extensively in birds, with particular attention to their effects on the patterns of competitive and co-operative behavior. One recently-reported long-term study of the Monteverde brown jay (*Cyanocorax morio*) in Costa Rica (Williams et al., 1994) documented significant behavioral changes over time as an expanding population reached habitat "saturation". In addition to demographic changes in the number of flocks, flock sizes and breeding constraints, the researchers also observed a sharp increase in interindividual aggression. However, their study also shed new light on the much-debated question of the relationship between habitat crowding and sociality (particularly communal breeding and helping behaviors). Their conclusion: "At high densities, habitat constraints on the population are associated with increased reproductive competition...and a decrease in the relationship between group size and reproductive success...At lower densities, however, intrinsic benefits to delayed dispersal are apparently sufficient to maintain sociality even in the absence of strict habitat constraints..." (p.321).

A second type of synergy involves "emergent phenomena." Although biologists frequently use the term broadly, it is restricted here to situations in which two or more "parts" merge in such a way that a new "whole" arises with distinctive new chemical or physical properties. Thus, stainless steel is an alloy of steel (itself an alloy) together with nickel and chromium, a combination which exhibits rust and tarnish resistance and increased durability. And duralumin, which is a compound of aluminum, copper, manganese and magnesium, combines the light weight of aluminum with the strength of steel. Similarly, the life-cycle of the cellular slime mold *Dictyostelium discoideum* includes an independent foraging phase, a process of aggregation among individual amoebae into a migrating pseudoplasmodium and, finally, the formation of a stalk with a spore-producing fruiting body at its head (Bonner 1988). Indeed, emergent phenomena are commonplace in the biological realm, ranging from protein molecules to the products of diploid reproduction to the elaborately constructed honey bee hives.

The Co-operative Gene

Spatial (and temporal) patterning -- that is, physical arrangements of various "parts" -- may also generate synergistic effects. Included in this category are phenomena such as the many forms of aggregation, grouping, or juxtaposition in nature, as well as the enormous variety of more precisely structured spatial configurations of different elements. The effects thus produced range from the emergent properties of crystals or proteins, on the one hand, to the collective results achieved by fish schools, leks, communal breeding colonies and foraging groups. Buckminsterfullerenes, the recently synthesized molecules of pure carbon (C_{60} and several variants) provide an apt example. These artifacts are named for the well-known engineer who invented geodesic domes (and incidentally promoted the concept of synergy). Nicknamed the "Bucky Ball," C_{60} was given its moniker because of its physical resemblance to a geodesic dome, or a soccer ball, which is what accounts for its extraordinary stability; it is the geometry of the whole that gives the Bucky Ball its distinctive properties (Curl and Smalley 1988).

Another type of synergy involves what might be called a "combination of labor." Many symbiotic partnerships fall into this category; mutualistic symbionts typically provide complementary functional capabilities or resources for one another. One case in point is lichens, where the fungal partner provides surface-gripping and water-retention capabilities while the cyanobacterium or green alga bring photosynthesizing capabilities to relationship. Moreover, a comparative study by Raven (1992) documented that lichen symbioses typically result in an enhancement of nutrient and energy uptake compared with the performance of asymbiotic forms. A second example was pointed out by Margulis and Sagan (1995). Eukaryotic microtubules have the distinctive property that they can either form centrioles or serve as the kinetosomes for undulipodia, but not both. However, colonial protist aggregates are often able to circumvent this constraint by combining and sharing their functional specializations.

Examples of synergistic combinations of labor among members of the same species include, among others, communal breeding, joint foraging, reproductive "coalitions", coordinated thermoregulation, mutual defense and mobbing behaviors, pleometrosis, and co-operative hunting. For instance, the studies of prairie dog colonies by Hoogland (1979a,b, 1981), cited above, showed that, as colony size increases, there is a pronounced decrease in individual alertness against potential predators, coupled with an overall increase in collective anti-predator alertness and protection. Similar results were obtained in Bertram's (1980) ostrich study and in Isbell and Young's (1993) study of vervet monkeys.

What is generally referred to as a "division of labor" is a particularly important generator of synergies -- in nature and human societies alike. As defined here, a division of labor differs from a combination of labor only in the sense that, in the latter case, the focus is on breaking up a global problem or task into parts in such a way that "differentiation" and specialization can be used to achieve efficiencies. To cite a few 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 multi-cellular 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, multi-cellular colonies are virtually immune from predation by filter feeders.
- Morphological specialization can sometimes play a key role in the 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 (*Eciton burchelli*), the so-called "sub-majors"

Peter A. Corning

(or porters), team up to carry sometimes very large prey which, if split up into pieces, would be more than each individual ant could carry alone (Franks 1989).

- A study of hunting behavior in lions by Stander (1992) speaks to the assertion 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 noncoordinated 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 many other species (e.g., dolphins and whales; see Würsig 1989).
- Naked mole rats (*Heterocephalus glaber*) represent a particularly significant example of a division of labor, because these diploid rodents 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 nonbreeders, both males and females, engage in co-operative digging, cleaning, carrying of pups, foraging and transporting of food (succulent tubers) within the colony's often extensive underground tunnel systems. The role of defense is 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 rat militia will also mobilize for defense against intruders from other colonies. Why do mole rats utilize this highly distinctive survival strategy? Sherman et al., (1992), who have studied the mole rats extensively, provide the following response: "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" (1992:78). (See also Sherman et al., 1991.)

As should be evident from these examples, synergistic effects are measurable and quantifiable even when we may not completely understand the underlying material causes. There are numerous measuring rods: economies of scale, reduced energy expenditures, higher yields, lower mortality rates, a larger number of viable offspring, and so on. More subtle measuring rods include enhanced stability properties, greater stress tolerance, increased fidelity in reproduction, augmented effects, etc. Consider the quantitative results mentioned in some of the examples above: the thermal efficiencies associated with emperor penguin huddling behaviors, reductions in predation rates among communally-nesting birds, reduced scanning time and individual alertness in colonial birds and mammals, the reduced mortality rate in vampire bats, the increased rowing speed of a varsity eight. Indeed, quantitative studies documenting various bioeconomic synergies have been growing in number recently. Below are a few examples:

- Nest construction in the social wasp (*Polybia occidentalis*) is a complex activity requiring the coordination of various tasks. To study the bioeconomics, Robert Jeanne (1986), conducted a comparative study of small versus large colonies, as well as the nest construction technique used by social wasps versus the less efficient method of solitary wasps. Jeanne found that small colonies required almost twice as many worker-minutes to complete the same amount of construction (due mainly to materials handling inefficiencies that larger colonies could minimize). In addition, he was able to determine that social wasps could collect and process a given amount of nest material with 2.6 times fewer foraging trips than were required by solitary wasps (with the added advantage that the social foragers were able to reduce their exposure to predators in the field).
- Marzluff and Heinrich (1991) tested the hypothesis that immature common ravens (*Corvus corax*) form social groups (in contrast with breeding adults that are territorial) in order to gain access to defended carcasses. They found that groups ranging from 9-29 immature birds were significantly more likely to overcome adult carcass defenders and were able to feed at higher rates than were smaller groups or solitary individuals. The group benefits resulted from a combination of reductions in the neophobia of the foragers and the reduced aggression of adult defenders as group sizes increased.
- In a comparative study of reproduction during a single breeding season among southern sea lions (*Otaria byronia*), Campagna, et al., (1992) observed that only 1 of 143 pups born to gregarious, group-living females died before the end of the season, as compared to a 60% mortality among the 57 pups born to solitary mating pairs. Pups in colonies were protected from harassment and infanticide by subordinate males and were far less likely to become separated from their mothers and die of starvation.

The Co-operative Gene

- In a singular variation on the example of the African honeyguide described above, Isack and Reyer (1989) conducted a quantitative analysis of a similar symbiotic partnership in northern Kenya between honeyguides and humans (the nomadic Boran people). They found that Boran honey hunting groups were approximately three times as efficient at finding bees' nests when they were guided by a bird. They required on average of 3.2 hours to locate the nest compared with 8.9 hours when not guided. (And the latter figure does not even include the days on which no nest was found.) The benefit to the honeyguides was even greater; 96% of the nests that were discovered during the study would not have been accessible to the birds had the humans not used tools to pry them open. Furthermore, the Boran's use of smoky fires to suppress the bees' defenses benefitted both the humans and their symbionts. (The human-honeyguide partnership was also aided by a two-way vocal communication system.)

Other quantitative examples include Bonner's (1988) observations that aggregates of myxobacteria, which move about and feed en masse, secrete digestive enzymes that enable them collectively to consume much larger prey than would otherwise be possible. Similarly, Schaller (1972) found that capture efficiency (captures per chase times 100) and the number of multiple kills achieved by Serengeti lion prides that he studied increased with group size. (Later studies have shown that hunting efficiencies are dependent on a variety of ecological factors, including the size and capabilities of the prey.) In the highly social African wild dog (*Lycaon pictus*), overall kill probabilities in hunting forays were found to be greatly superior (between 85 and 90 percent) to those achieved by less social top carnivores (Estes and Goddard 1967). Kummer (1968, 1971) documented that collective defense in hamadryas baboons (*Papio hamadryas*), as in many other species, greatly reduces the joint risk to each group member of being a victim of predation. In the same vein, Partridge and his colleagues (1982) showed that fish schooling, which may include active forms of coordinated behavior, is highly adaptive for the individual participants. For instance, evasive maneuvers utilized by dwarf-herring (*Jenkinsia lamprotaenia*) against predatory barracudas dramatically reduced the joint risk of being eaten. And von Wagner (1954) observed that the Mexican desert spiders (*Leiobunum cactorum*), by clustering together in the thousands during the dry season, are able to avoid dehydration.

SYNERGY AND THE EVOLUTIONARY PROCESS

To return to our leading question: "Why are selfish genes so often co-operative?" the answer in a nutshell is because of the functional synergies that co-operation may produce. Furthermore, from a broader perspective synergistic effects have also played a significant causal role in the overall evolutionary process. Elsewhere (Corning 1983, 1995) it was proposed that synergistic effects of various kinds have been of central importance in the evolution of complex systems generally -- that a common functional principle has been associated with the various steps in this important directional trend. The reasoning behind this hypothesis can be briefly summarized.

We must begin by returning to the Darwinian conceptualization of natural selection -- not as a "mechanism", or as a competitive struggle between genes, or as a genetic bookkeeping exercise -- but as an aspect of a dynamic historical process. In the Darwinian model, natural selection can be viewed as an umbrella term which refers to whatever functionally-relevant factors may be responsible in a given context for the causing the differential survival and reproduction of various "units" of biological organization. Natural selection is a way of characterizing a causal dynamic that involves changes in relationships -- changes in the functional interactions that occur within an organism, and between an organism and its environment, inclusive of other organisms. It is the functional consequences of various bioeconomic processes that constitute the "causes" of natural selection. Another way of putting it is that causation in evolution runs backwards from our conventional view of things. To use Ernst Mayr's well-known distinction, it is the "proximate" functional effects produced by changes in organism-environment relationships that are responsible for the "ultimate" (transgenerational) genetic changes which constitute organic evolution. These relational changes could be initiated by a functionally-significant mutation, a chromosomal transposition, a new gene combination, a change in the physical environment, a change in one species that affects another species, or it could be a change in behavior. However, it is the consequences of these changes that matter.

This model of evolutionary causation applies to synergistic phenomena as well. Co-operative interactions in nature that produce positive functional effects, however they may arise, can become "units" of selection that differentially favor the survival and reproduction of the "parts" (and their genes). In other words, it is the proximate advantages (the payoffs) associated with various synergistic interactions (in relation to the particular

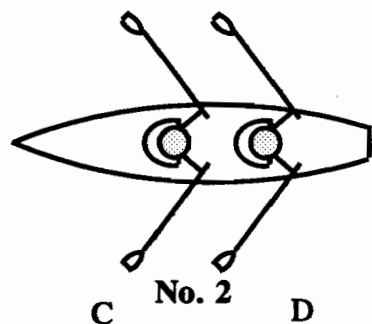
organism's needs) that constitute the underlying cause of the evolution of co-operative relationships, and complex organization, in nature. The functional synergies are the very cause of their systematic evolution over time, via their impacts on differential survival and reproduction.

Moreover, many of these evolutionary changes originate (and are initially adopted) at the behavioral level. For, as Ernst Mayr (1974) has observed, behavioral innovations are often a "pacemaker" of evolutionary change. In C.H. Waddington's words: "It is the animal's behavior which to a considerable extent determines the nature of the environment to which it will submit itself and the character of the selective forces with which it will consent to wrestle" (1975:170). The idea that behavioral innovations might be a significant cause of evolutionary change can be traced back to Lamarck. Darwin also alluded to the idea in *The Origin*. At the turn of the century, a movement among evolutionists of that day known as "Organic Selection Theory" was developed in an effort to highlight the creative role of behavior in evolutionary change. (It was subsequently buried by "Weissmannism" and, much later, was resurrected, downgraded and renamed the "Baldwin Effect" by George Gaylord Simpson and other exponents of what was then called "the modern synthesis.") Waddington himself developed a variation on this theme in the 1950s, which he dubbed "genetic assimilation." And Ernst Mayr has repeatedly argued the case for behavior as a cause of evolution in his various writings (reviewed in Corning 1983; see especially Mayr 1960; also see Plotkin 1988; Bateson 1988; cf., Skinner 1981).

One way of bringing this theoretical perspective into better focus might be to revisit the plethora of formal game theory models of co-operative behavior that have appeared in recent years. 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 you look 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) formulation, 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 bioeconomics of the game are a critically important aspect.

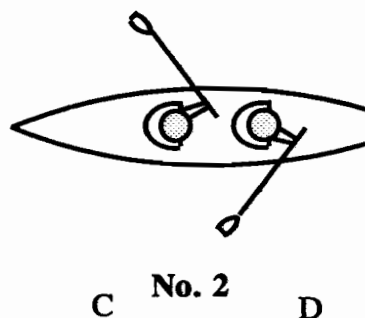
In their new volume on *The Major Transitions in Evolution*, Maynard Smith and Szathmary (1995) make a similar argument. They note that the evolution of co-operation depends less on relatedness than on the functional costs and benefits -- ie., the values in the payoff matrix. As they put it, if an individual 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.

How can "cheating" or "defection" (the Prisoner's Dilemma) be prevented? Maynard Smith and Szathmary's response is rendered in terms of game theory. They posit two different kinds of game situations, as illustrated in the diagrams below. (I have taken the liberty of revising the payoff values that were utilized by Maynard Smith and Szathmary to accord with a more explicit assumption about the object of the game, namely, that the oarsmen



		No. 2	
		C	D
No. 1	C	7 / 7	4 / 7
	D	7 / 4	0 / 0

Sculling Game



		No. 2	
		C	D
No. 1	C	7 / 7	0 / 0
	D	0 / 0	0 / 0

Rowing Game

The Co-operative Gene

are both seeking to cross a river.) The first diagram represents a "sculling" model in which two oarsmen each have two oars and row in tandem. In this model 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. In this case, mutual co-operation becomes an evolutionarily stable strategy and defection is unrewarding.

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." Peck also noted (as have others) that co-operation can best be maintained among individuals who have a continuing relationship, regardless of kinship. (The "policing" of co-operative relationships will be discussed further below.)

Game theory provides one possible means for testing specific hypotheses of synergistic interactions. Another involves either experiments or "thought experiments" in which a major part is removed from the whole and the consequences are observed. 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 water supply from a human settlement. A third means of testing for synergistic effects 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 notable for pioneering; their ability to survive in these more rigorous circumstances is dependent on their joint capabilities.

Additional support for this theoretical paradigm can be found in the increasing use of the synergy concept among biologists during the past decade or so. (Indeed, a computer search of a biological sciences data base for the year 1993 identified 10,958 "synerg" references, although most were associated with biochemistry, endocrinology, pharmacology and related disciplines, where the concept has a long history.) Some explicit uses of the synergy concept in evolutionary biology and sociobiology include Kondrashov's (1982, 1988) hypothesis regarding the basis of sexual reproduction, which relies on synergistic linkages between deleterious mutations. Similarly, Maynard Smith and Szathmáry's (1993) theory of the origin of chromosomes postulates a synergistic relationship among primordial genes. Szathmáry (1993a) also utilizes the concept in a model derived from metabolic control theory which suggests that, under some conditions, two mutations affecting a metabolic pathway could act synergistically. Elsewhere, Szathmáry (1993b) utilizes the concept in a model involving frequency and density-dependent effects in viral dynamics. Rosenberg (1991) postulates a necessary role for "synergistic selection" in the evolution of warning coloration (aposematism) in marine gastropods. The synergy arises when a potential predator has multiple "distasteful" encounters with the same morph, which enhances the joint selective value for each bearer. (See the further discussion of this issue in the contributions by Guilford and Cuthill 1991, and Tuomi and Augner 1993.) Hurst (1990) suggests that parasite diversity in a given cell or organism may be more burdensome than a similar quantity of uniform types, because various synergistic interactions among different parasites may enhance their mutual effects. Hurst proposes that diploidy, multicellularity and anisogamy may be anti-parasite mechanisms. They might serve to reduce parasite diversity.

Leo Buss (1987) utilized the concept of synergy (or what he called "synergisms") in a broader theoretical context, as an explanatory principle in connection with the evolution of metazoa and "higher units" of selection. Though he never explicitly defined the term, his usage was idiosyncratic; he equated synergy with positive, or mutually beneficial relationships between lower and higher levels of organization, or wholes and parts, as contrasted with "conflicts" between levels. "The organization of any unit will come to reflect those synergisms between selection at the higher and the lower levels which permit the new unit to exploit new environments and those mechanisms which act to limit subsequent conflicts between the two units" (1987:viii).

Synergy has also been deployed in some recent sociobiological studies. Gordon (1987) observed "synergistic interactions" among three major activities in colonies of red harvester ants (*Pogonomyrmex barbatus*) in response to various "perturbations". Santillán-Doherty and his colleagues (1991), in a study of stump-tailed macaques (*Macaca arctoides*), found non-linear synergistic effects among three variables -- kinship, sex and rank -- in shaping the behavioral interactions among the animals in their study population. Packer and Rutan (1988) also explicitly recognized the role of synergy in co-operative hunting. They observed that, when individual hunting success is already high, there is little to be gained by co-operating. Co-operation depends on synergy -- an

increase in the average individual feeding efficiency through joint efforts. "An increase in hunting success with group size therefore indicates synergism from co-operation, whereas a decrease indicates some form of interference [negative synergy]" (1988:183).

A number of other theorists have recognized synergistic effects implicitly in their studies and analyses without explicitly using the term. Thus, Page and Robinson (1991) refer to "non-additive inter-individual effects" in relation to possible genetic influences on the division of labor in honey bees. Bell (1985) focusses on the non-additive functional efficiencies that arise with specialization and a division of labor in *Volvocales*. Hoogland (1981) stresses that there is a strong relationship between group-size in prairie dog colonies and both functional improvements in the detection of predators and decreased individual scanning activity -- efficiencies that are in fact synergistic. Fairbanks (1990) found that vervet monkey mothers (*Cercopithecus aethiops sabaues*) in captive groups that had access to allomothering were able to shorten their birth intervals, while females who had more experience in caretaking and carrying as juveniles were more likely to rear their own first born infants successfully. And Fanshawe and Fitzgibbon (1993) documented at least two forms of synergy in relation to group-size in wild dogs (*Lycaon pictus*), namely, the type of prey that could be captured and killed and the ability to defend carcasses against interspecific competitors.

Maynard Smith's use of the synergy concept deserves a special note. First, Maynard Smith (1982) coined the term "synergistic selection" more or less as a synonym for D.S. Wilson's (1975, 1980) concept of "trait group selection" and a similar formulation by Matessi and Jayakar (1976), both of which sought to account for the evolution of altruism without the need for inclusive fitness theory. The general approach involved temporary (functional) interactions among non-relatives in non-reproductive groups. The key feature of the "synergistic selection" model, according to Maynard Smith, was a fitness gain to interacting altruists that was greater than the gain to an altruist and a non-altruist. (At this point, Maynard Smith, like many other theorists, was conflating altruism and co-operation.)

Maynard Smith discussed the concept of "synergistic selection" further in a 1983 paper. Again, he built on Wilson's trait group selection model, identifying non-additive interaction effects (labelled "r" in his equations) as the critical factor. And again, he assumed that the interaction involved altruism. Subsequently, Queller (1985) elaborated on Maynard Smith's ideas in an analysis of inclusive fitness theory, where he proposed that synergistic effects might provide an alternative to altruism as an explanation for the evolution of social behaviors. Queller suggested the use of a coefficient of synergism ("s") to reflect any joint effects produced by co-operators.

In Maynard Smith's 1989 textbook on evolutionary genetics, there is a significant shift of focus. Here he follows Queller's lead and moves the concept out of the classical population genetic framework and into game theory, with its emphasis on finding an ESS (evolutionarily stable strategy). No longer is synergistic selection associated with altruism; the stress is on co-operation as a class of behaviors with a variety of potential payoff distributions. Now synergy (re-labelled "s") is defined as the non-additive payoff increment to co-operating "partners". Maynard Smith concludes that, if the synergistic increment is greater than the cost, the behavior will be an ESS. Although inclusive fitness is not required for such interactions to occur, he suggests that relatedness could be significant as a facilitator, especially in initiating co-operation.

Finally, Maynard Smith and Szathmáry make liberal use of the synergy concept in their new volume on *The Major Transitions in Evolution*, a work that was done independently of my own earlier effort along these lines in *The Synergism Hypothesis* (1983). The evidence they amass, and their accompanying analyses, strongly support the hypothesis that the evolution of co-operation generally and of complex organization in particular, has been driven by bioeconomic synergies. (Maynard Smith, in a personal communication, acknowledges that the "universal" significance of synergy only became apparent to them after their volume was completed.)

SOME IMPLICATIONS

Among the numerous implications, and ramifications, of this theoretical framework, I will briefly mention five. One implication was suggested in the discussion above, namely, that synergy is a pan-disciplinary phenomenon. It can be observed at all levels of living systems, from DNA to ecosystems and, indeed, in human societies as well. Some of the most important examples have been responsible for what could be characterized as key innovations -- functional breakthroughs that have become building blocks for a new type, or "level" of organization. Some of these breakthroughs include the origin of reproductive "templates", the development of metabolic networks, the origin of sexual reproduction, the origin of eukaryotes, the emergence of metazoa, the

The Co-operative Gene

development of social organization and the evolution of human language.

Needless to say, synergy has also been involved in many less sweeping evolutionary innovations as well. For instance, Nee and Harvey (1994) have noted Karl Liem's analyses of how synergistic changes in the jaw musculature of cichlid fishes were probably responsible for opening up an array of new feeding niches into which that group could radiate. Similarly, the "domestication" of fire by evolving hominids has long been considered a major factor in the expansion and radiation of human populations (by allowing access to new sources of food as well as to less hospitable environments).

A second point is that synergistic effects, like all other biological phenomena, are always historically-contingent and context-specific. To illustrate, the so-called VAM (vesicular-arbuscular mycorrhizal) fungi are generally considered to be models of mutualism with many species of plants. Careful studies have shown that VAM fungi do in fact enhance plant growth in low phosphorous soils, but in high phosphorous soils or in low sunlight conditions (when photosynthetic activity is reduced), they may actually become parasitic and reduce plant growth (Bethlenfalvay et al., 1982a,b, 1983; Daft and El-Giahmi 1978). In a similar vein, avian brood parasitism, such as the cowbirds' practice of infiltrating their eggs into other species' nests, is ordinarily harmful to the hosts, who end up nurturing somebody else's nestlings. But cowbird chicks also eat botfly larvae, which can infect a host's nestlings and lower their fitness. So, whenever there are heavy botfly infestations, the parasitic cowbirds may actually enhance their hosts' reproductive success (N.G. Smith 1968).

A corollary of this point is the fact that synergy is a phenomenon that can have both positive and negative consequences from the point of view of different participants. This is obviously the case in zero-sum types of parasitism, where the parasite's gain is at the expense of the host. It is also true in the many cases, some of which were described above, where co-operative behaviors involve trade-offs. Thus, the benefits of joint protection against predation may be offset by an increased susceptibility to parasites, or increased competition for mating privileges, or perhaps even increased conspicuousness to potential predators. Often, the balance between positive and negative synergies may be critical in determining the net benefits, if any, and the ultimate likelihood that co-operation will occur. Also, there are many threshold phenomena, where more of a good thing may become a bad. For instance, Shields and Crook (1987) found that breeding success in Barn Swallows (*Hirundo rustica*) was better among those that did so in small groups than in large groups; larger nests were more heavily infested with parasites. Also relevant is Dunbar's (1992) analysis, described above, of group-size effects in baboon troops.

A third point is that synergistic relationships often involve third-parties -- mediators, catalysts, facilitators, or even antagonists of various kinds. One example is the bark beetle of the genus *Dendroctonus*, which utilizes a symbiotic fungus (genus *Ceratocystus*) to suppress tree tissue resistance to invasion by the beetle, so that it can breed in healthy trees while, at the same time, spreading the fungus to new trees (Price et al., 1986, 1988). Conversely, many mutualistic relationships in nature appear to have evolved as a means of counteracting parasites -- e.g., the 50-odd species of cleaner fish that remove parasites from their larger (often predatory) hosts (Limbaugh 1961; Losey 1987), the numerous bird species that remove parasites from large ruminant animals, or the many social animals that engage in mutual grooming (reviewed in Dunbar 1992).

At the micro-level, there is increasing evidence that plasmids and viruses often play a role in facilitating DNA transfers -- for example, between bacteria and yeast (Heinemann and Sprague 1989) -- as well as being mediators in symbiotic partnerships -- e.g., between *Azolla* and *Anabaena* (Carrapiço 1991) and between mycorrhiza and plant roots (Garbaye and Duponnois 1992). Symbiotic relationships may also be impacted by the effects of inorganic minerals or biochemical substances. For instance, an iron deficiency in the soil may decrease the productivity of *rhizobium*-legume symbioses (Tang et al., 1992). On the other hand, a study by Lynd and Ansman (1994) showed that the productivity of mycorrhizal symbioses between the perennial foliose lichen (*Parmelia incurva*) and the Showy Partridge Pea (*Cassia Chamaecrista fasciculata*) was drastically reduced by the addition of phosphorus and nitrate-nitrogen as soil amendments.

Another implication of this paradigm relates to the controversial issue of group selection (see Wilson and Sober 1994, plus commentaries). Maynard Smith's "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 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.

This conceptualization can be illustrated by returning to the "sculling" and "rowing" games described above.

Peter A. Corning

What if the object of the game were changed? Rather than merely crossing a river, now the two oarsmen share the objective of winning a race against another boat. In this situation, if either oarsman were to defect, their "team" might lose the race; only all-out co-operation might provide rewards for either player. Now the sculling and the rowing games are functionally equivalent in the sense that the performance of each boat depends on both oarsmen; they are both trait groups, or a functional groups. There is "synergistic selection." Below are a few concrete examples:

- 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 linked 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 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. The bottom line was that larger colonies were more effective overall in deterring predators.
- Scheel and Packer (1990), 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.

A final implication of this paradigm has to do with the problems of "cheating", "defection", and "free-riders" -- phenomena that the selfish gene metaphor has helped to illuminate. As Maynard Smith and Szathmáry suggest, 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 set of assumptions can be found 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). In a nutshell, if the potential payoffs (synergies) for each of the participants in a co-operative relationship are high enough, this could provide sufficient incentives for the imposition of "government" in the "common 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). Smith argued for the necessity of government -- "mutual coercion mutually agreed upon" in Garrett Hardin's (1968) phrase -- to constrain the unfettered greed of the market place.

This reasoning is reflected in a new 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-

The Co-operative Gene

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). 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)

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 common interest" might have significant fitness-enhancing value for groups that are in competition with other groups, or other species (viz., the revised "sculling" game mentioned above, in which free-riding may be severely penalized).

An important aspect of the "policing" issue is what could be called the "paradox of dependency." Although co-operative interactions may produce positive 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 associated with these changes.) Margulis (1993) has made a similar argument with respect to the organelles in eukaryotic cells. An obvious implication is that the "incentives" (both proximate and ultimate) for imposing "government" on the parts are likely to increase in relation to the degree of interdependency among the parts.

CONCLUSION

So, why are selfish genes so often co-operative? The answer, it has been suggested here, is that, because of the synergies that may result, co-operation represents an often advantageous survival strategy; it may be a way to compete more effectively. The paradox, however, is that by co-operating in the pursuit of their own interests, co-operative genes may also advance the interests of others. Moreover, invention has become the mother of necessity. Selfish genes have come to be dependent upon one another. And so, a complex organism or "superorganism" also represents a "collective survival enterprise," a functional unit of survival and reproduction in which the corporate interest of the "whole" becomes a filter or screen that differentially affects the survival and reproduction of the parts. Accordingly, this way of viewing the Necker cube might be characterized as "Holistic Darwinism." It might be useful to focus more intently on this aspect of the evolutionary process.

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Peter A. Corning

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The Co-operative Gene

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