

ECONOMICS FROM A BIOLOGICAL VIEWPOINT*

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I. ECONOMICS AND BIOLOGY

The field variously called population biology, sociobiology, or ecology is concerned to explain the observed inter-relations among the various forms of life -- organisms, species, and broader groupings and communities -- and between forms of life and their external environments. The subject includes both material aspects of these inter-relations (the geographical distributions of species in relation to one another, their respective numbers, physical properties like size differences between the sexes) and behavioral aspects (why some species are territorial while other flock, why some are monogamous and others polygamous, why some are aggressive and others shy).

From one point of view, the various social sciences devoted to the study of mankind, taken together, constitute but a subdivision of the all-encompassing field of sociobiology.^{1/} The ultimately biological subject matter of economics in particular has been recognized by some of our leading thinkers.^{2/} There is however a special link between economics and sociobiology.

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^{1/} See Chapter 27 of E. O. Wilson's authoritative text (1975), and also (1977).

^{2/} "But economics has no near kinship with any physical science. It is a branch of biology broadly interpreted." (Marshall /1920/, p. 772). See also Boulding (1950, Ch. 1). Also relevant of course are the famous passages in The Wealth of Nations where Adam Smith attributed the emergence of the division of labor among mankind, and its failure to develop among animal species, to a supposedly innate human "propensity to truck, barter, and exchange" (1937 /1776/, Book 1, Ch. 2).

over and above the mere fact that economics studies a subset of the social behavior of one of the higher mammals. The fundamental organizing concepts of the dominant analytical structures employed in economics and in sociobiology are strikingly parallel.^{3/} What biologists study can be regarded as "Nature's economy" (Ghiselin [1974]). Oswald Spengler perceived (and regarded it as a serious criticism) that Darwin's contribution represented "the application of economics to biology."^{4/} Fundamental concepts like scarcity, competition, equilibrium, and specialization play similar roles in both spheres of inquiry. And terminological pairs such as species/industry, mutation/innovation, evolution/progress, mutualism/exchange have more or less analogous denotations.

Regarded more systematically, the isomorphism between economics and sociobiology involves the intertwining of two levels of analysis. On the first level, acting units or entities choose strategies or develop techniques that promote success in the struggle or competition for advantage in given environments. The economist usually calls this process "optimizing"; the biologist, "adapting." The formalizations involved are equations of constrained maximization. The second, higher level of analysis examines the social or aggregate resultant of the interaction of the striving units or agents. The formalizations here take the form of equations of equilibrium. (In more general versions, the static solutions may be embedded in "dynamic" equations showing the time-paths of approach to solution states.) The solutions on the two levels are of course interdependent. The pursuit of advantage on the part of acting units takes place subject to opportunities and constraints that emerge from the social context, while the resulting social configuration (constituting at least part of the environment for each separate agent) depends in turn upon the strategies employed by the advantage-seeking entities.

^{3/} A somewhat similar argument is made in the very recent paper by Rapport and Turner (1977).

^{4/} Spengler, The Decline of the West, quoted in Himmelfarb (1959), p. 418.

Among the methodological issues that might arise at this point are two with somewhat opposed thrusts: (1) Given the validity of a sociobiological outlook on human behavior, are we not claiming too much for economics? What role is there left for the other social sciences if economics can be regarded as essentially coextensive with the sociobiology of human behavior? (2) But alternatively, are we not claiming too little for economics (and a fortiori for the other social sciences) in adopting the reductive interpretation of human behavior implicit in the sociobiological approach? May it not be the case that the cultural evolution of the human species has carried it into a realm where biological laws are determinative of only a minor fraction of behavioral phenomena? (Or perhaps economics is the discipline that regards mankind as merely sociobiological in nature, while the other social sciences treat of the higher aspects of human culture?)

Consideration of the second group of questions will be reserved for the concluding sections of this paper. With regard to the first -- a seeming claim that the domain of economics is coextensive with the total sphere of all the social sciences together -- a unified social-science viewpoint is adopted here, in which economics and other social studies are regarded as interpenetrating rather than compartmentalized. The traditional core area of compartmentalized economics is characterized by models that: (a) postulate rational self-interested behavior on the part of individuals with given preferences for material goods and services, and (b) attempt to explain those interactions among such individuals that take the form of market exchanges, under a fixed legal system of property and free contract. That only a very limited portion of human behavioral association could be adequately represented under such self-imposed analytical constraints has often been pointed out to economists by other social scientists. In recent years economics

has begun to break through these self-imposed barriers, to take as subject matter all human activity that can be interpreted as goal-directed behavior constrained by, and yet in the aggregate determinative of, resultant social configurations. Significant innovative instances of the application of techniques of economic analysis to broader social issues include Schelling (1960) and Boulding (1962) on conflict and warfare, Downs (1957) and Buchanan and Tullock (1965) on political choice, and Becker on crime (1968) and marriage (1973). And each of these has been followed by a growing literature, in which both economists and other social scientists have participated.^{5/} The upshot is that (at least in their properly scientific aspect) the social sciences generally can be regarded as in the process of coalescing. As economics "imperialistically" employs its tools of analysis over a wider range of social issues, it will become sociology and anthropology and political science. But correspondingly, as these other disciplines grow increasingly rigorous, they will not merely resemble but will be economics. It is in this sense that "economics" is taken here as broadly synonymous with "social science."^{6/}

^{5/} In the earlier "classical" era the compartmentalization of economics within such narrow boundaries had not yet taken place. Adam Smith in particular discussed law, government, psychology, and the biological instincts promoting and hindering social cooperation--as well as economics in the narrow sense -- throughout his works. (See Coase [1976] and Billet [1976].) In a sense, then, economics is in the process of returning to the classical view of the whole man.

^{6/} Marx's "economic interpretation of history" can be regarded as an earlier instance of intellectual imperialism of economics, but its connection with this modern development is limited. Marx's economic interpretation was a materialistic one. He contended that the essentially autonomous progress of the methods and organization of material production was decisive for shaping the entirety of social relationships in every era. True or false, this is a substantive proposition essentially independent of the methodological stance of modern economic imperialists. The latter analyze marriage, fertility, crime, law, revolution, etc., with the tools of economic analysis without necessarily asserting that these patterns of social interaction are determined by "materialistic" considerations (such as the ownership of the means of production) as contended by Marx.

One of the obvious divergences between economics and sociobiology, it might appear, is that men can consciously optimize -- or so we often like to think -- whereas, for all but a few higher animals, the concepts of "choice" or "strategy" are only metaphorical. What happens in the biological realm is that, given a sufficiently long run, natural selection allows survival only of entities that have developed successful strategies in their respective environments. So the result is sometimes (though not always, as we shall see) as if conscious optimization were taking place. The idea that selective pressure of the environment can do the work of conscious optimizing (thus freeing us of any need to postulate a "rational" economic agent) has also received some controversial discussion in the economics literature. This topic will be reviewed in Section III.

After these preliminaries, the central portions of the paper will survey some of the main parallels and divergences in economic and sociobiological reasoning. Since this is written by an economist with only an amateur interest in the biological sciences, attention will be devoted to "what message sociobiology has for economics" rather than to "how we can set the biologists straight."

II. SOME MUTUAL INFLUENCES

The most famous example of the influence of an economist upon biological thought is of course the impact of Malthus upon Darwin and Wallace. The co-discoverers of evolution each reported that Malthus' picture of the unremitting pressure of human population upon subsistence provided the key element leading to the idea of evolution by natural selection in the struggle for life.^{7/} Malthusian ideas of compounded growth also play a role in modern biological theory. The "Malthusian parameter," as defined by biologists, represents the exponential rate at which a population will grow as limited by its genetic capabilities and constrained by the environment.^{8/}

In the very recent period a number of biologists have come to make significant use of tools and approaches of economics. Michael T. Ghiselin has urged fellow-biologists to adopt the "methodological individualism" of economics in preference to the open or disguised "teleologism" of assuming optimizing behavior on the part of higher-level groupings and species.^{9/} A few instances of recent biological optimization studies that seem to be consciously modelled upon economic analytical techniques can be cited: (1) Rapport (1971) showed that the extent of "predator switching" from one prey species to another in response to

^{7/} Oddly enough, this example is not really a valid one, for the borrowing was already from biology to economics in Malthus' own thought! Malthus drew his ideas about human populations from a biological generalization attributed to Benjamin Franklin on the first page of the Essay on the Principles of Population: "It is observed by Dr. Franklin that there is no bound to the prolific nature of plants or animals but what is made by their crowding and interfering with each other's means of subsistence." See Himmelfarb (1959), Ch. 7.

^{8/} The classic definition by R.A. Fisher (1958 [1929], Chapter 2) as applied by him to a population of mixed ages, corresponds to what the economist would call the internal rate of return on investment (the growth rate of invested capital). Fisher, in fact, uses the metaphor of a business loan to explain the concept.

^{9/} Ghiselin (1974). See also the review by Demsetz (1975).

changes in relative abundance could be expressed in terms of shapes of the predator's indifference curves and opportunity frontier; (2) Gadgil and Bossert (1970) interpreted various characteristics of organisms' life-histories -- such as the timing and scale of reproductive effort and the determination of survival probabilities at various ages -- as the resultant of a balance between "profit" (i.e., gain) and "cost" (i.e., foregone gain or opportunity cost) in choosing strategies to maximize the Malthusian parameter of population growth. (3) Trivers (1972) demonstrated that various aspects of parental behavior, in particular the differing extent in various species of male versus female "investment" in care of offspring, could be explained in terms of differences in the selectional return on investment to the male and female parents (i.e., in terms of the comparative propagation of their respective genetic endowments); (4) Cody (1974) examined the conditions determining the relative competitive advantages of "generalist" versus "specialist" strategies in the exploitation of a mixed-resource environment. (5) E. O. Wilson (1975, Ch. 14) employed linear programming models to determine the optimum numbers and proportions of castes in the division of labor among social insects. (6) Charnov (1976) develops an optimality theorem for foraging animals, in which the forager terminates exploitation of a given food patch when the marginal energy intake falls to equality with the average return from the habitat.

But the more significant intellectual influence has been in the other direction, from biology to social science. The success of theories of evolution and natural selection in the biological realm led quickly to the body of thought called "Social Darwinism" -- the most characteristic figures being the philosopher Herbert Spencer in England and the economist William Graham Sumner in America. On the scientific level Social Darwinism represented an attempt to explain patterns of social stratification as the consequence of the selection of superior human

types and forms of organization through social competition. To a considerable extent, its exponents went on to draw the inference that such existing stratification was therefore ethically justified. The political unpalatability of this conclusion has led to an exceptionally bad press for Social Darwinism. (At the hands of other social scientists, jurists, and philosophers -- as economists after Sumner have scarcely discussed the question.) The Social Darwinists, or some of them at least, did confuse descriptive with moral categories so as to attribute excessive beneficence to natural selection on the human level. In the real world, we know, success may sometimes be the reward of socially functional behavior, but also sometimes of valueless or disruptive activities like monopolization, crime, or most of what is carried on under the heading of politics.

It would be incorrect to assume that Darwinism is necessarily conservative in its social implications. The implications would seem to be radical or conservative according as emphasis is placed upon the necessity and importance of mutability and change (evolution) or upon final states of harmonious adaptation as a result of selection ^{ion} (equilibrium).^{10/} Similarly, racist and imperialist theories on the one hand, and pacifist and universalist theories on the other hand, could both be founded on Darwinian ideas.^{11/} The first would emphasize the role of ongoing struggle, and the latter the role of the social instinct and mutual aid, in promoting selection of human types. And even among those for whom the key lesson of Darwinism is the competitive struggle for survival, there are a variety of interpretations. These range from individualistic versions of Spencer and Sumner to a number of collectivist versions: the idea of superior or fitter social classes (Karl Marx), or systems of law and government (Bagehot [1948 (1875)]).

^{10/} On this see Lewontin (1968).

^{11/} See Hofstadter (1955), Ch. 9 and especially Himmelfarb (1959), Ch. 19.

or of course racial groups.^{12/}

In the spectrum of opinion that went under the name of social Darwinism almost every variety of belief was included. In Germany, it was represented chiefly by democrats and socialists; in England by conservatives. It was appealed to by nationalists as an argument for a strong state, and by the proponents of laissez-faire as an argument for a weak state. It was condemned by some as an aristocratic doctrine designed to glorify power and greatness, and by others, like Nietzsche, as a middle-class doctrine appealing to the mediocre and submissive. Some socialists saw in it the scientific validation of their doctrine; others the negation of their moral and spiritual hopes. Militarists found in it the sanction of war and conquest, while pacifists saw the power of physical force transmuted into the power of intellectual and moral persuasion.^{13/}

But the too-total rejection of Social Darwinism has meant a lack of appreciation of its valid core of scientific insights: (1) That individuals, groups, races, and even social arrangements (democracy versus dictatorship, capitalism versus socialism, small states versus large) are in never-ending competition with one another. While the results of this competition have no necessary correlation with moral desert, the competition itself is a fact with explanatory power for social phenomena. (2) That the behavior of mankind is strongly influenced by the biological heritage of the species, and that the forces tending toward either cooperation or conflict among men are in large part identical with phenomena observable in the biological realm.

The sweeping rejection of biological categories for the explanation of human phenomena, on the part of social scientists, is strikingly evidenced by the concluding paragraph of Hofstadter's influential and penetrating study:

Whatever the course of social philosophy in the future, however, a few conclusions are now accepted by most humanists: that such biological ideas as the "survival of the fittest," whatever their

^{12/} The subtitle of the Origin of Species is "The Preservation of Favoured Races in the Struggle for Life," and there is no doubt that Darwin himself applied this conception to the competition among races of mankind (Himmelfarb [1959], p. 431).

^{13/} Himmelfarb (1959), p. 431.

doubtful value in natural science, are utterly useless in attempting to understand society; that the life of man in society, while it is incidentally a biological fact, has characteristics that are not reducible to biology and must be explained in the distinctive terms of a cultural analysis; that the physical well-being of men is a result of their social organization and not vice versa; that social improvement is a product of advances in technology and social organization, not of breeding or selective elimination; that judgements as to the value of competition between men or enterprises or nations must be based upon social and not allegedly biological consequences; and, finally, that there is nothing in nature or a naturalistic philosophy of life to make impossible the acceptance of moral sanctions that can be employed for the common good. ^{14/}

This statement is on solid ground in rejecting attempts to draw moral claims from biological premises. But it promotes confusion in confounding these claims with -- and therefore rejecting out of hand -- the entirely scientific contention that man's biological endowment has significant implications for his social behavior.

Darwinian evolution involves four main factors (Nicholson [1960]): the occurrence of variations, some mechanism of inheritance to preserve variations, the Malthusian tendency to multiplication (leading sooner or later to competition among organisms), and finally environmental selection. From this broad point of view it is clear that there may be cultural evolution even apart from any biological change. Hofstadter seems to regard the forms of human association and the patterns of human social and cultural change as almost entirely free of biological determinants -- apart, presumably, from permanent human characters like degree of intelligence that determine and constrain the possibilities of cultural advance. In contrast, the sociobiological point of view is that cultural and biological change cannot be so totally dichotomized; cultural tracking of environmental change is a group-behavioral form of adaptation, which interacts in a variety of ways with genetic and populational responses. ^{15/} There is cultural evolution

^{14/} Hofstadter (1955), p. 204.

^{15/} See E. O. Wilson (1975), p. 145.

even in the non-human sphere, as animals discover successful behaviors which then spread by learning and imitation. Apart from the direct implications for population composition (those individuals who succeed in learning more efficient behavior survive in greater numbers), there may be genetic consequences in that the behavioral changes may modify the conditions of selection among genetic mutations and recombinations (Mayr [1960], p. 371).

Along this line, the anthropologist Alland (1967, Ch. 9) emphasizes that culture itself should be regarded as a kind of biological adaptation. And there is a long tradition among biologists who have urged attention to the implications of human biological origins for social behavior and institutions. Among the important recent instances are J. Huxley (1939), Fisher (1958 [1929]), Dobzhansky (1962), Lorenz (1966), Tiger and Fox (1971), and of course E.O. Wilson (1975). On the more popular level are such works as Ardrey (1961 and 1970) and Morris (1967). But these ideas have won relatively little acceptance among social scientists.

Turning now to economics, the relevance of quasi-biological (selectional) models has been the topic of controversial discussion since Alchian's paper (1950). Alchian argued that environmental selection ("adoption") could replace the traditional analysis premised upon rational profit-maximizing behavior ("adaptation") as a source of verifiable predictions about visible characteristics of business firms. This discussion, which has interesting parallels within biology proper, will be reviewed next.

III. BIOLOGICAL MODELS OF THE FIRM: OPTIMIZATION VERSUS SELECTION

Alchian (1950) contended that optimization on the part of the business firm (profit maximization, in the traditional formulation) was an unnecessary and even unhelpful idea for purposes of scientific explanation and prediction. While profit is undoubtedly the firm's goal, the substantive content of profit maximization as a guiding rule erodes away when it is realized that any actual choice situation always involves profit as a probability distribution rather than as a deterministic variable (p. 212). And even if firms never attempted to maximize profit but behaved purely randomly, the environment would nevertheless select ("adopt") those hitting upon relatively correct decisions in the sense of meeting the positive realized profit condition of survival (p. 217). Without assuming profit maximization, therefore, the economist can nevertheless predict that relatively correct (viable) adaptations or decisions will tend to be the ones observed -- for example, the employment of low-skilled workers becomes less viable a practice after imposition of a minimum-wage law.

Enke (1951) expanded on Alchian's discussion, with a significant shift in point of view. He suggested that, given sufficient intensity of competition, all policies save the optimum would in time fail the survival test. As firms pursuing successful policies expand and multiply, absorbing a larger fraction of the market, a higher and higher standard of behavior becomes the minimum criterion for competitive survival. In the long run, viability dictates optimality. Consequently, for long-run predictive purposes (under conditions of intense competition) the analyst is entitled to assume that firms behave "as if" optimizing (p. 571).

"As if" optimization is of course what the biologist ordinarily has in mind in postulating that organisms (or, sometimes, genes or populations) "choose" strategies leading to evolutionary success. Two levels of the optimization metaphor in biology may be distinguished: (1) First, there are axes along which

the organism can be regarded as having a degree of actual choice (what size of territory to defend, how much effort to devote to the struggle for a mate, what intensity of parental care to confer upon offspring). Here we speak only of "as if" optimizing because we do not credit the animal with the intelligence necessary for true (non-metaphorical) optimization. (2) Second, there are axes along which the organism cannot exercise choice in any meaningful sense at all (whether or not to be an unpalatable insect, whether or not to be a male or a female). Nevertheless, such is the power of selection that the optimization metaphor often seems workable for "choice" of biological characters even on this second level.

There is, however, a serious problem here not yet adequately treated in either economics or biology. If, as applies in almost all interesting cases, the strategic choice is among probability distributions, what is the "optimum"? According to what criterion does natural selection select when strategies **have** uncertain outcomes?

In evolutionary theory, the "as if" criterion of success (the maximand) is generally postulated to be fitness: the ratio of offspring numbers to parent numbers at corresponding points in the generational life cycle.^{16/} In a deterministic situation, no doubt it is better adaptive strategy to choose higher fitness over lower. (Or, translating from metaphorical to literal language, in the long run the environment will be filled by those types of organisms who have developed and passed on to descendants traits permitting higher multiplication ratios.) But what if the situation is not deterministic, so that some or all of the strategies available generate probability distributions rather than definite deterministic numbers for the fitness ratio? In such circumstances the strategy that is optimal in terms of mean fitness -- that yields the highest mathematical

^{16/}See Fisher (1958 [1929]), p. 37; Wilson and Bossert (1971), pp. 51, 73-76.

expectation of offspring per parent -- might be quite different from the strategy that rates highest in terms of viability (that minimizes the probability of extinction). Where such a conflict arises, some biologists have suggested that viability considerations dominate over mean fitness.^{17/}

No solution to this general problem in evolution theory will be offered here.^{18/} The point to be underlined is that Enke envisaged a situation where the outcome of each alternative policy option for the firm is objectively deterministic, although subjectively uncertain from the point of view of the firm's decision-maker (acting under limited information). Under these conditions there really does exist an objectively optimum course of action leading to maximum profit, which intense competition (even in the absence of knowledge) ultimately enforces -- in Enke's view -- upon all surviving firms. Alchian sometimes seems to have the same idea (p. 212). In saying that maximum realized profits is meaningful while maximizing profit is not, he means that one cannot "maximize" a probability distribution representing subjective uncertainty about profit,

^{17/} See, for example, Williams (1966), p. 106.

^{18/} A number of the complex issues involved may be briefly alluded to. In balancing extinction probability against multiplication ratio, a long-term (multi-generational) point of view must be taken. In any such long-term comparison there will be some prospect of changes in the external environment and even in the genetic constitution of the organism's descendants over time. Even if a high-mean-fitness strategy pays off, the extinction risk being avoided, eventually diminishing-returns constraints (what the biologists call "density-dependent effects") are likely to be encountered -- so that the one-generation high multiplication ratio cannot be indefinitely maintained. On both these grounds the probability distribution for "fitness" measured in terms of a single generation's multiplication ratio may give misleading results. A high extinction probability is more acceptable if descendants will spread into a number of different environments or otherwise diversify so that the extinction risks have a degree of independence of one another. In this case, while many lines of descent may be extinguished, others are likely to survive and multiply. Finally, flexibility is an important consideration; a very advantageous strategy might include a capacity to mutate between high-mean-fitness and low-extinction-probability characters over time.

but there is nevertheless a deterministic or objective "maximum" of profit that could be attained if the knowledge were available. Usually, however, Alchian seems to have in mind the quite different case in which the outcomes are intrinsically or objectively probabilistic, rather than merely subjectively uncertain because of imperfect knowledge. Here there does not exist any unequivocal optimum, and Enke's argument does not apply. For Alchian, it is in such an environment that viability (positive realized profit) becomes the relevant success criterion.

Independent of Alchian's introduction of the viability argument, but parallel in its implications, was Herbert A. Simon's contention (1955, 1959) that firms are better regarded as "satisficing" than as optimizing. Starting from a psychological rather than evolutionary orientation, Simon contended that decision-makers are conservative about modifying established routines yielding satisfactory results -- unless forced to do so by exogenous changes that threaten unacceptable outcomes. The reason given was informational: the decision-maker who recognizes the inadequacy of his knowledge, or the costs of performing the computations necessary for determining optimality even if he had all the relevant data, does not find that it pays even to attempt to optimize.^{19/} Simon did allow for a long-run approach toward optimization under stationary conditions, in the form of a gradual shift of the decision-maker's "aspiration level" toward the best outcome attainable. But, he emphasized, business decisions take place in a context of ever-recurring change; the process of gradual approximation of optimality can never progress very far before being confounded by events. Thus, for Simon as for Alchian, the environment primarily plays a selective role in rewarding choice of viable strategies. Simon, in contrast with Alchian, chooses to emphasize how

^{19/} Of course, behavior might be optimized subject to these informational constraints. While it seems possible to adopt such an interpretation, there may be operational or even logical difficulties in calculating "the optimal amount of departure from optimality" (see Winter [1975], pp. 81-85).

this process has in effect been internalized into the psychology of decision-makers.

A closely related aspect of the optimizing-selection process is the question of "perfection." It is possible in evolutionary models alternatively to emphasize the achieved state of adaptation, or the process of adaptive change toward that state. In the biological realm a high state of perfection on the organismic level has been attained:

"...organisms are, in fact, marvellously and intricately adapted, both in their internal mechanisms, and in their relations to external nature." (Fisher, 1958 [1929] p. 44).

The high degree of perfection is evidenced by the fact that the vast majority of mutations, which follow a random law, are harmful to the organism rather than beneficial. An important and less obvious consequence of the high degree of perfection is that the environment, as it changes under a variety of random influences, is always (from the organism's viewpoint) tending to deteriorate. So even relatively well-adapted organisms, or particularly such organisms, require the ability to track environmental changes. In the economic sphere, in contrast, we do not -- though perhaps we should -- think in terms of a very high degree of perfection in the adaptations of individuals or firms.^{20/} The argument in terms of perfection has been at the heart of much of the critical discussion of the biological model in economics.

Penrose (1952, 1953) criticized Alchian by contending, in effect, that the achieved state of economic adaptation is generally too perfect to be accounted

^{20/} But note that a high degree of such "selfish" adaptation, on the part of private economic agents, need not imply optimality of the Invisible-Hand variety on the social level. Similarly in the biological domain, perfection on the level of the organism does not imply that the entire biota, or even smaller aggregates like single species, have been optimally adapted to the environment. See Tullock (1971), Ghiselin (1974). This point will be discussed further below.

for by merely random behavior on the part of businessmen. Although high states of adaptation are indeed attained in the biological sphere even without rational optimizing, that is due, she argued, to the extreme intensity of competition forced by organisms' innate urge to multiply -- the Malthusian principle. This urge being lacking in the economic sphere, and competition therefore less intense, the businessman's purposive drive to make money is required to supply the analogous driving force (1952, p. 812).

Of course, the desire to make money is not enough. The key point of the Penrose criticism is that this desire must, for the most part, be realized. Businessmen must expect to be successful if they are to enter the competitive arena. And any such expectation would be too regularly refuted to persist if actual outcomes realized were no better than would ensue from random action. So the Penrose image is one of a changing environment (else there would not be much in the way of profit opportunities) very effectively tracked by rationally optimizing businessmen.

The selectional processes of Nature, driven by random variation and Malthusian competition, are profligately wasteful of life and energy.^{21/} An implication of the Penrose thesis is that the wastage cost of economic selection should be considerably less than that of biological selection.^{22/} Quantitative estimates of the selectional wastage cost (bankruptcies, abandonments, etc.) would be of interest, therefore, in providing some measure of the prevalence

^{21/}See Haldane (1957); Feller (1967).

^{22/}Not all biological adaptive mechanisms are random in their working, however. Mutations and genetic combinations are completely random, but patterns of activity (e.g., feeding, mating) often are not. Even lower animals display simple purposive behavior, such as escape maneuvers when threatened. And there is a great deal of adaptive learning on the non-human level.

and success of rational optimization.^{23/}

Where Penrose argued that the observed degree of adaptation in the economy is too perfect to be accounted for by blind environmental selection, Winter's critique (1964, 1971, 1975) is based on the opposite contention -- that the state of adaptation is too imperfect to be accounted for by a process that leads to the same outcomes "as if" firms actually optimized. His argument is therefore directed against Enke's extension of the selectional model, against the idea that in the long run viability requires optimality, rather than against Alchian's original version. The main evidence of imperfection cited by Winter is the prevalence in business practice of conventional rules of thumb (e.g., a pricing policy of fixed percentage markups) even where seemingly in conflict with profit-maximizing behavior (1971, p. 241).

Winter contributed interesting suggestions about the nature of inheritance and variation in economic selectional models. For Alchian, the inherited aspect of the firm was described as "fixed internal conditions" (p. 216) -- in effect, simple inertia due to the fact that the firm is more or less the same from one day to the next. Variation was attributed to imitation of successful firms,^{24/} or simply to trial-and error exploration. For Winter the inherited element, analogous to the biological genotype, is represented by certain more permanent aspects of the firm (its "decision rule"). This is to be distinguished from the specific decision made in a given context, which is analogous to the biological phenotype. What the environment selects is the correct action, even though it be the chance result of a rather inferior decision rule. In natural

^{23/} To some extent, market experiments -- while failing to capture the full richness and variety of economic environments -- do provide insight as to the rapidity of convergence to optimal solutions. V. L. Smith in surveying such experiments (1976), is generally quite impressed by the ability of experimental subjects to approximate optimal (rather than merely viable) behavior. Experiments on economic choices even on the part of animals provide evidence of a considerable degree of "rationality" (Kagel et. al. [1975]).

^{24/} And "innovation" to imperfect imitation that happens to be successful!

selection as well, more and less well-adapted genotypes might be represented at a given moment by the same phenotype. But, over a number of generations, natural selection working together with the Mendelian laws of inheritance will tend to fix the superior genotype in the population.^{25/} The economic mechanism of repeated trials is somewhat different, as no genetic recombination is involved. But surely we can expect that, as a variety of selectional tests are imposed over time, those firms providing a merely lucky action-response to a particular environmental configuration will tend to be selected against as compared with those following a more correct decision rule.^{26/}

In his first article Winter employed the term "organization form" for what his later papers call "decision rule" or "rule of action." While the intended referent is the same, and is indeed better described by the words "decision rule" or "rule of action," the initial term had interesting implications that might well have been pursued. "Organization form" would ordinarily be understood to mean something like corporation or partnership, large firm or small, etc. This is a more visible and operational concept than "decision rule" Since even the best decision rule (in the usual sense of that term) might not make possible survival of a firm with an ill-adapted organization form, we should really think of three levels of selection -- action, decision rule, and organization form.^{27/}

^{25/} Suppose a dominant allele A at a certain gene locus is the superior type, and the recessive allele a is inferior. Then the heterozygote Aa will be represented by the same phenotype (and so be subjected in the current generation to the same selection) as the homozygote AA. But in the next and succeeding generations, the descendants of AA will on the average do better than those of Aa -- ultimately extinguishing the inferior allele.

^{26/} Winter appears to doubt this (1975, p. 97; 1964, pp. 257-58).

^{27/} Stigler (1958) employed, though without placing any emphasis upon biological analogies, a selectional model called the survivor principle to draw inferences about efficient plant and firm sizes in a variety of industries. The same method could evidently be applied to other firm characteristics that could be described as "organizational forms."

The broadly similar views of Alchian and Winter represent, it might be noted, a Lamarckian evolutionary model. Lamarck believed (as did Darwin) that acquired characters can be inherited, and also that variations tend to appear when needed. Failure-stimulated search for new rules of action (Winter), taking in particular the form of imitation of observed success (Alchian), is -- if the results are assumed to be heritable -- certainly in the spirit of Lamarck. The Lamarckian model is inapplicable to inheritance and variation (whether somatic or behavioral) mediated by the genetic mechanism, but it seems to be broadly descriptive of cultural evolution in general, and of economic responses in particular.^{28/}

Perhaps Winter's most important contribution in this area is his actual modelling of possible selectional equilibrium situations. Space does not permit adequate exposition or review of these formulations here, but the following summary may be suggestive:

Those organization forms which have the lowest zero growth price are viable, others are not. Or, to put the matter another way, price will tend to the lowest value at which some firm's organization form still yields non-negative growth. Firms whose organization forms result in decline at that price will approach zero scale as time goes on, leaving the firms which have the minimum zero growth price to share the market. (1964, p. 253).

This language suggests the "long run zero-profit equilibrium" of the competitive industry, reinterpreted in terms of the biologists' population equilibrium condition of zero growth. But Winter is at pains to show that even a firm with the lowest possible zero-growth price (lowest minimum of Average Total Cost curves) might -- as a result of using an inappropriate decision rule -- not actually be a survivor in selectional equilibrium. So the traditional compet-

^{28/} Since behavioral changes, by modifying the conditions of selection, may lead to changes in genetic compositions of populations, to a degree Lamarckism plays a role even in the modern theory of genetic evolution (see Waddington [1961], Ch. 4).

itive equilibrium might not be generated, or, once generated, might not respond in the standard way to changes in exogenous determinants.^{29/} One reason for this divergence from the traditional result, however, is that Winter's model is limited to the single adjustment mechanism of firm growth. Among the factors not considered, entry pressure on the part of new firms and (a more surprising omission in view of the previous emphasis) failure-stimulated search on the part of unsuccessful existing firms would tend to force a progressively higher state of adaptation upon survivors.

In his 1971 article Winter indicates that in order to achieve the optimality properties of the standard competitive model an "innovating remnant" is needed. This category consists of firms that are, for unexplained reasons, inveterate searchers who will ultimately hit upon any as-yet-undiscovered superior decision rules (p. 247). But new entrants, upon whom standard theory relies to discipline firms already in the industry, can also serve this exploratory role. A fruitful approach, consistent with biological observation, would be to recognize that one of the many possible survival strategies adopted by organisms (firms) is a tendency to search -- and at any moment of time there will be a balance between organisms searching for new niches and organisms adapting to existing ones. (This point will come up again when competitive strategies are discussed below.)

It is a rather odd accident that biological models entered into economic thought in connection with the theory of the business firm -- a highly specialized and consciously contrived "cultural" grouping. To some extent, as just seen, evolution theory is applicable to firms: inheritance, variation,

^{29/} In more recent work R. R. Nelson and Winter (1974) have developed simulation models of growth in which firms and industries evolve over time by a selectional process, one not describable as a path of moving equilibrium.

competition, selection, adaptation all play roles in explaining the observed patterns of survivorship and activity. Still, if biological models were being explored afresh for possible relevance to economic behavior, one's first target for consideration would naturally be the individual together with the family -- entities of direct biological significance. Without any preconceived limitation of attention to the business firm, several aspects of economic theorizing will now be examined from a biological orientation: the nature and provenance of preferences; the evolution of patterns of competition, cooperation, and conflict; and resulting tendencies toward equilibrium, cycles, and progressive change.

IV. ELEMENTS OF ECONOMIC THEORIZING: A BIOLOGICAL INTERPRETATION

The contention here is that the social processes studied by economics, or rather by the social sciences collectively, are not mere analogs but are rather instances of sociobiological mechanisms -- in the same sense in which chemical reactions have been shown to be a special class of processes following the laws of physics.^{30/} For this to be in any way a useful idea, it remains to be shown that a more general sociobiological outlook can in fact provide social scientists with a deeper and more satisfactory explanation of already-known results, or better still can generate new ones.^{31/}

IV.A. Utility, Fitness, and the Provenance of Preferences -- Especially, Altruism

Modern neoclassical economics has forsworn any attempt to study the source and content of preferences, i.e., of the goals that motivate men's actions. It has regarded itself as the logic of choice under conditions of "given tastes." But many of the great and small social changes in history have stemmed from shifts in people's goals for living. The very terminology used by the economist -- preferences, wants, tastes -- tends not only to trivialize these fundamental aims and values, but implies that they are arbitrary or inexplicable (de gustibus non est disputandum). Nor have the other social sciences, to whom the economists have unilaterally delegated the task of studying preferences, made much progress in that regard. The healthy aggrandizing tendency of modern economics requires us, therefore, to overstep this boundary like so many others.

^{30/} Compare Alland (1967), pp. 194-97 and E. O. Wilson (1977).

^{31/} And, of course, it is possible that the more general science of sociobiology might benefit from results independently achieved in the special fields of the human sciences.

No doubt there is a large arbitrary element in the determination of wants. Individuals are idiosyncratic, and even socially influenced preferences may reflect chance accidents in the histories of particular societies. But it is equally clear that not all preferences for commodities represent "mere taste." When we learn that Alabamans like cooling drinks more than Alaskans do, it is not hard to decipher the underlying physiological explanation for such differences in "tastes." Unfortunately, the refusal of modern economics to examine the biological functions of preferences^{32/} has meant that the bridge between human physiology and social expressions of desires has been studied by no-one (except, perhaps, by practitioners of empirical "human engineering").

On a very abstract level, the concept of homeostasis has been put forward as the foundation of wants: the individual is postulated as acting to maintain vital internal variables within certain limits necessary for optimum functioning, or at least for survival (Day [1975]). But homeostasis is too limited a goal to describe more than very short-run human adaptations. And in any case, the internal "production function" connecting these internal variables with external social behavior has somehow fallen outside the domain of any established field of research.

Of more critical importance to social science than tastes for ordinary commodities are preferences taking the form of attitudes toward other humans. Anger and envy are evidently anti-social sentiments, while benevolence and group identification promote socialization. Socially relevant attitudes differ from culture to culture: in some societies hierarchical dominance is a prime

^{32/} Recent reformulations of consumer theory by Lancaster (1966) and Becker (1965) treat commodities as packages of more fundamental characteristics which constitute the true desired entities. But without a biological interpretation, this reformulation merely pushes the arbitrariness of tastes one step farther back.

motive for action, in others not; in some, marital partners value fidelity highly, in others promiscuity is regarded as normal; in some cultures people cluster closely together, in others they avoid personal contact. The programmatic contention here is that such preference patterns, despite seemingly arbitrary elements, have survived because they are mainly adaptive to environmental conditions. (No strong emphasis will be placed upon the issue of whether such adaptations are cultural or genetic in origin, in line with the argument above that the ability to evolve cultural traits is itself a kind of genetic adaptation.) This contention will surely not be always found to hold; in the biology of plants and animals as well, it is often unclear whether a particular morphological or behavioral trait is truly adaptive or merely an accidental variation. Nature is unceasingly fertile in producing random modifications. But if a trait has survived, as a working hypothesis the biologist looks for an adaptive function.^{33/}

As a nice example, in a famous passage in The Descent of Man Darwin asserted that for hive-bees the instinct of maternal hatred rather than maternal love serves an adaptive function. He went on to generalize that, for animals in general (and not excluding mankind), "sentiments" or social attitudes are but a mechanism of adaptation (see Ghiselin /1974/, pp. 218-219).^{34/} The anthropologist Ronald Cohen (1972, pp. 46-51) has similarly pointed to variations among cultures in degrees of "affect" (i.e., of interpersonal emotional attachment) as adaptive responses to environmental circumstances.

^{33/} Though whether the function is adaptive to the individual only, or alternatively to some larger social group to which he belongs, may remain subject to controversy.

^{34/} Adam Smith, it might be noted, argued that the desires (or passions, appetites, or sentiments) driving men have been implanted (as by a wise Providence) to promote the survival of the species. See Coase (1976).

The biological approach to preferences, to what economists call the utility function, postulates that all such motives or drives or tastes represent proximate aspects of a single underlying goal -- fitness. Preferences are governed by the all-encompassing drive for reproductive survival. This might seem at first absurd. That all humans do not solely and totally regard themselves as children-making machines seems evidenced by phenomena such as birth control, abortion, and homosexuality. Or, if these be considered aberrations, by the large fractions of income and effort devoted to human aims that compete with child-rearing -- among them entertainment, health care beyond the child-bearing age, personal intellectual advancement, etc. Yet, all these phenomena might still be indirectly instrumental to fitness. Birth control may be a device leading on net balance to more descendants rather than fewer; health care beyond the child-bearing age may more effectively promote the survival and vigor of children or grandchildren. And, as we shall see shortly, even a childlessness strategy may be explicable in fitness terms!

In any attempt to broaden the application of economic reasoning, to make it a general social science, a key issue is the problem of altruism (the "taste" for helping others): its extent, provenance, and determinants. Old-fashioned, narrow economics was often criticized for employing the model of economic man -- a selfish, calculating, and essentially non-social being.^{35/} Of course, it was impossible to postulate such a man in dealing with that essential social grouping, the family. Neoclassical economics avoided the difficulty by abandoning attempts to explain intra-family interactions! Some economists formalized this evasion by taking the household rather than the individual as the fundamental unit of economic activity; in effect, they postulated total altruism within and total selfishness outside the family.

^{35/} A criticism quite inapplicable, as already observed, to Adam Smith's view of man. (See footnote 5.)

Modern economic "imperialists" have been dissatisfied both with the excessively restrictive postulate of individual selfishness and with the exclusion of intrafamily behavior from the realm of economic analysis. The modern view postulates a generalized preference or utility function in which selfishness is only the mid-point of a spectrum ranging from benevolence at one extreme to malevolence at the other.^{36/} But, standing alone, this is really an empty generalization. Where any individual happens to lie on the benevolence-malevolence scale with regard to other individuals still remains a merely arbitrary "taste." And yet we all know that patterns of altruism are not merely arbitrary. That a parent is more benevolent to his own child than to a stranger's is surely capable of explanation.

From the evolutionary point of view, the great analytical problem of altruism is that, in order to survive the selectional process, altruistic behavior must be profitable in fitness terms. It must somehow be the case that being generous (at least sometimes, to some beneficiaries) is selectively more advantageous than being selfish!

A possible semantic confusion arises here. If altruism were defined simply as accepting injury to self in order to help others, without countervailing benefit of any kind, then indeed natural selection would quickly eliminate altruist behavior. When biologists speak of altruism they do not mean to rule out offsetting or redeeming mechanisms making unselfish behavior profitable in some sense; indeed, their analysis requires that such exist.^{37/}

^{36/} See, for example, Becker (1974).

^{37/} Still another semantic difficulty is suggested by a remark like the following: "If an individual's utility function has the well-being of another party as argument, there need be no conflict between (selfishly) maximizing utility and (unselfishly) helping the other." Here maximizing utility is taken as the definition of selfish behavior, a verbal device that only evades the real substantive issue: to explain how it is that aiding others can viably enter an individual's utility function.

The redeeming mechanisms identified by biologists seem to fall into two main categories. In the first, altruistic behavior survives because, despite initial appearances, a fuller analysis shows that the preponderance of benefit or advantage is really conferred on the self. We may, though paradoxically, call such behavior "selfish altruism"; being ultimately selfish, such altruism does not require compensation or reciprocity to be viable. In the second class of redeeming mechanism compensation does take place; Trivers (1971) has termed such behavior "reciprocal altruism." Reciprocal altruism, apart from motivation, approaches what economists would of course call exchange. It will be discussed, in connection with that topic, in Section B following.

The clearest cases of selfish altruism, of behavior only seemingly selfish, stem from the fact that in the biological realm there are two levels of self! On one level is the morphological and physiological constitution of the organism (the phenotype); on the other level the organism's genetic endowment (the genotype). The genetic constitution may contain recessive genes that are not expressed in the phenotype; perhaps even more important, the phenotype is subjected to and modified by environmental influences that leave the genotype unaffected. "Unselfish" action defined as behavior that injures the organism's phenotypical well-being may yet tend to propagate the organism's genotype. Indeed, since all living beings eventually die, ultimately the only way to achieve a payoff in fitness terms is to help certain other organisms -- most notably, of course, one's offspring -- carry one's genetic endowment beyond the death barrier.

The mechanism rewarding this type of altruist behavior is called kin selection (Hamilton /1964/). Maximization of fitness from the point of view of the genotype often dictates a degree of altruism from the point of view of the phenotype -- not only to offspring, but more generally to close relatives. Setting aside a number of qualifications, we might say that any individual

should be willing to give his life to save two of his brothers (since full sibs have at least half their genes in common), or four half-brothers, or eight cousins, etc. Put another way, the "as if" maximand governing choice of evolutionary strategy is not the organisms's own fitness but its inclusive fitness -- the reproductive survival, with appropriate discounting for distance of relationship, of all those organisms sharing its genetic endowment.

Before proceeding to draw out some of the implications of altruism motivated by kin selection, a word of caution. Actual behavior always represents the interaction of two determining factors -- on the one side preferences, on the other side opportunities (constraints). We cannot directly infer altruistic preferences from cooperative behavior; in some environments the limited opportunities available may dictate that even enemies cooperate in the interests of selfish survival. Nor can we directly infer malevolence from hostile behavior; in some environments even brothers may be impelled to fight one another for survival.

Compare parent-to-offspring altruism with sib-to-sib altruism. Parental altruism is behaviorally much the more evident, and yet the degree of kinship (proportion of shared genes) in the two cases is exactly the same! The reason for the difference is that brothers and sisters are ordinarily in much closer competition with one another^{38/} than parents are with children. Why then the famed maternal hatred and sisterly altruism among ants? The explanation is remarkable. Due to the unusual method of sex determination called haplodiploidy (Trivers and Hare [1976]), sisters in ant colonies (the queen and worker castes) are more closely related to one another than they are to their own offspring (or would be, if they had offspring)! The notoriously lazy

^{38/} For many species, the struggle for food or shelter among members of a litter is a matter of life or death.

male drones, on the other hand, have only the ordinary degree of kinship with other colony members.

Yet it must not be assumed that parents and offspring never compete. Each offspring's selfish interest lies in having its parents' full devotion. But the parent aiming at reproductive survival strives for an optimal allocation of care and protection over all his or her offspring -- past, present, and future. One nice implication is described by Trivers (1974). Intergenerational conflict occurs during the period when additional parental care, still desirable from the offspring's point of view, is no longer optimal for the parent (who must consider his opportunity cost in the form of the potential fitness gain in caring for a new batch of offspring). But the intensity of such "weaning conflict" is a function of the offspring's expected degree of relationship with his sibs of the later batch. If an offspring in a promiscuous species foregoes maternal care, his sacrifice will probably operate to the benefit of mere half-sibs; in permanently mating species, to the benefit of full sibs. Hence the prediction, which is in fact confirmed, that offspring will be somewhat less "selfish" (weaning conflict will be less intense) in species following the stable-family pattern.^{39/}

Another point of interest: why are parents generally more altruistic to offspring than offspring to parents -- since the degree of relationship is the same? The reason turns on their disparate opportunities for helping one another. The offspring may initially require care simply in order to survive, while the parents usually have energy available over their own immediate survival needs. As the offspring develop self-sustaining capacity over time, parental devotion diminishes. Still another factor is the asymmetry in time.

^{39/} In human polygamous families, full sibs reputedly display greater mutual altruism than half-sibs. But I am unaware of any hard evidence on this point.

In terms of fitness comparisons, offspring generally have greater "reproductive value,"^{40/} i.e., offspring are more efficient at producing future descendants for parents than parents are in producing future relatives (sibs and their descendants) for offspring. This is of course clearest when parents have entirely completed their reproductive activity. And, as seen above, the sibs are likely anyway to be pretty close competitors. Yet, in appropriate biological environments, offspring sometimes do curtail personal reproduction to help parents rear sibs (E. O. Wilson /1975/, p. 125).

What of altruism within the parental pair? From the biological viewpoint, alas, the parental partner is just a means to the end of selfish reproductive survival. He or she is undoubtedly to be valued, but only as a kind of specialized livestock! Trivers (1972) has explored in detail the mixed cooperative-competitive incentives for parents. Each requires the other to achieve reproductive survival, yet each is motivated to load onto the other a disproportionate share of the burden. The relatively smaller male investment in germ cells (sperm vs. egg) tends to lead to desertion, promiscuity, or to polygyny as ways for males to maximize numbers of descendants. The female, having already made a substantial somatic commitment in each reproductive episode, is less well placed than her mate to refuse additional parental commitment. (Females sometimes have means of cheating through cuckoldry, however.) The actual expression of one or more of these non-altruistic tendencies depends upon the specific opportunities provided by the environmental situations of each species. There are situations in which parental pairs are models of mutual devotion, most notably in difficult environments where the survival of offspring requires full concentrated teamwork on the part of both parents (E. O. Wilson /1975/, p. 330).

^{40/} Fisher (1958 [1929]), pp. 27-30.

Let us now go beyond the kin-selection mechanism favoring altruism directed at close relatives. Wynne-Edwards (1962) propounded the broader view that altruistic behavior may be favorably selected because it promotes the good of the species as a whole even though adverse to individual fitness -- an example being voluntary restriction of offspring numbers in times of food scarcity. Or, more generally, it has been argued that in environments where within-group altruism strongly promotes group success (as will often be the case), altruism tends to evolve through a process of group selection. For example, ant colonies that cooperate more effectively will thrive and multiply, in comparison with colonies whose altruism is not so fully developed.

But biologists recognize a serious difficulty here, equivalent to what economists call a "free-rider problem." To wit, the bearer of a gene dictating altruistic behavior tends to be negatively selected within his group as against fellow group members who are non-altruists. Thus, individual selection opposes group selection; the altruistic groups may thrive, but always tend to become less and less altruistic while doing so. Even if the altruist groups drive all others to extinction, they themselves tend to end up non-altruistic.

One important consideration might make it appear, at first sight, that the argument for selection of kin-directed altruism (that it is really selfish behavior, genotypically speaking) extends with almost equal force to broader within-group altruism -- and indeed, even to cooperation on the level of the species as a whole. There is a strong degree of relationship (in the sense of correlation of genetic endowments) even among "unrelated" members of the same species. At many, or even the great majority of loci, genes are fixed in any given species (Fisher /1958 (1929); p. 137/); everyone has both genes in common at any such locus. So even individuals chosen at random in a species may well share 70% or 80% of their genetic endowments.

This fact would seem to imply a very heavy "selfish" payoff, genotypically speaking, for altruistic behavior toward any conspecifics whatsoever. (And, of course, the correlation will tend to be closer, and so the payoff greater, within localized social groupings having any degree of inbreeding.) The flaw in this argument is that group selection for altruistic behavior is not governed by overall correlations of genetic endowments, but by the presence or absence of the specific gene or genes determining altruist behavior. The "free-rider problem" operates equally effectively to favor non-carriers of the altruist gene, whether or not the individuals concerned otherwise have high or low correlations of genetic endowments. The altruist gene, metamorphically speaking, only "wants" to help its close relatives -- ~~organisms likely to be~~ bearing the same specific gene. Given that the altruist gene is initially rare, it is highly unlikely that both parents carry it. Thus there is only a 50% chance that one's full brother is a fellow-carrier, and essentially no chance that a random conspecific is.

Still, it remains true that, from the point of view of the organism's overall genotype, altruism has a higher value for promoting fitness the higher the genetic correlation with the beneficiary. The mechanism governing the spread of the specific altruist gene might be thought of as the "supply" factor, with the overall genotypical benefit as the "demand" factor, in the process. The idea is that the free-rider problem is more likely to be overcome, the greater the benefit from doing so.^{41/}

Two different types of process for overcoming the free-rider problem seem to have been identified by biologists: genetic drift, and group dispersal-reassortment. Genetic drift refers to variation of gene frequencies due

^{41/} I am indebted to Joel Guttman for this point.

simply to random fluctuations in the process of genetic recombination associated with mating. It may so happen that, despite the free-rider factor acting systematically to reduce within-group frequency of the altruist gene, by sheer random fluctuation the gene may nevertheless become fixed in the group (J. M. Smith /1964/). Once every member of the mating group possesses only altruist genes, there can be no within-group selection against altruists (unless the non-altruist gene is reintroduced by mutation or by entry of outsiders.) Such a development is highly improbable, unless the group is very small. And yet, Nature's experiments over time have been so unimaginably numerous that the improbable does happen from time to time. The improbability is sharply reduced for colonial species that "bud off" mating pairs to found new colonies (Lewontin /1970/ pp. 13-14). Here the altruist gene need only become fixed from time to time in a minimally-sized group -- a mating pair. Such a pair may then found a colony which will be favorably group-selected in competition with other colonies. With successive "buddings off" from such a thriving colony, the altruist genes may spread and eventually preponderate.

The second process, often mixed with the first, involves regular dispersal and reassortment of groups having larger and smaller proportions of altruist genes (D. S. Wilson /1975/). Within each of the two classes of groups, prevalence of the altruist gene is progressively reduced by individual selection. Yet, if the collective advantage of altruist behavior is sufficiently large, it may be that groups with larger altruist representation increase in numbers so much relative to the others that the overall representation of the altruist gene increases in the population at large. If the groups regularly disperse and reassort themselves at some stage in the life cycle, this process can continue. (Failing dispersal and reassortment, on the other hand, individual

selection will ultimately tend to drive out the altruist genes.)

A quite different sort of altruistic behavior, not necessarily involving close kin or even fellow-carriers of the altruist gene, still falls into the selfish category. An instance appears in the development of alarm calls in birds (Trivers /1971/). A caller who alerts the flock to a predator, it is hypothesized, is thereby subjected to a higher risk (by attracting attention to itself). This behavior can be viable in fitness terms, in certain circumstances, provided that it is only comparatively (not absolutely) disadvantageous to the caller. Thus, the altruism is merely incidental to selfish behavior. (The alarm may discourage the predator entirely or at least reduce his efficiency, so that the caller benefits on balance.) Still, under such "incidental altruism" even the comparative disadvantage tends to lead to elimination of the altruistic caller types by natural selection in favor of other group members (free riders). The saving feature here is that flocks are fluid, ever-changing aggregations. The caller gets only a small benefit, but gets it every time; the non-caller occasionally gets a big benefit from a free ride, but otherwise loses by refraining from calling. This tends to lead to an interior solution with a mixed population of callers and non-callers, for, as the callers increase in numbers, the marginal advantage of being a non-caller (receiving more free rides) increases. (See also Charnov and Krebs /1975/.)

Incidental altruism of the alarm-call type is an instance of what economists would term the private provision of a public good. Olson (1971 /1965/, Ch. 1) argues that such provision is more likely to be found in small groups, and particularly so where there are size or taste disparities within the group. (The larger members, or of course the more desirous ones, are the most

motivated to provide the public good; the smaller or the less desirous are more likely to be the free riders.) Buchanan (1968) has a somewhat different analysis, showing that substantial amounts of the public good might be provided even without such disparities. For Buchanan the main factor is the wealth enhancement that each group member derives from the purchase of the public good by others. On the one hand such purchases by others impel him to cut back his own purchases (the free-rider effect), but on the other hand the wealth enhancement stops him from cutting back all the way to zero (income effect).

Summing up, we have seen how altruistic behavior may prove to be viable in selectional terms even in the absence of any reciprocation. Over the course of human and pre-human evolutionary development, drives or instincts promoting such behavior have evolved and ultimately taken the form that the economist so inadequately calls preferences. And what is true for the specific "taste for altruism" holds in considerable degree for preferences in general -- that these are not arbitrary or accidental, but rather the resultants of systematic evolutionary processes. This does not mean that such attitudes are now immutable. On the contrary, the inbuilt drives themselves contain the capability of expressing themselves in diverse ways depending upon environmental circumstances, which will in turn be modified by cultural evolution. The main lesson to be drawn, therefore, is not that preferences are biologically determined in any complete way -- but rather, that they are scientifically analyzable and even in principle predictable in terms of the inheritance of past genetic and cultural adaptations together with the new adjustments called for by current environmental circumstances.

IV.B Exchange and Other Competitive Strategies

Exchange, the sole form of social ^{or} interaction traditionally studied by economists, is a particular competitive strategy in the great game of life -- one involving a mutually beneficial relation among two or more organisms. It fits into the more general category called "mutualism" by biologists, of which there are both interspecific and intraspecific examples. Among the former are the symbiosis of alga and fungus that constitutes a lichen, the pollination-nectar exchange between bees and flowers, the presence of nitrogen-fixing bacteria on the roots of leguminous plants, and the resident protozoa in the gut of the termite that facilitate digestion of cellulose. Particularly interesting are the complementary associations among somewhat higher animals, which can be regarded as involving a degree of consciousness and discretionary choice. Here mutualism approaches the economic concept of exchange.

In the absence of legal enforcement of compensation for acts conferring advantages on others, such patterns of mutual aid in the biological realm ^{42/} may represent instances of altruism on the part of one or more of the participants. A nice example of what Trivers (1971) called reciprocal altruism is the interaction wherein certain fish species feed by grooming other, larger species -- who in return refrain from eating their cleaners. ^{43/}

^{42/} But even in human interactions, exchange very often takes place without legally enforceable contracts. This is true not only for trading among primitive peoples, but for highly sophisticated transactions under the most modern conditions (Macaulay [1963]). And in the sphere of "social exchange" among humans (Homans [1958]) legal enforcement is ordinarily out of the question.

^{43/} Trivers also classes alarm calls in birds under reciprocal altruism. But, as argued above (and in line with his detailed analysis), the benefit to the calling bird in no way depends upon reciprocation in the form of self-sacrificing behavior on the part of other birds. Alarm calls appear to represent incidental altruism, under the more general heading called "selfish altruism" in the previous section.

The key question for the selectional advantage of such reciprocal aid (in economic terms, for the viability of a pattern of exchange or "market") is control of cheating. As Trivers points out, this is a Prisoner's Dilemma -- a special case of the more general public-good situation. However great the advantage jointly to the trading pair of establishing a reciprocal relationship, it pays each member to cheat if he can. The big fish, once having been properly groomed, would seem to be in a position to profit by snapping up his helper. (The little cleaner fish often does his work actually within the mouth of his client.) On the other side of the transaction, mimics have evolved that imitate the characteristic markings of the true cleaners. Upon being permitted to approach the big fish, the mimic takes a quick bite and then escapes!

The problem here is essentially the same as the cheating, sale of "lemons", or "moral hazard" that arises in a number of market contexts.^{44/} While these phenomena threaten market viability, given the mutual advantage of trade the market can tolerate some slippage through cheating provided it is kept within bounds.^{45/} A number of devices have evolved, in both market and biological contexts, to limit the degree of slippage. The market cheater may be punished by law, the mimic cleaner fish by being (with some probability) caught and eaten. Non-cheaters in markets establish personal reputations and brand names, while cleaner fish develop (so it is claimed) a regular clientele of satisfied customers.

Mutually advantageous exchange is facilitated by altruistic motivations; the emotions of affection and sympathy have evolved, Trivers contends, because they provide a better guarantee of reciprocity than any mere calculated advantage

^{44/} See Akerlof (1970), Darby and Karni (1973).

^{45/} Zeckhauser (1972).

of doing so. Put another way, altruism economizes on costs of policing and enforcing agreements (see also Kurz [1975]).

Becker (1976) has contended that sympathetic motivation may be required only on one side of reciprocal-altruism interactions. The other party can be quite selfish in his aims, yet may still find cooperative behavior advantageous. Consider a selfish beneficiary of a parent's benevolence (a "rotten kid"). The key proposition is that the rotten kid may still act benevolently toward the parent, simply in order to maximize the latter's capacity to bestow benefits upon him. And, in these circumstances, the mutual advantage of cooperative behavior may be such that even the "unselfish" parent ends up selfishly better off than he would if he were not altruistic! Consequently, in biological terms, no loss of fitness on either side is involved. This altruistic "contagiousness" -- unselfish motivation on one side breeding cooperative behavior on the other side -- would seem to promote the evolution of mutual aid patterns. Let one party be so motivated, for whatever reason (for example, altruism on the part of the parent could evolve simply from kin selection), and we will tend to observe reciprocity and mutual aid.^{46/}

More generally, Trivers argues that human evolution has developed a balance between the abilities to engage in and to detect and suppress subtle cheating while participating in reciprocal interactions. The sense of justice, what Trivers calls "moralistic aggression", is an emotion that involves third parties as additional enforcers to punish cheaters. Finally, the selectional advantage of these emotions has led to evolution of the ability to simulate or mimic them --

^{46/} There is one important limitation, however. The benevolent party must be in a position to have the last word, the last move in the interaction. If "rotten kid" has the last free choice of action, he may ruthlessly destroy his parent (Shakespeare's Regan and Goneril in relation to King Lear), so that the interaction would not be viable in selectional terms. (See Hirschleifer [1977].)

to hypocrisy. Note once again how these emotional qualities, absent from the make-up of "economic man," turn out to have an important place in the biological economy of human relationships. Economics can, as the economic imperialists allege, deal with the whole human being, and indeed must do so even to explain the phenomena in its traditional domain of market behavior.

The chief biological example of intraspecific exchange is of course mating interaction. Here vying for trading partners, sexual competition, not only has market parallels but is of course an important economic phenomenon in its own right. In some human societies marriage partners are explicitly sold, but more generally the marriage relationship constitutes a form of "social exchange".^{47/} The competition for mates in the biological realm displays many familiar and some unexpected parallels with market phenomena.

Health and vigor in sexual partners are obviously desirable qualities, correlated with the probability of generating and rearing viable offspring. As a means of demonstrating these qualities (i.e., of advertising), sexual displays, combats, and rituals have developed.^{48/} There is a nice analogy here with recent economic theories of "competitive signalling."^{49/} Some characteristics may be acquired by economic agents not because they confer competitive superiority, but only because they demonstrate a pre-existing superiority (in potential for mutually advantageous exchange). Just as success in display or combat, even in cases where biologically useless in itself, may signal sexual vigor -- so educational attainment, even where of itself useless in contributing to productivity, may yet be a signal of useful qualities like intelligence.

^{47/} An economic analysis quantifying some of the determinants of polygynous marriages appears in Grossbard (1976).

^{48/} "Advertising" is also observed in some interspecific exchanges, e.g., showy flowers and fragrances designed to attract the attention of pollinating insects.

^{49/} See Spence (1974), Stiglitz (1975), Riley (1976).

Another desirable quality in a mate is possession of territory, generally by the male.^{50/} This is advertised in birds by the call. Presumably it is not the artistic excellence of the male's call that attracts the female, but the mere announcement effect -- since the quality of the product (of the territory) is evident on inspection.^{51/} But for goods whose quality can be determined only by experience, the main message conveyed by advertising is simply that the product is worth the effort of advertising! (On this see P. Nelson [1970, and more especially 1974].) Sexual displays seem to fall in this category.

Sexual competition also provides parallels with what are sometimes called "excessive" or "destructive" competition for trade. Cheating is once again a factor, as it pays males to mimic vigor by convincing displays even if they do not actually possess it. (The "coyness" of the female is said to have evolved to prevent premature commitment of her limited reproductive capacity to males with only a superficially attractive line.)^{52/} Sexual combats may go beyond mere demonstration and actually harm the vanquished party, or sometimes the victor as well. Biologists have devoted considerable attention to cases like the peacock, where the extreme development of sexual ornaments appears to be dis-functional to the species or even to the individual. The explanation seems to be that positive sexual selection can to a degree overcome a disadvantage in terms of natural selection -- the peacock with a splendid tail does not survive so well or so long, but is more likely to find a mate. Such a development requires

^{50/} While the most obvious illustrations of sexual competition involve male competition for females, females compete for males as well. This is reasonably evident in the human species.

^{51/} It seems, however, that there may be some selection for excellence in the call. The reason appears to be that well-developed calls are correlated with age, which is a good indicator of ability in birds. (Personal communication from M. Cody.)

^{52/} E.O. Wilson (1975), p. 320.

that male ornamentation and female preference evolve in parallel, which when carried to an extreme degree may represent a rather unstable equilibrium.^{53/}

In economic exchange, another mechanism of competition is entry and exit -- variation of numbers to equalize on the margin the net advantages of the various types of activity. This also operates in sexual competition; the sex ratio varies to equalize the advantage of being a male or a female! Other things equal, the equilibrium male/female sex ratio is 1/1. Taking any offspring generation, exactly half its genetic endowment is provided by male parents and half by female parents. Hence, if one sex were scarcer than the other in the parent generation at mating age, its per-capita representation in the offspring generation's genes (genetic fitness) would be greater. If the disproportion persisted, it would pay in fitness terms to have offspring of the scarcer sex, and an adaptive response in this direction would correct the disparity. Even such practices as disproportionate infanticide of females will not affect the equilibrium 1/1 ratio. (This outcome displays the power of individual as opposed to group selection, since a 1/1 ratio is not the most "efficient" from the point of view of species growth. In terms of group selection it would generally be much more desirable to have a larger proportion of females.)

One factor that does distort the equilibrium sex ratio has been described by Trivers and Willard (1973). It is nearly universal among mammals that male parents have a higher variance in number of offspring than female parents. (A single male can father hundreds or even thousands of offspring, but the female's reproductive capacity is much more severely limited.) Also, healthy vigorous parents tend to have healthy vigorous offspring, and physically weak parents weak offspring. Taken together, these two considerations imply that it pays stronger

^{53/} See Fisher (1958 [1929]), p. 152.

parents to have male offspring; strong male children will tend to engender a relatively larger number of descendants. Conversely, it pays weaker parents to have female offspring, to minimize exposure to this variance. Thus an explanation is provided for the otherwise mysterious tendency of the human male/female sex ratio to rise with socioeconomic status^{54/} (since status tends to be correlated with health and vigor). More generally, the normally higher early male mortality is explained. Pre-natal and post-natal mechanisms discriminating against males permit stronger parents (who will suffer relatively less early mortality among their offspring) to end up with relatively more male children and permits weaker parents relatively more female children.

Even interest, Trivers (1971) suggests, ultimately has a biological origin. Reproductive value (the average number of offspring an organism will engender in the future) declines with age in the child-bearing life phase. A loan today involves a cost to the lender in fitness terms; since his reproductive value upon repayment will be less, the repayment would have to be proportionately greater to make up the difference.

So exchange in a variety of forms, and with many familiar implications, exists in the biological realm. But what does seem to be a specifically human invention is the organized market, a form of exchange involving "middlemen" specialized to trading activity. This must have been what Adam Smith really had in mind in his otherwise too-sweeping assertion that "the propensity to truck, barter, and exchange" is specifically associated with the human species.^{55/}

^{54/} Shapiro, Schlesinger, and Nesbitt (1968).

^{55/} "It is common to all men, and to be found in no other race of animals, which seem to know neither this nor any other species of contracts." ([1937 (1776)], Book I, Ch. 2). Simmel, who adopted a broad view of exchange as equivalent to compromise, also regarded the process as a human invention (1955 [1922], p. 115). But compromise surely occurs in non-human interactions.

Sexual competition and cleaning symbioses provide sufficient evidence to the contrary. And associations such as pack membership also undoubtedly involve "social exchange."

But competition for trading partners remains only one very special type of biological competition. The more general concept used by biologists is illustrated in Figure 1.^{56/} Let N_G and N_H signify numbers of two populations G and H. Then if \dot{N}_G , the time-derivative of N_G , is a negative function of N_H , and \dot{N}_H of N_G , the two populations are called competitors. In the diagram we can draw for population G what the economist would call a "reaction curve" showing the population levels for which $\dot{N}_G = 0$, and similarly for population H. Since the populations are competitors, the reaction curves have negative slope. Their intersection will be a state of equilibrium. (Whether the equilibrium is stable or unstable depends upon the relative slopes at the point of intersection -- as will be explored further in the next Section.) If the reaction curves are positively sloped as in Figure 2, the two populations are complementary rather than competitive. (Again, depending upon the relative slopes, the intersection point may be stable or unstable.) Finally, there is a mixed case, typified by predator-prey interactions, where the reaction curve of the predator has \dot{N}_G as an increasing function of the prey population N_H , while \dot{N}_H is a falling function of N_G . (Again the equilibrium at the intersection may or may not be stable.)

Competition in the general sense exists because some resource of relevance for two or more organisms is in scarce supply. The consequent universality of competition (the "struggle for existence") was of course the main message Darwin drew from Malthus. The ecologists speak of an organism's "fundamental niche" as the volume of abstract resource space in which it can exist -- and of the

^{56/} These curves have already been expounded and analyzed in the economic literature by Boulding (1950 and 1962).

"realized niche" as the volume which it actually occupies. Where niches overlap, there is competition. These considerations have one very essential implication: that competition is generally more severe the more similar the organisms. The more similar the organisms, the greater the niche overlap. In particular, intraspecies competition tends to be more intense than interspecies competition.^{57/} For example, territorial birds exclude conspecifics but to greater or lesser extent tolerate birds of other species. And, we have seen, competition tends to be particularly severe within families and especially among litter-mates; the high correlations of genetic endowments and of positions in the generational life cycle, plus physical proximity, make for near-identity of resource requirements (niches).

There are two opposing forces which together constitute what might be called the "Dilemma of Sociality." On the one hand, altruistic preferences or motivations stem mainly from degree of relationship (from correlation of genetic endowments), not only among close kin but extending to more distant relatives. And even, perhaps, to a degree over the entire species. (Other things equal, a man's genes would tell him to favor his fellow man fighting with a bear.) This is the main socializing force. On the other hand, competition, which opposes socialization, tends to be most intense precisely where degree of relationship is closest. (The other man will often be a closer competitor than the bear.) In consequence, as organisms strike some balance between cooperative and competitive strategies, there is an element of instability in the outcome. The degree of conflict or of social cooperation is not a simple function of closeness of relationship, but depends upon the specific details of kinship as related to the environmental situation.

^{57/} Darwin (1958[1859], Ch. 3.) In exceptional cases, however, as when population density is held down by other forces such as predation, intraspecies competition may not be very severe.

Competition-limiting strategies range over a spectrum, from minimal patterns of "holding back" to full cooperation. "Holding back" means that the economic unit or biological organism merely competes somewhat less intensely for resources than short-run selfish interest would dictate. An obvious economic example is cartelization, but more praiseworthy forms of holding back -- e.g., refraining from blowing up your competitor's premises -- also fall into this category. In human societies the institutions of government and law provide reinforcers for what might otherwise be the too-frail force of altruism in limiting the extent of destructive forms of competition. Unfortunately, as evidenced most strikingly by the phenomenon of war, human genetic and cultural evolution have not progressed as far in this direction as might be desired.

Limits on competition have also evolved in the biological realm. In what is called "exploitation competition" organisms scramble to utilize resources but ignore competitors, whereas, in "interference competition," they gain resources precisely by hampering competitors.^{58/} Interference may take the milder form, as in territoriality, of fighting only as necessary to deny a limited zone of resource access to others. But more aggressive versions also exist, of direct attack upon conspecifics -- even of cannibalism, where the competitor himself is converted into a resource. This is relatively rare, however. Presumably, extreme forms of interference strategies have mainly proved dysfunctional to the groups or species evolving them, and have therefore been selected against. (Group selection need not be involved here, as there is a fitness loss to the individual to the extent that his own descendants are inclined to eat one another up.) Biologists have observed that interference competition is more likely to evolve when resource limitations are particularly severe. In economic affairs as well,

^{58/} McNaughton and Wolf (1973), Ch. 11; E.O. Wilson (1975), Ch. 11-12.

"cut-throat competition" is a product of hard times. When organisms are occupying unfilled environments, on the other hand, or firms are interacting in a growing market, competition takes place mainly through the externality of resource depletion (in economic terms, bidding up prices of inputs or driving down prices of products).

Another important means of limiting competition is specialization. It is useful to distinguish the specialization that results from competitive pressure, on the one hand, from the kind of cooperative specialization more properly called the division of labor. Unfortunately, there has been some confusion on this score. The valuable pioneering study on biology and economics by Houthakker (1956) confounds the two categories. The very important analysis by the biologist Ghiselin (1974, pp. 233-240), on the other hand, distinguishes what he calls the competitive division of labor (represented by the subdivision of ecological niches in the biological sphere, corresponding to product or locational differentiation in the economy) from the cooperative division of labor. In the former case (which, preferably, ought to be termed simply competitive specialization) there is no mutual dependence or complementarity among the entities. Each would be better off if the others were to vanish. The latter type of differentiation, the division of labor proper, is associated with true alliance -- to achieve a common end, or at least for mutual benefit where a degree of complementarity exists.

In competitive specialization in the biological realm, each of the contending species is forced away from the zone of resource overlap -- not only in locational terms, but in the form of divergent evolution of characters. This process of character displacement, resulting in an equilibrium separation distance between the species,^{59/} is completely parallel to the economic mechanisms

^{59/} See MaNaughton and Wolf (1973), pp. 312-314.

described in our textbooks under the heading of product-differentiation competition and locational competition ("monopolistic competition"). But on the other hand, the biologists emphasize, such specialization is constrained by the possibility that a generalist of intermediate character might outcompete the set of specialist types (Cody, [1974]). Relative abundance and certainty of resources favor specialists; relative scarcity and unpredictability favor generalists.

Biologists, having developed a more subtle and elaborate approach to this question of specialization/generalization strategies than economists, recognize a variety of different dimensions of "generalist" competition against specialists. Individuals of a species might tend to a ~~common~~ intermediate character, able to make tolerably good use of a range of resources. Or the individuals might be specialized, yet the species show enough inter-individual variety to generalize its command over resources. Still another form of generalization is plasticity, whereby the species is enabled to change its character in response to environmental shifts.^{60/} Such plasticity might be genetically determined if the population maintains a reserve of variety in the form of a largely heterozygotic genetic composition. Or failing this, it may have evolved a high mutation rate as a way of tracking the environment. Finally, even with a fixed genetic constitution the capability for learning and behavioral adaptation may exist to a greater or lesser extent. The human species, of course, has concentrated upon becoming a generalist of this last type.

Turning now to cooperation in the true sense, we arrive at what is properly called the division of labor. Since competition is most intense when organisms are attempting all to do the same thing (to occupy the same niche, to use the same resources), one way out is for individuals or groups to cooperate by doing

^{60/} Compare the discussion of "adaptability" in Stigler (1966), pp. 129ff.

different things. For the group, or rather for each member thereof, command over resources is thereby extended.

The division of labor in Nature penetrates profoundly into the deepest aspects of the differentiation of living matter. In multi-celled organisms the parts unselfishly cooperate to serve the whole, which is of course warranted by the fact that all the cells of an individual organism are genetically identical (save the germ cells, of course). Sexual differentiation also represents an evident instance of the cooperative division of labor in the interests of reproductive survival. Here altruism is less perfect, in that each member of the parental team is altruistic toward the other only to the extent necessary for promoting the reproductive survival of his or her own genetic endowment (Trivers [1972]). Nevertheless, the mechanism works well enough to have won out, for the most part, over asexual reproduction. Going beyond this most elemental social unit -- the male-female pair -- the family involves a related type of role differentiation: that associated with the generational life-cycle. This provides a temporal division of labor; each generation plays its role, in due course, in promoting the reproductive survival of the parent-offspring chain. While altruism between generations is by no means unlimited, as seen above, the differentiation of tasks ties together the interests of the family group.

For larger cooperative associations, necessarily among more remotely related organisms, specialization through the division of labor with its concomitant of social exchange must, to be viable, become compensatingly productive as the force of altruism is diluted. Traditional economics, epitomized by Adam Smith, demonstrated the economic advantage of the division of labor even for a group of entirely selfish individuals. The sociologist Durkheim (1933 [1893], Introduction and Book 1), in contrast, claimed that the division of labor generates a kind of superorganismic "solidarity." He argued that the economic benefits of

the division of labor are picayune compared to this solidarity, a union not only of interests but of sentiments (as in the case of friends or mates). As so often occurs in social analysis, however, Durkheim is failing to distinguish properly between desires (preferences) and opportunities. If there is any superorganismic tie between individuals, it can only be (according to the hypothesis accepted here) their sharing of genetic endowments. Yet in many important instances of the division of labor (e.g., bees and flowers) there is no genetic association at all. The cooperative division of labor in such cases is no more than an alliance for mutual benefit. With genetic sharing it is no doubt easier for cooperation to evolve, but superorganismic ties are not sufficient causes and certainly not necessary consequences of the division of labor.

The human species, of course, has carried the division of labor to extraordinary lengths. The extent to which this represents genetic versus cultural evolution is not a simple matter to resolve. The regulation of cheating, necessary to make exchange and therefore the division of labor possible has, as we have seen, been achieved in Nature to some degree. Even emotional supports for exchange, like the sense of justice ("moralistic aggression") may represent genetically evolved characters. On the other hand, human culture has evolved institutional supports for exchange and the division of labor -- property, law and government.

Analysis on the part of economists of the determinants of the division of labor has gone little beyond Smith's famous proposition (1937 [1776], Book I, Ch. 3): "That the division of labour is limited by the extent of the market." Houthakker (1956), taking the standpoint of the individual, views him as the potential beneficiary of a number of activities some or all of which may however be disharmonious if undertaken together. The choice to be made is for individuals either to act as nonspecialists and incur costs of internal coordination, or

else to separate and distribute the activities via a division of labor that entails costs of external coordination. Here Smith's "extent of the market" is taken as the inverse of inter-individual transaction costs, the absence of which would facilitate specialization with external coordination. Stigler's analysis (1951) is fundamentally similar, though concentrating on firms as decision units rather than individuals. Again there are a number of activities, all desirable or even essential in the production of output, but diverging mainly in offering economies or diseconomies of scale. The firms would do better to divest themselves of at least the increasing-returns activities, if a specialized external supplier were available. As the industry expands, such specialized suppliers become economically viable entities. Thus, for Stigler, "extent of the market" signifies aggregate scale of output.

The discussion by the biologist Ghiselin (1974, pp. 233-247) provides many apt illustrations: for example, that an insect colony must reach a certain size before it pays to have a specialized soldier caste. But Ghiselin is inclined to stress that there are important advantages of nonspecialization, such as the existence of complementarities among certain activities (e.g., teaching and research). In addition, there may be sequential rather than individual specialization, as when members of an ant colony all progress through a common series of different productive roles in the course of the life cycle.

Following up a suggestion by Ghiselin, it might really be better to think in terms of "combination of labor" rather than "division of labor." Division is the first step; it is the combination (external coordination) that produces the result. Apart from the division of labor as a form of complementary combination of individuals undertaking different specialized tasks, there is also the possibility of supplementary combinations whereby individuals reinforce one another in performing the same task. A simple example would be men tugging on a rope to

move a load; such "threshold phenomena" are quite important and widespread. Wherever scale economies for a given activity dictate a minimum efficient size greater than the full output of a single individual, we would expect to see a mixture of complementation and supplementation, of specialization and multiplication of numbers, in the general process of cooperation through the combination of labor.

A number of other dimensions of choice have been explored by biologists. On such is between "K-strategies" and "r-strategies." K symbolizes the carrying capacity of the environment, i.e., the species number N^* at which the time-rate of change $\dot{N} = 0$. The symbol r signifies the maximum rate of Malthusian growth, that obtained under conditions where the environment is not constraining. The r-strategists are opportunist species, who pioneer and settle new unfilled environments. The K-strategists are solidier citizens, who compete by superior effectiveness in utilizing the resources of relatively saturated environments. The former thus make their living from the recurrence of disequilibrium situations (entrepreneurial types, we would say). But their success can only be transient; ultimately they will be displaced by the more efficient K-strategist species. The r-strategists tend to be characterized by high early mortality, as they must continually disperse and take long chances of finding new unsaturated habitats. A high birth rate is therefore a necessity. Among other tendencies are rapid maturity, small body size, early reproduction, and short life. K-strategists, in contrast, tend to develop more slowly, have larger body size, and longer life.^{61/} Their inclination is to produce a smaller number of more carefully optimized offspring.^{62/}

^{61/} See E.O. Wilson (1975), p. 101.

^{62/} Compare the discussion of "high-quality" and "lower-quality" children in Becker (1960) and Nerlove (1974).

Analogs in the world of business exist for a number of these strategies. In the high-fashion industry we observe high birth rates and death rates of firms, in public utilities the reverse. In general, pioneering strategies tend to be more suitable for small firms -- which survive better in highly changeable environments.

But as applied to firms, as emphasized previously, biological reasoning is only a metaphor. In particular, firms do not follow the reproductive laws of biology: small firms do not give birth to other small firms, and firms of one "species" (industry) may transfer to another. By way of contrast, human individuals, families, races, etc. are biological entities which may be regarded as choosing competitive strategies. Martial races may concentrate on success through politics, conflict, or violence ("interference strategy"); others may have proliferated and extended their sway through high birth rates; others through lower birth rates but superior efficiency in utilizing resources ("exploitation strategy"). The r-strategist pioneering human type was presumably selected for in the early period of American history -- a period long enough for genetic evolution, though cultural adaptation may have been more important. This type was not entirely anti-social; altruist "pioneer" virtues such as mutual defense and sharing in adversity can emerge under r-selection. In the present more crowded conditions the preferred forms of altruism represent "urban" virtues of a negative rather than positive sort: tolerance, non-aggressiveness, and reproductive restraint.^{63/} Even today it seems like that a suitable comparison of populations in environments like Alaska on the one hand and New York City on the other

^{63/} See E.O. Wilson (1975), pp. 107-08.

would reveal differential genetic (over and beyond merely cultural) adaptations.^{64/}

IV.C. The Results of Social Interaction -- Equilibrium Versus Change

Equilibrium in biology has one striking feature with no close counterpart in economics: a dualism between processes taking place simultaneously on the level of organisms and on the level of genes.

In dealing with the interactions of organisms the biologist generally uses a partial-equilibrium model, taking genetic compositions as fixed. He then asks such questions as: (1) For a given species G, what will be the limiting population number in a particular environment (the "carrying capacity" of the environment for that species)? (2) Or, with two or more interacting populations, G and H, what will be their respective equilibrium numbers N_G and N_H . And, in particular, will one ~~drive~~ the other to extinction, or might they even both become extinct? (The last possibility may seem surprising. Yet a predator might conceivably be so efficient as ultimately to wipe out its prey, in which case its own extinction may follow.) (3) Where new species may enter an environment by migration, thus offsetting loss of species from extinction, what is the equilibrium number of distinct species, and how do the species partition the total biomass?

^{64/} Many such associations of human genetic types with historical and geographical determinants are elaborated in Huntington (1945). While his work remains highly controversial, and not all of his instances are convincing, that some racial characters are indeed adaptive (e.g., the dark skin of Africans, the body shape of Eskimoes) is evident.

To take up the second of these three questions, it was remarked above that the intersection of the two reaction curves of Figure 1 (two competitive populations) might be a stable or an unstable equilibrium point. It will be evident, by consideration of the nature of the interaction (as illustrated by the arrows showing the directions of change of the two populations from any N_G, N_H point in the positive quadrant), that the intersection equilibrium as shown is stable. Thus, we have here a coexistence solution at point E. If the labels on the reaction curves were reversed, however, it may be verified (by making appropriate changes in the arrows showing the directions of change) that the coexistence equilibrium would be unstable. Depending upon the initial situation, population H would drive G to extinction at point K, or population G would drive H to extinction at point L.

Similar analysis of the complementary populations in Figure 2 will show that the coexistence equilibrium at point E is again stable. But if the labels on the reaction curves were reversed, the populations would jointly (depending upon the starting point) either decay toward zero or explode toward infinity. (Of course, in the latter case another branch of at least one of the reaction curves would eventually be encountered, beyond which the rate of change of population would again become negative.)

The arrows of directional change in the predator-prey diagram of Figure 3 show that a kind of spiral or cobweb exists around the intersection point E. Depending upon the slopes of the curves, the cobweb could: (a) repeat itself indefinitely, (b) converge to the coexistence equilibrium at E, or (c) oscillate explosively. In the latter case the result may be extinction of the predator (if the spiral first hits the prey axis, since the prey can continue to survive without the predator), or the extinction of both (if the spiral first hits the predator axis,

in the case where the predator cannot continue to survive without prey). The theoretical tendency of predator-prey interactions toward cycles in population numbers has in fact been confirmed in empirical observations.^{65/}

These models have rather direct analogies with a number of processes in the realm of the human sciences. The reaction-curve format closely parallels Lewis F. Richardson's models of arms races^{66/} and Lanchester's equations of combat.^{67/} Economists will of course recognize the duopoly solutions associated with Cournot.^{68/}

Biological models of equilibrium on the genetic level are again of a partial-equilibrium nature, since they typically involve only processes within a single population. The simplest version of such models is known as the Hardy-Weinberg Law. If at a particular gene locus two alleles A and a exist, under sexual reproduction there are three possible genotypes: AA, Aa, and aa. With random mating, if selective and other pressures determine the proportions p and q (where $p+q = 1$) for the prevalence of alleles A and a respectively, then the equilibrium proportions for the genotypes will be p^2 for AA, $2pq$ for Aa, and q^2 for aa. This equilibrium is reached extremely rapidly, in fact -- apart from random fluctuations -- in the first filial generation.^{69/}

The proportions p and q will not in general remain stable, however. They are affected by mutation (A may change into a, and vice versa), by gene flow due to

^{65/} See McNaughton and Wolf (1973), Ch. 10.

^{66/} Richardson (1949). See, on this, Rapoport (1960), Ch. 1. Some extensions are provided in Boulding (1962), Ch. 2, 4, 6. Boulding (1950) proposed that these models serve as the core of an "ecological" reorientation of economics.

^{67/} See Lanchester (1916), Morse and Kimbell (1951).

^{68/} See Allen (1938), pp. 200-04.

^{69/} Feller (1950), pp. 94-95.

migration, by random fluctuation ("genetic drift"), and most importantly by natural and sexual selection associated with differing fitnesses of the three genotypes.

Selection operates on the gene proportions through differential survival of the phenotypes. A dominant deleterious (low-fitness) gene will tend to be extinguished relatively rapidly, in terms of generational time. But a recessive deleterious allele expresses itself as a phenotype only in the case of the aa genotype, and so tends to be eliminated only slowly. There may be other complicating features. For example, the allele causing human sickle-cell anemia is a recessive lethal in the homozygote (aa) form, but tends to confer a degree of immunity against malaria in the heterozygote (Aa) form. Where malaria is a serious cause of reduced fitness, the a-type allele will not be eliminated.^{70/}

"Genetic drift" occurs because the actual numbers of the phenotypes AA, Aa, and aa will differ stochastically to a greater or lesser degree from the respective mean values p^2 , $2pq$, and q^2 . The most important consequence is a tendency toward the loss of heterozygosity, i.e., genetic drift tends ultimately to fix a single allele in the population. Genetic drift operates more powerfully upon smaller populations, of course, and elimination obviously is much more likely to occur for an allele that is already rare. Note that even a superior-fitness allele, if sufficiently rare, might well be eliminated by stochastic fluctuations. (It was genetic drift that was called on above to explain the occasional fixing of low-individual-fitness "altruist" genes in some populations.)

Somewhat tenuous analogies exist between genes and ideas, between mutation and invention, etc.^{71/} A human population might increase fitness by "mutations"

^{70/} Wilson and Bossert (1971), pp. 68-70.

^{71/} See Boulding (1950), p. 7.

like a new form of social organization or the invention of a new tool or weapon. And ideas, like genes, are subject to the selectional test of competition. But the laws of the generation and propagation of ideas are so different from those of genes that the comparison does not really seem fruitful.

Some broader parallels might still be of interest, however. Sexual reproduction may be interpreted as a device that (among other things) provides populations with a reserve of variability of characters. Heterozygosity makes a range of different phenotypes available for selection in each generation, thus permitting the tracking of environmental shifts while delaying the loss of potential characters that might turn out to be useful in the future. Asexual organisms lacking this reserve of variability, are more vulnerable to environmental shifts. In effect, sexual reproduction provides species with "memory," though at the cost of some loss of efficiency. In each generation, as was seen above, each of the combinations AA, Aa, and aa will generally be "recalled" and tried again -- so long as $0 < p < 1$. And in actuality, more than two alleles are often "stored" at a given locus, and in addition there may exist other more complex forms of genetic recombination or recall. The widened opportunities provided by sexual reproduction are related to the issue of satisficing versus optimizing discussed at several points previously. In the absence of "memory" of alternative possibilities, a biological entity could not successfully stray very far from any current combination that leads to even minimally satisfactory outcomes -- since it cannot remember anything old, it can scarcely afford to learn something new. The mental development of the human species, culminating in speech and writing, has permitted the vast development of cultural memory independent of genetic storage of variability, thus widening the ability to explore alternatives and approach closer to true optimization.

Another feature that operates to store variety in the economic system is the law of diminishing returns, in its various forms. Rising marginal cost tends to lead to interior or coexistence solutions; entities or forms of organization that are favored by environmental changes tend to increase in prevalence, but not ordinarily so totally as to drive out all others. Thus, a capacity for rapid response to change tends to be preserved.^{72/} The concept corresponding to diminishing returns in biology is called "density dependence," though biologists tend to call upon this mainly to explain why single populations do not increase without limit.^{73/} With respect to competing populations the biologists have a proposition that seems to run counter to diminishing returns in economics -- Gause's Exclusion Principle. The idea is that no two species that fill the same ecological niche can permanently coexist.^{74/} Here, at least, it would seem that the biologists can learn from us. Because of diminishing returns to any form of expansion (density-dependent effects), coexistence equilibria in the same niche should be perfectly possible. Ultimately, the same forces preventing a single organism from monopolizing a niche against conspecifics also tends to control the expansion of the species as a whole as against its competitors.^{75/}

Biologists, as compared with economists, seem to devote relatively more effort to the description of processes of ongoing change as opposed to processes leading to equilibrium in the sense of stationary states. This is historically understandable, in that modern biology was faced at the outset with the great polemical

^{72/} On the other hand, the less stringent inheritance process in economics -- the ability of a "mutation" to spread by mere imitation -- means that storage of alternative productive techniques or forms of organization is not so vital.

^{73/} Wilson and Bossert (1971), pp. 106-08.

^{74/} Ibid., pp. 156-58.

^{75/} While the law of diminishing returns makes coexistence equilibrium possible, corner solutions are not necessarily ruled out.

problem of winning public acceptability for the fact of evolutionary change. In consequence, perhaps, the biologists do not seem to have developed (or at any rate do not pay much attention to) concepts of general equilibrium. They do not seem, to cite one example, to have felt the need for integrating the two partial-equilibrium developments described above -- one on the level of population numbers the second on the level of genetic composition. On the other hand, they have developed models showing the working of a rich variety of mechanisms of change -- mutation and recombination, selection and migration, learning, genetic drift, etc. -- as well as useful generalizations concerning the extent and prevalence of certain patterned responses to change such as mimicry, convergence, character release, speciation, and the like.

Related to the intellectual problem of the relative importance of equilibrium versus change is an issue that has concerned both disciplines -- the question that biologists call teleology. In Panglossian terms, is this 'the best of all possible worlds? Or, if not the best just yet, does our world at least progress toward such a desirable goal?

In biology, the teleological theme seems to underly the concluding sentence of The Origin of Species:

Thus, from the war of nature, from famine and death, the most exalted object which we are capable of conceiving, namely, the production of the higher animals, directly follows. There is grandeur in this view of life, with its several powers having been originally breathed by the Creator into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being evolved.

Darwin's language suggests, though it does not quite say, that evolution is directed by some higher force and that its results represent in some sense progress. Herbert Spencer and others went further to develop an evolutionist ethics -- moral conduct is defined as that which contributes to better adaptation.

and progress toward higher forms. T. H. Huxley, Darwin's great supporter, declared: "The absolute justice of the system of things is as clear to me as any scientific fact."^{76/}

The alternative mechanistic view, that evolution is an entirely undirected process, is almost universally and emphatically postulated by modern biologists.^{77/} Ghiselin (1974) contends further that hidden teleology lurks wherever adaptation is explained in such terms as "the good of the species" or "the good of the community." But this accusation does not seem warranted. The scientific question is simply whether the mechanistic processes of evolution can lead to the emergence of characters benefiting larger groups although harming the individual bearer. That this is at least possible, as in the devotion of parents to offspring, can scarcely be denied. More generally, the genetic-relationship argument for altruism (kin selection) shades gradually in diluted form to groups up to the level of the species, and possibly beyond. Since Nature does select simultaneously on both the organism and the gene level -- and on higher population and community levels as well -- and since groups of genes or groups of individuals may become coadapted in a variety of ways and so coselected, it would seem that some of Nature's productions could validly be interpreted as responding to "the good of the group" rather than solely of the organism (or the gene).

Yet, it is evident, the argument of "perfection" does not hold with any force above the organism level. The many forms of destructive competition in Nature -- from sexual combats within species to predation between species --

^{76/} Quoted in Himmelfarb (1958), p. 403. Huxley was later to totally reverse his position, going on to argue that ethical progress required combating the natural tendency of the cosmic processes (ibid., p. 406).

^{77/} Mechanism is not, any more than its opposite (the postulate of design or purposiveness) a scientifically provable proposition. It is a working hypothesis.

preclude any inference of a universal harmonious adaptation to the non-living environment (see Tullock [1971]). Still, it seems that there may be at least some slow long-run pressure in this direction (see Frech [1973]).^{78/}

A related question is the degree to which cultural evolution, which necessarily concerns group rather than individual traits, is adaptive. Again, one can hardly make any strong arguments for perfection of cultural adaptation. And yet, selection processes are certainly at work tending to destroy societies that have somehow evolved seriously maladapted cultures.^{79/}

The main classical tradition in economics has similarly been subjected to criticism on grounds of teleology. Adam Smith's view, that under laissez faire an "invisible hand" leads to a kind of harmony of private interests,^{80/} has been attacked as apologetics for the capitalist system -- as a tendentious attempt to prove that what exists is indeed the best of all possible worlds. Setting questions of motivation aside, it is indeed true that much of the intellectual effort of modern theorizing has gone into proving social optimality -- in the very special sense of Pareto-optimality -- of idealized versions of the laissez-faire capitalist economy. (Or, in some cases, of the welfare-state or even the socialist economy!) More specifically, what has been shown is that the equilibrium outcome under an unregulated economy with fully defined property rights is a social optimum in the sense that it would not be possible to improve the situation of any individual (in his own eyes) without harming one or several

^{78/} One possible instance is the tendency of disease parasites to evolve in the direction of reduced virulence (E. O. Wilson [1975], p. 116). It is sometimes contended that the beneficial bacteria living within our bodies have evolved from harmful ones.

^{79/} See Alland (1967), p. 171; E. O. Wilson (1975), p. 560; Cohen (1972); Durham (1976).

^{80/} "By pursuing his own interest he frequently promotes that of the society more effectually than when he really intends to promote it." (1937[1776], Book IV, Ch. 2.)

individuals (in their own eyes).

However, these results might equally well be interpreted as anti-apologetics. For, the idealized conditions necessary to make them valid evidently do not fully apply to any actual capitalist (or welfare-state or socialist) economy. And in fact, economists have devoted major energy to examination of forces leading to failures of Pareto-optimality -- natural monopoly, oligopoly, externalities, and public goods being leading examples.

The lack of the institution of property -- founded, in turn, upon the larger institutions of law and government -- in the economy of Nature is an important element explaining the "imperfection" of social adaptations in the biological realm. Some observers have regarded animal territoriality as closely analogous to property, but this is incorrect. Territory in Nature is held only so long as it is continuously and effectively defended by the force of its possessor. Property does sometimes need to be defended by force, but what makes it property is the availability of impersonal enforcement through the law of the community.^{81/} To the extent that the property system is effective, a degree of progressive cultural adaptation tends to take place over time. Individuals need not expend energy in combat or other contests for possession, but are instead motivated to search out mutually advantageous ways of employing property so as to achieve a more complete division of labor. In particular, they are motivated to find ways around the failures of Pareto-optimality mentioned above (Coase [1960]).

Yet, lest this seem too unguardedly hopeful, it must be pointed out that the institutions of law and government are powerful mechanisms that may be employed

^{81/} Fredlund (1976) claims to have found that property in this sense does exist, at least in primitive form, in some animal communities.

achieving many private or group ends quite apart from Pareto-optimality. Law and government may destroy some individuals for the benefit of others, may penalize rather than promote the division of labor, may undermine rather than support the institution of property. Nor can we say on scientific grounds that law and government "ought not" do so. But to the extent that they do not, the progress of adaptation to the environment will be hampered or even reversed.

V. POINTS OF COMPARISON -- A TABULAR VIEW

Tables 1 and 2 have been designed as a way of pulling together, without undue repetition, the strands of the preceding discussions. The first Table is an attempt to systematize, in a comparative way, the entities or units of action as viewed by biologists and by economists. The second Table is intended to display, again in a comparative way, the processes of action and interaction involving these entities.

For the economist the fundamental acting unit or agent is of course the individual. Individuals organize into many types of composite units for purposes of joint action -- these are the "Cooperative Groups" in Table 1. A useful though somewhat rough distinction can be made between "unselfish" groupings, whose dominant feature is the existence of altruistic preference functions connecting the goals of the members, and "selfish" aggregations where cooperative action is motivated only by mutual anticipations of selfish gain.

The family is of course the standard example of a supposedly "unselfish" grouping. As explained at length above, some or all participating family members may actually be motivated to a greater or lesser degree by considerations of personal advantage rather than by other-regarding love and concern. But for the most part, family associations respond to supra-individual goals (kin selection). A variety of other communal associations ("brotherhoods") -- social, religious, and the like -- also exist, at least purportedly, to unite the members thereof in unselfish fellowship.

Economics, in contrast with other social sciences, has concentrated attention upon the "selfish" associations in the next line of the Table. These include alliances of all sorts: the firm in the realm of economics, the gang for criminal activity, political parties and other associations for achieving or exercising power. "Exchange associations" are links in the division of labor.

Just as the "unselfish" associations are in fact not completely so, similarly the "selfish" combinations typically have and may indeed require a certain social cement in the form of feelings of fraternity and community (altruism). This cement is perhaps least binding in the case of exchange associations, but even there at least a simulation of uncalculated fellowship between the parties may be essential for good business. While the state or polity falls into the "selfish" grouping, its survival in the face of military competition probably requires a high degree of unselfish patriotic sentiment.

The next major heading represents "Competitive Clusters." The term, for lack of a better, is intended to represent aggregations of units that are mainly striving against rather than cooperating with one another. Here there may be no sense of actual association on the part of the participants, the cluster being rather merely a discrete classification as viewed by an observer. Such an aggregate of closely competing firms we call an industry, of competing workers a craft or profession, etc. We lack accepted single words for clusters of competing gangs, of competing parties and political associations, of competing nations, etc. (Sometimes we refer to them as the players in the political game, the diplomatic game, and so forth.) The members of cooperating groups may do different things, so as to complement one another; or they do the same thing, where scale economies make supplementation a more advantageous cooperation technique than complementation. But members of competitive clusters are trying to do the same thing in a rivalrous sense, in a context where the success of one entity to some extent precludes that of others.

Here again, the distinction is not always so sharp. Contending groups or individuals generally have some mutual interest in limiting at least the degree of competition. They are better able to find this opportunity for mutual gain if an element of "brotherhood" is thought to exist among the competitors. Trade

Table 1

ACTING ENTITIES, UNITS, AND GROUPS

	ECONOMIC SYSTEM	BIOLOGICAL SYSTEM A	BIOLOGICAL SYSTEM B
AGENTS	Individuals	Organisms	Genes
COOPERATIVE GROUPS			
"Unselfish"	Families, "brotherhoods"	Reproductive associations	(NONE)
"Selfish"	Firms, parties and other political associations, gangs, exchange associa- tions	Packs, mutualists	Organisms, chromosomes and other gene linkages
COMPETITIVE CLUSTERS	Industries, crafts and professions, other contending sets (of gangs, parties, nations, etc.)	Sexes, species, set of niche competitors	Set of alleles, of genotypes.
UNIVERSAL GROUP	Society	Biota	Gene pool

unions (often actually called "brotherhoods") call on class sentiment to limit the competition among workers.

Finally, at the bottom line we have the "Universal Group" -- society itself. Society as an entirety is a complex structure of cooperating and competing elements.

In the biological realm, as was indicated earlier, there are two interwoven systems of thinking -- here simply denoted A and B. In A the organism is the fundamental unit, in B it is the gene. In system A the egg serves to reproduce the chicken, in system B the chicken is the means of reproducing the egg (i.e., the gene). Genes are chemical units that have somehow evolved ways of reproducing themselves. (Not that they "want" to do so, of course, but rather that once self-reproduction somehow came about it tended to be selected by Nature for survival.) In system A there are "unselfish" (kin-selected) cooperative groupings like the family, here more abstractly called reproductive associations. But in system B there are no "unselfish" genes!

Now consider the "selfish" cooperative groupings of individual organisms in system A -- packs or other alliances (within or between species) whose members gain by mutual association in feeding or defense or reproduction. The leading analog in system B is the organism itself. That is, the individual organism represents a kind of alliance of the various genes making up its genetic endowment! As a rather less important point, study of the details of the process of genetic reproduction reveals that the genes are themselves not isolated but are organized into chromosomes and other linkages whose prospects for reproduction are connected in various ways.

The most obvious instance of the "Competitive Cluster" category in system A is the species itself -- regarded as the aggregate of its competing individual members. While competition is severest within a species, interspecific

competition also occurs where the potential niches of different species overlap. Each sex also represents a competitive cluster (i.e., all males compete against one another, as do all females) within a sexually reproducing species. In system B the set of competing alleles at a given locus, and the set of alternative genotypes, are instances of competitive clusters. Finally, the "Universal Group" is the entire biota in system A. In System B the gene pool represents the universe in which various forms of cooperation and competition may take place.

In Table 2 the chief point of interpretation to be emphasized is that the biological processes and mechanisms represent more general classes into which the economic ones fall as particular instances. Where standard economics takes the satisfaction of preferences as the primitive objective or "utility function" of the acting individuals, biological theory suggests that what seems like mere preference or taste evolves out of the objective dictates of reproductive survival. As to the principle of action or behavior, the process of calculated optimization postulated in standard economics can be regarded as a special instance of the uncalculated "as if" optimization dictated by the selective forces of Nature. The thrust of the "satisficing" controversy in descriptive economics is that, even in the economic sphere, explicit optimization cannot always serve as the principle of action.

The opportunities available for organisms in the biological realm can be categorized in ways that seem familiar to the economist. Exploitation of resources is akin to production; mutualism corresponds to exchange; predation and war have obvious analogs in human society. Biology's emphasis on reproduction corresponds to the range of choices involved in family formation in the social context.

In terms of selective processes at work, the biological environment chooses for superior fitness, the analog being superior economic efficiency in the

processes studied by standard economics. However, since economic efficiency is not propagated by mechanisms closely analogous to inheritance in biology, the processes of competition in the two areas are not closely comparable.

Economics distinguishes three levels of equilibrium: (1) short-run exchange equilibrium (market-clearing); (2) long-run entry/exit equilibrium, in which there is no longer any net advantage from redirection of resources (zero-profit condition); and (3) a hypothetical very long-run stationary state where there is no longer any advantage to the formation of new resources (by accumulation). There seems to be no close analog in biology to the short-run concept. The equivalent of the long-run equilibrium condition of economics can be taken to be the biological situation where each type of population (on the organism level) or each type of allele (on the genetic level) has a reproductive ratio ("fitness") equal to unity. And one can also imagine a hypothetical very-long-run equilibrium condition, in which the environment is so totally saturated as to leave no niche for the formation of new life entities.

"Progress" takes place in the economy in two main ways: accumulation of resources by saving, and technological advance. In biology the analogous process is of course evolution, the improvement of adaptation to environment by a variety of processes.

Finally, we have the question of social optimality. In biology, the standard mechanistic view seems to leave no room for such a concept. In economics we have the one rather debatable, and in any case highly limited, criterion of Pareto-optimality. While Pareto-optimality is usually regarded as a normative concept, it does have positive content in one respect -- that there is at least a weak tendency in the competitive economy to move toward Pareto-optimal outcomes. Despite the "teleological" ring of the argument, it is conceivable that a similar

Table 2
PROCESSES AND RELATIONSHIPS

	ECONOMIC SYSTEM	BIOLOGICAL SYSTEM
OBJECTIVE FUNCTION	Subjective preferences ("tastes")	Reproductive survival ("fitness")
PRINCIPLE OF ACTION	Optimization [alternatively, "satisficing"]	"As if" optimization
OPPORTUNITIES	Production Exchange via market Crime, war Family formation	Exploitation of resources Mutualism Predation, war Reproduction
PRINCIPLE OF COMPETITIVE SELECTION	Economic efficiency	Superior "fitness"
PRINCIPLES OF EQUILIBRIUM		
a) Short-run	Markets cleared	?
b) Long-run	Zero-profit	Reproductive ratio = 1
c) Very long-run	Stationary state	Saturated environment
"PROGRESS"	Accumulation, technological advance	Evolution: improved adaptation via mutation, recombination, migration, drift, and behavioral adjustment
SOCIAL OPTIMALITY CONCEPTS	Pareto-optimality	None (?)

tendency, toward solving the Prisoners' Dilemma by arriving at cooperative rather than conflictual outcomes, may be operating, however weakly, in the biological realm.

VI. ECONOMY, BIOLOGY, AND SOCIETY

I have tried here to trace some of the implications of Alfred Marshall's view that economics is a branch of biology. Or, in more sweeping terms, of the contention that the social sciences generally can fruitfully be regarded as the sociobiology of the human species.^{82/} Yet at the same time, it was suggested, we might well claim that certain laws of the economizing process -- optimization on the individual level, and equilibrium on the societal level -- apply to biology as well.^{83/} Viewed this way, economics can be regarded as the general field, whose two great subdivisions consist of the natural economy studied by the biologists and the political economy studied by economists proper.^{84/} Considerable light has been shed, I believe, upon many of the questions and results of the social sciences. These involve broad issues like the provenance of tastes (including, what is particularly essential for social processes, individuals' "taste" for altruism), the balance between optimization and selection in governing social outcomes, the forces favoring cooperation versus conflict as competitive strategies in social interaction, and the determinants of specialization in human productive activities. And some specific phenomena as well: the correlation of the male/female sex ratio with socioeconomic status, the recent tendency to have smaller numbers of "higher-quality" children, the predominance of small firms in transient economic environments, positive interest or time-preference, and minimum separation distances in locational or product-differentiation situations.

It was not very debatable, perhaps, that the sociobiological approach does have some utility for social science purposes. But how much? The central question is whether or not the human species has entered a new domain of experience.

^{82/} Compare E.O. Wilson (1975, Ch. 27 and 1977).

^{83/} See Cody (1974) and Rapoport and Turner (1977).

^{84/} This is consistent with the approach of Ghiselin (1974).

where general biological laws will have only negligible relevance or have even been abolished by the unique developmental advances achieved by mankind. Among such might be included: (1) the transcending importance of cultural as opposed to genetic change; (2) the degree of intelligence and awareness, suggesting that man can henceforth regulate and control the evolutionary process by deliberate cultural and even genetic modifications of the human material itself -- quite apart from operations on the environment; (3) the invention of weapons of intraspecies competition that threaten the survival of all mankind; and (4) what might hopefully be a countervailing factor, man's possession of moral, spiritual, and ethical values.

At this point it is possible only to pose the question, not to answer it. In terms of the proximate goal of research strategy, perhaps it is sufficient to say that the sociobiological approach holds out great hope for breaking down not only the "vertical" discontinuity between the sciences of human behavior and more fundamental studies of life but also the "horizontal" barriers among the various social studies themselves.

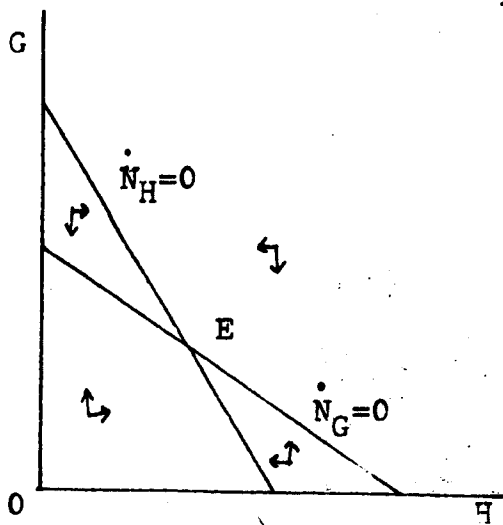


Figure 1

Two Competitive Populations
Stable Coexistence Equilibrium

Figure 2

Two Complementary Populations
Stable Coexistence
Equilibrium

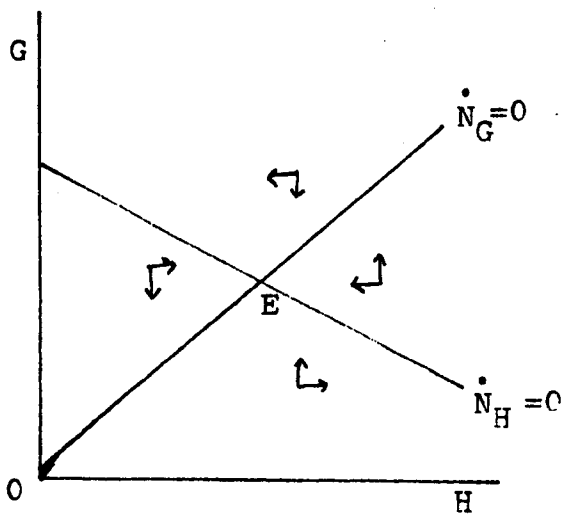
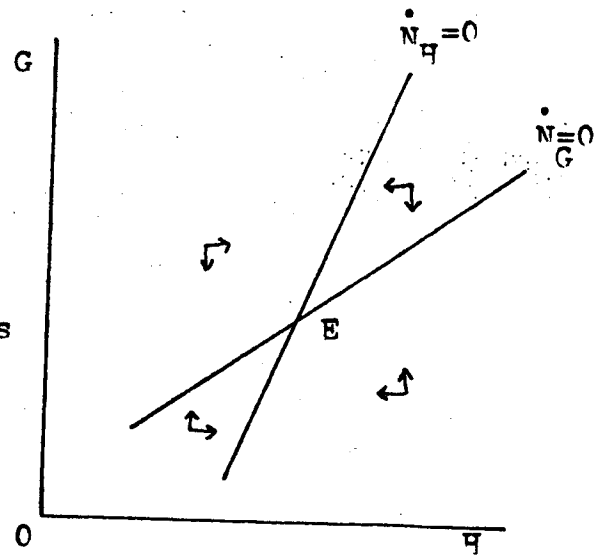


Figure 3

Predator-Prey Interaction

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