

ECONOMICS AND SOCIOBIOLOGY

by

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**UCLA
Economics Department
Working Paper #80
September, 1976**

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Contents

	<u>Page</u>
I. SOME MUTUAL INFLUENCES	6
II. BIOLOGICAL MODELS OF THE FIRM: OPTIMIZATION VERSUS SELECTION	11
III. ELEMENTS OF ECONOMIC THEORIZING: A BIOLOGICAL INTERPRETATION	21
A. Utility, Fitness, and the Provenance of Preferences	21
B. Competition and Competitive Strategies	30
C. The Results of Social Interaction -- Equilibrium versus Change	45
IV. POINTS OF COMPARISON -- A TABULAR VIEW	56
V. ECONOMY, BIOLOGY, AND SOCIETY	64

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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 (the geographical distribution of species in relation to one another, their respective numbers, physical properties like size differences between the sexes) and behavioral aspects of these inter-relations (e.g., 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 together constitute but a subdivision of sociobiology. The ultimately biological subject matter of economics in particular has been recognized by some of our leading thinkers.^{1/} There is however a special link between economics and sociobiology, 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. What biologists study can be regarded as "Nature's economy" (Ghiselin, 1974). (Oswald Spengler considered it a serious criticism that

^{*/} Thanks for comments and suggestions are due to Armen Alchian, Gary Becker, Eric L. Charnov, Harold Demsetz, Michael Ghiselin, Bruce Herrick, David Levine, and Robert Trivers, all of whom are nevertheless guiltless of the final product.

^{1/} "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

Darwin's contribution represented "the application of economics to biology.")^{2/} 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, mutualism/exchange have strikingly 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 competing for advantage in given environments. The economist usually calls this process "optimizing";^{3/} 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.

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

^{2/} Spengler, The Decline of the West, quoted in Himmelfarb (1959), p. 418.

^{3/} As we shall see, however, there is debate over the meaning or relevance of "optimization" under conditions of limited information.

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 portion of this paper. With regard to the first -- are we really claiming as the domain of economics the total sphere of all the social sciences?-- that will indeed be the working hypothesis! (Subject, however, to the proviso that we are working throughout within the sociobiological view of human activity.) Of course the assertion that economics is, at least in one aspect, coextensive with whatever is scientific in the social sciences means adopting a rather broad interpretation of economic behavior. Attention here will not be limited to the production-consumption-exchange relationships of economics as the subject might be narrowly defined. Rather, the view of modern "economic imperialists" will be adopted, which takes as subject matter all human activity that can be interpreted as optimization (or, more generally, as goal-directed behavior) constrained by, and yet in the aggregate determinative of, resultant social configurations. Significant instances of such "imperialist" forays by economists include Schelling (1960) and Boulding (1962) on conflict and warfare, Buchanan and Tullock (1965) on political choice, and Becker on crime (1968) and marriage (1973). (Many other

examples will be cited below.)^{4/5/}

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 (at least, sometimes) 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 economic literature. This topic will be reviewed in Section II.

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

^{4/} 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 minimal. 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 phenomena are determined by "materialistic" considerations (such as the ownership of the means of production) as contended by Marx.

^{5/} An alternative view, adopted in Wilson's authoritative text, is that sociology is the human-species subdivision of sociobiology (1975, Ch. 27). This interpretation is entirely valid if sociology is defined in terms of its broad subject matter -- the study of all human association. But if sociology is defined as a body of scientific methods and results, the interpretation is much less satisfactory. For lack of any central organizing conceptualization, the achievements of scientific sociology remain largely on the natural-history level. In a sense, what is being contended here is that sociology and economics are in process of coalescing as the scientific methods of economics are applied to all the subject matter of sociology.

biological sciences, attention will be devoted to "what message sociobiology has for economics" rather than to "how we can set the biologists straight." The concluding Section will briefly review the success of the enterprise.

I. 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.^{6/} Malthusian ideas of compounded growth also play a role in modern biological theory. R. A. Fisher in his classical work (1958 [1929]) defines the "Malthusian parameter of population increase" for a population of mixed ages in terms essentially equivalent to what an economist would call the internal rate of return on investment.^{7/}

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.^{8/} A few instances of 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 changes in relative abundance could be expressed in terms of shapes of the predator's indifference

^{6/} 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.

^{7/} Fisher uses the metaphor of a business loan in explaining the concept (p. 27).

^{8/} Ghiselin (1974). See also the review by Demsetz (1975).

curves and opportunity frontier; (2) Trivers (1972) demonstrated that various aspects of male and female behavior, in particular the differing extent in various species of male versus female "investment" in care of offspring, could be explained in terms of the selectional return on investment to the male and female parents (i.e., in terms of the comparative propagation of their respective genetic endowments); (3) Cody (1974) examined the conditions determining the relative competitive advantages of "generalist" versus "specialist" strategies in the exploitation of a mixed-resource environment. (4) 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.^{9/} (5) 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 conspicuous 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 existing patterns of social stratification as the consequence of the selection of superior human types through economic competition. To a considerable extent, its exponents went on to draw the inference that such stratification was

^{9/} Considering the enormous emphasis placed on it by Adam Smith, economists have done astonishingly little since to advance our understanding of the division of labor. (One exception is Stigler [1951]). Ghiselin (1974, Ch. 8), on the other hand, closely analyzes Smith's ideas in terms of their applicability to insect and other animal societies. I will give this topic some emphasis below.

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 and certainly attributed excessive beneficence to the working of the Invisible Hand. 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 more of what is carried on under the heading of politics.

It must not be assumed that Darwinism is necessarily conservative in its social implications, however.^{10/} 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 (equilibrium).^{11/} 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. 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.^{12/}

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

^{10/} Karl Marx sought to dedicate Das Kapital to the author of The Origin of Species (Himmelfarb, 1959, p. 421).

^{11/} On this see Lewontin (1968).

^{12/} See Hofstadter (1955), Ch. 9 and Himmelfarb (1959), Ch. 19.

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 groups or 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 in 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 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."^{13/}

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.

As against this view, the anthropologist Alland has contended that culture itself must be regarded as a kind of biological adaptation, though subject to somewhat different selectional processes than biological characters in the narrow sense (1967, Ch. 9). But this remains a minority view among social scientists.

^{13/} Hofstadter (1955), p. 204.

Biologists, in contrast, have generally urged attention to the implications of biological origins for social behavior and institutions. Among the important recent instances are J. Huxley (1939), Fisher (1958 [1929]), Dobzhansky (1962), Lorenz (1966), and of course Wilson (1975). Of late date there has been something of an intellectual fad in this direction, evidenced by such works as Ardrey (1961 and 1970), Tiger and Fox (1971), and Morris (1967). But their ideas have won little acceptance among social scientists.

A few instances of biological (selectional) models in positive social analysis may be mentioned. (1) To start with a thinker sometimes classed with the Social Darwinists, Bagehot's Physics and Politics (1948 [1875]) traced law, the origin of the state, and the prevalence of different forms of politics to the process of selection by competition -- in particular, competition through military force.^{14/} (Bagehot's analysis, it may be remarked, was entirely scientific; there was no confusion whatsoever of the "what is" with the "what ought to be.") (2) Leaping a considerable time span, and turning from politics to economics (in the narrower sense), Stigler (1958) employed -- though without emphasis upon any biological analogy -- a selectional model called "the survivor principle" to draw inferences about efficient firm and plant sizes in a variety of industries. (3) Boulding (1962, Ch. 6) provides an abstract analysis, applicable to various branches of social theory, showing how alternative forms of group interaction (such as competition, cooperation, predation, etc.) may lead either to extinction or to coexistent configurations of populations. (4) The most fully developed application, one that has received a good deal of controversial discussion, started with the argument by Alchian (1950) that selection by environment ("adoption") could replace the traditional analysis premised upon profit-maximizing behavior ("adaptation") as a source of verifiable predictions about the behavior and interaction of firms. This discussion, which has significant implications for biology as well as for economics, will be reviewed in the next Section.

^{14/} A more recent work in a similar vein is Carneiro (1970).

II. BIOLOGICAL MODELS OF THE FIRM: OPTIMIZATION VERSUS SELECTION

Alchian contended (1950) 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 ~~the~~ 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 hard to struggle for a mate, what intensity of parental care to devote to 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 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 -- among strategies with 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.^{15/} 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 organisms who have developed traits permitting higher multiplication ratios in competition with organisms having lower 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

^{15/} See Fisher (1958 [1929]), p. 37; Cody (1974); Wilson and Bossert (1971), pp. 51, 73-76.

the highest mathematical expectation of offspring per parent -- might be quite different from the strategy that rates highest in terms of viability (probability of non-extinction).^{16/} 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. The point to be underlined is that Enke's analysis 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 exists an unequivocally optimum course of action leading to maximum profit, which intense competition (even in the absence of knowledge) ultimately enforces 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, but there is nevertheless a deterministic or objective "maximum" of profit attainable. 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. For Alchian, in such an environment it is viability (positive realized profit) that becomes the relevant success criterion.

^{16/} Suppose an organism has a "choice" of strategies A or B. Strategy A involves a 90% chance of extinction (fitness ratio $m=0$) and a 10% chance of 100-fold multiplication ($m=100$). The mean fitness, $E(m_A)$, is therefore 10. Strategy B entails only a 10% chance of extinction ($m=0$), with a 90% chance of 10-fold multiplication ($m=10$) -- so $E(m_B) = 9$. In terms of expectations A looks better, yet B is far superior in terms of viability.

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

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 to lead to 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.^{18/} 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 almost always 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 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 has been attained:

^{18/} 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).

"...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).

This explains why the vast majority of mutations, which follow a random law, are harmful rather than beneficial. (Another interesting consequence emphasized by Fisher of the high degree of achieved perfection is that the environment is always, from the viewpoint of most organisms, tending to deteriorate.) 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.^{19/} 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 too perfect to be accounted for by merely random behavior on the part of businessmen. Although high states of adaptation are attained in the biological sphere 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

^{19/} 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 adopted to the environment (Ghiselin, 1974).

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 random selectional processes of Nature, driven by Malthusian competition, are profligately wasteful of life and energy.^{20/} An implication of the Penrose thesis is that the wastage cost of economic selection should be considerably less than that of biological selection.^{21/} Quantitative estimates of the selectional wastage cost (bankruptcies, abandonments, etc.) would be of interest, therefore, in providing some measure of the prevalence and success of rational optimization.

In complete contrast with Penrose, Winter's critique (1964, 1971, 1975) is based on the 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 "long run" implication of the biological model, rather than against Alchian's original version that emphasized viability rather than profit-maximization.) The main evidence cited by Winter is the prevalence in business practice of conventional rules of thumb (such as fixed percentage markups) even where seemingly in direct 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

^{20/} See Haldane (1957); Feller (1967).

^{21/} 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 adaptive learning to some extent on the non-human level.

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,^{22/} 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 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.^{23/} 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.^{24/}

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

^{22/} And "innovation" to imperfect imitation that happens to be successful!

^{23/} 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.

^{24/} Winter appears to doubt this (1975, p. 97; 1964, pp. 257-58).

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"; hypotheses as to differential survival of organization forms are what are in fact tested, for example, by the use of Stigler's "survivor principle." 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.

The broadly similar views of Alchian and Winter represent, it might be noted, a Lamarckian evolutionary model. Lamarck believed that acquired characters can be inherited (so did Darwin), 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 -- of which the behavior here examined is one aspect.^{25/}

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.

^{25/} There is cultural evolution even in the non-human sphere; animals can discover and pass on successful behaviors. And this may have consequences for genetic inheritance since behavioral changes may modify the conditions of selection among genetic mutations and recombinations (Mayr, 1960, p. 371). To this extent Lamarckism plays a role even in the modern theory of genetic evolution (see also Waddington, 1961, Ch. 4).

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 competitive equilibrium might not be generated, or, once generated, might not respond in the standard way to changes in exogenous determinants.^{26/} 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

^{26/} In certain more recent work 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.

of the many possible survival strategies adopted by organisms (firms) is 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, 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 obvious biological significance. Without any preconceived limitation of attention to the business firm, I now propose to view several aspects of economic theorizing 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.

III. ELEMENTS OF ECONOMIC THEORIZING: A BIOLOGICAL INTERPRETATION

Analogies are interesting and suggestive. But 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^{27/} -- in the same sense in which chemical reactions have been shown to be a special class of processes following the laws of physics. 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.^{28/} That is the object of this Section.

A. Utility, Fitness, and the Provenance of Preferences

Economics traditionally 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 merely arbitrary (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.

^{27/} Compare Alland (1967), pp. 194-97.

^{28/} 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 culturally 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 tastes^{29/} 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 the "preferences" that relate to patterns of human interaction. These differ from culture to culture: in some societies, parents try to have large families, in others small; in some, marital partners value fidelity highly, in others not; in some cultures people cluster closely together, in others they avoid personal contact. My programmatic contention is that such preference

^{29/} 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.

patterns, despite seemingly arbitrary elements, have survived because they are mainly adaptive to environmental conditions of particular societies. While this will surely not literally always prove true, such a working hypothesis will (it is contended) prove methodologically fruitful. In biology as well, it is often unclear a priori whether a particular trait is truly adaptive or merely accidental. Nature's experiments may randomly produce almost any conceivable outcome in a given instance. But if a trait has survived, as a working hypothesis the biologist always looks for an adaptive function. (Though whether adaptive solely to the individual, or alternatively to some larger social group to which he belongs, may remain subject to controversy.)

The biological approach to what economists call "utility" hypothesizes that tastes represent proximate aspects of a single underlying goal -- fitness. That is, 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 even more fundamentally, 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 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 can permit parents to 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!

The biologist thinks of the problem of achieving fitness as requiring tracking of environmental changes (Wilson, 1975, p. 145). On a short time scale fitness is achieved by organismic responses, ranging from quick biochemical and behavioral

adjustments dictated by the need to maintain homeostasis (e.g., taking a cooling drink in the Alabama sun) to more gradual accommodations like individual learning or family planning. On a longer time scale population responses are observed, ranging from moderately fast societal adjustments and demographic changes to long-run genetic modifications of physical or behavioral characters. But even this last is not so slow-moving a process as to be an entirely negligible consideration for social science; according to Wilson, evolutionary responses are perceptible over periods as short as ten generations. (And even more quickly, surely, under conditions of extreme selective pressure -- as by disaster.)

A key issue, in any attempt to broaden the application of economic reasoning to general problems of the social sciences, is the question of the "taste" for altruism.^{30/} Old-fashioned, narrower economics was often criticized for employing the model of "economic man" -- a selfish, calculating, and essentially non-social being. Of course, it was impossible to postulate such a man in dealing with that essential social grouping, the family. The older 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 without the family.

Modern economic imperialists have been dissatisfied both with the excessively restrictive postulate of individual selfishness and with the exclusion of intra-family 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

^{30/} Kurz (1975) and Becker (1976) provide economic analyses of altruism founded on biological considerations. The biological literature on the topic is enormous; selected citations will be provided below.

the other.^{31/} 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.

It turns out, biology tells us, that there is not so great a distance after all between the old-fashioned "man is selfish" postulate on the one hand, and the position of those critics of economic man who emphasized the fundamentally social nature of the human being ("men are brothers"). The genes are indeed ruthlessly selfish. But men are to greater or lesser degree "brothers" in the sense of sharing a common genetic endowment.

This has been formalized in the concept called kin selection (Hamilton, 1964). Optimal selfish behavior on the genetic level requires a degree of altruism toward close relatives on the organism level. Put another way, the appropriate "as if" maximand for the organism is not its own fitness but its inclusive fitness -- the reproductive survival of its genetic endowment. The obvious example is parental sacrifice on behalf of children. More generally, and with some oversimplification, 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.

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 -- preferences and opportunities (constraints). We cannot directly infer altruistic preferences from cooperative behavior; in some environments, even enemies may be forced to cooperate in the

^{31/} See, for example, Becker (1974).

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, if only one can survive.

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 sibs are ordinarily in much closer competition with one another^{32/} than parents are with children. Why then the famed sisterly altruism among ants? The explanation is remarkable. Due to the unusual method of sex determination called haplodiploidy, 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 and selfish 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. Any individual offspring's 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, always desirable from the offspring's point of view, is no longer optimal for the parent (who must consider his potential fitness gain in caring for other offspring). But the intensity of such "weaning conflict" is a function of the offspring's expected degree of relationship with sibs. In promiscuous species any withholding of maternal care is likely to redound to the benefit of mere half-sibs; in permanently

^{32/} For many species, the struggle for food or shelter among members of a litter is a matter of life or death.

mating species, of full sibs. Hence the prediction, which is in fact confirmed, that offspring will be less "selfish" (parent-offspring conflict will be less intense) in species following the "stable family" pattern.^{33/}

Another point of interest: why are parents generally more altruistic to offspring than offspring to parents -- since the degree of relationship is the same? Part of the reason is of course the disparity of initial endowments and capacities. 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. In comparison with parents, offspring generally have greater "reproductive value," 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 (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 tempted to load onto the other a disproportionate share of the burden. The relatively smaller male investment in germ cells (sperm vs.

^{33/} In polygamous human families full sibs reputedly display greater mutual altruism than half-sibs, but I am unaware of any hard evidence on this point.

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 (Wilson, 1975, p. 330).

The question of altruism other than to close kin remains quite controversial in biology. In environments where within-group altruism tends to promote group success, as will often be the case, one would expect such altruism to evolve readily from competition among groups ("group selection"). But there is a serious difficulty, what economists call a "free-rider problem." For, the bearer of a gene dictating altruistic behavior will be negatively selected within the group as against free-riding non-altruists ("individual selection").

Sharp disagreement persists among biologists as to whether non-kin altruism can emerge from group selection despite the adverse pressure of individual selection. Wynne-Edwards (1962) is the best-known proponent of this view; in contrast, Williams (1966) denies it as other than a theoretical possibility. An intermediate position, though leaning toward the negative, is taken by Wilson (1975, Ch. 5). He describes a number of possible models in which altruist genes may become fixed^{34/} (or nearly so) in small sub-populations which are then strongly group-selected over competing sub-populations. (When the altruist gene is fixed

^{34/} A gene is fixed in a population if all genetic endowments are homozygotic at that locus. In other words, all competing alleles have been eliminated.

within the group, there is no longer any individual-selection disadvantage of altruist behavior.) But his conclusion is that the evolution of altruism is highly improbable, requiring a very narrow "window" of parameters; he seems to allow it only as a temporary springboard permitting the development of other means of social cooperation.^{35/}

Since the qualified experts disagree, an outsider's opinion on the issue may be less unwarranted. My view is that, with the exception of altruism toward one's own direct descendants, no clear distinction can be drawn between kin selection and group selection. It should be noted that 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 two genes in common at any such locus. So "unrelated" individuals chosen at random in a species may well share 70% or 80% of their genetic endowments, and the correlation will be even closer within a localized social grouping likely to profit from altruistic interactions. This correlation does not of itself overcome the free-rider problem, since non-altruist individuals will still be selected over the altruists within any such group. But this same free-rider problem applies to the expression of altruism toward sibs or cousins; within the family as social unit, non-altruists will survive differentially at the expense of their altruist brothers.^{36/} Only parent-to-offspring altruism is largely free of this

^{35/} In particular, "reciprocal altruism" (i.e., exchange) to be discussed below.

^{36/} If a parent could pass genetically determined altruism on to all his offspring so that the altruist gene is fixed within the family group, this difficulty would be obviated. But when the altruist gene first arises by mutation, the one parent will only be heterozygotic for it while the other will be homozygotic for the non-altruist gene. So three-quarters of the offspring's genes will be of the non-altruist variety, on the average.

difficulty. But altruism toward kin even apart from direct offspring undoubtedly exists. Since the well-attested fact of kin selection differs only in degree from altruism toward conspecifics with correlated genetic endowments, it seems very likely that -- despite the improbabilities involved -- altruism experiments have been replicated so unimaginably often over the sweep of evolutionary time that there have been some significant successes! That is, even against the odds, altruist genes have from time to time become fixed (or nearly so) in non-kin social groupings which then succeed thanks to group selection.^{37/} If descendants are budded off into independent colonies, later reverse-mutations toward selfishness would tend to destroy the affected descendant colonies. But those colonies retaining their altruist character would continue to thrive and multiply.

What are the implications for economics, or the social sciences generally? The main proposition is that "tastes" are (sometimes, or often, or perhaps even always) not only explicable but explicable in economic terms. What are conventionally regarded as desired commodities or services or relationships are only intermediate goods serving the ultimate end of maximized fitness -- reproductive survival. The case for this contention is naturally more evident for preferences closely tied to biological functions, e.g., altruism toward offspring. But the working hypothesis, that all so-called tastes are ultimately adaptive to the goal of fitness, is likely to bear substantial fruit.

B. Competition and Competitive Strategies

Economics traditionally has concentrated attention upon one form of social interaction -- exchange. In this context competition arises only as transactors

^{37/} Charnov (1976) has demonstrated that the probabilities favor an altruist gene spreading only if altruist actions differentially favor fellow-altruists. Such a reciprocity requirement brings us close to exchange interactions (see below). The odds are against survival of "true" (i.e., unreciprocated) altruism.

vie for trading partners by offering better terms in the market. In its imperialist extensions economics has begun to devote attention to all of the interactions studied by the social sciences, e.g., those suggested by terms like love, power, exploitation, and conflict. The entirety of social interactions are involved in the all-encompassing biological competition among organisms.

Exchange is thus a particular competitive strategy, one involving a mutually beneficial relation among at least two organisms. It fits into the more general category called "mutualism" by biologists, of which there are both interspecific and intraspecific examples.

Among the instances of mutualist interaction between species 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 in the light of the preceding discussion of altruism 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.

A nice example is the reciprocal aid wherein certain fish species feed by grooming other, larger species -- who refrain from eating their cleaners. Such exchange interactions may shade into altruistic behavior. Indeed, Trivers (1971) has described them as "reciprocal altruism." But it is conceptually clearer to maintain the distinction; exchange requires reciprocity, whereas altruism is aid provided even in the absence of reciprocity by the benefited party.^{38/}

^{38/} Trivers' examples of "reciprocal altruism" include, apart from cleaning symbioses in fish, alarm calls in birds. The latter would seem to represent true altruism; the bird sounding the alarm on the average loses thereby, since it runs the risk of drawing the predator's attention to itself. Another example, though not "chosen," is the development of distastefulness in moths. The distasteful moth teaches predators to avoid its conspecifics, but that may be too late for itself!

The key question for the selectional advantage of 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 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.^{39/} 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.^{40/} 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!

Cooperative exchange shades into altruistic motivations, at least on the human level, in that (Trivers contends) the emotions of affection and sympathy have evolved because they provide a better guarantee of reciprocity than any mere calculated advantage of doing so. More generally, he argues that human evolution has developed a balance between the abilities to engage in and to detect and

^{39/} See Akerlof (1970), Darby and Karni (1973).

^{40/} Zeckhauser (1972).

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. (See also Kurz, 1975.) Finally, the selectional advantage of these emotions has led to evolution of the ability to simulate or mimic them -- 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 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" (Homans, 1958).^{41/} The competition for mates in the biological realm displays many familiar and some unexpected parallelisms 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.^{42/} There is a nice analogy here with recent economic theories of "competitive signalling."^{43/} Some characteristics may be

^{41/} An economic analysis of polygyny is provided in Grossbard (1976).

^{42/} "Advertising" is also observed in some interspecific exchanges, e.g., showy flowers and fragrances designed to attract the attention of pollinating insects.

^{43/} See Spence (1974), Stiglitz (1975), Riley (1976).

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.

Another desirable quality in a mate is possession of territory, generally by the male.^{44/} 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.^{45/} 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! (See 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. 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.)^{46/} Sexual combats may go beyond mere demonstration and actually harm the vanquished party, or sometimes the victor as well.

^{44/} 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.

^{45/} 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.)

^{46/} Wilson (1975), p. 320.

Biologists have devoted considerable attention to cases like the peacock, where the extreme development of sexual ornaments appears to be disfunctional 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 that male ornamentation and female preference evolve in parallel, which when carried to an extreme degree may represent a rather unstable equilibrium.^{47/}

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 at mating age than the other in the parent generation, 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.^{48/} Even such practices as disproportionate infanticide of females will not affect the equilibrium 1/1 ratio.

One factor that does distort the equilibrium sex ratio has been described by Trivers (1973). It is nearly universal among mammals that male parents have a

^{47/} See Fisher (1958 [1929]), p. 152.

^{48/} Note that a 1/1 ratio is not the most "efficient" from the point of view of species growth. From this group-selection point of view, it would generally be desirable to have more females.

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 strictly 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 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 (since status tends to be correlated with health and vigor).⁴⁹ More generally, the normally higher early male mortality is explained. This is a device that permits stronger parents (who suffer relatively less mortality among offspring) to have more male children and permits weaker parents more female children.

Even interest, Trivers (1971) suggests, ultimately has a biological origin. Reproductive value (average number of potential offspring an organism will in the future have) 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.^{50/} This must have been what Adam Smith really had in mind in his

^{49/} Shapiro, Schlesinger, and Nesbitt (1968).

^{50/} See Clower (1976).

otherwise too-sweeping assertion that "the propensity to truck, barter, and exchange" is specifically associated with the human species.^{51/} Sexual competition and cleaning symbioses provide sufficient evidence to the contrary. And associations such as pack membership also undoubtedly involve "social exchange" (Homans, 1958).

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.^{52/} Let N_G and N_H signify number 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.)

^{51/} "It is common to all men, and to be found in no other race of animals, which seems to know neither this nor any other species of contracts." (Smith, 1937 [1776], 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.

^{52/} These curves have already been expounded and analyzed in the economic literature by Boulding (1950 and 1962).

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 "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.^{53/} 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 from degree of relationship -- from correlation of genetic endowments -- not only among close kin but extending in substantial degree over the entire species. 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! In consequence, as organisms strike some balance between cooperative and competitive strategies, there is an element of instability in the

^{53/} Darwin, Origin of Species, Ch. 3. But if population density is held down by other forces such as predation, intraspecies competition may not be very severe.

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.

There are two main categories of cooperative strategies, in Nature and in the economy. A "hold-back" strategy is a kind of negative cooperation. Given the mutual interest in restraining individual striving for advantage, the organisms somehow find a behavioral solution to the Prisoners' Dilemma. Each competes 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, law, and property 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 ignore competitors but simply utilize resources; in "interference competition" they gain resources by hampering competitors.^{54/} Interference may take the milder form, as in territoriality, of fighting only as necessary to deny a limited zone of resource access to competitors. 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, in comparison with territorial conflict. Presumably, these extreme forms of interference strategies have mainly proved disfunctional to the species evolving them, and have therefore been selected

^{54/} McNaughton and Wolf (1973), Ch. 11; Wilson (1975), Ch. 11-12.

against. In exploitation or "scramble" strategies, the organisms compete solely by relative efficiency in utilizing resources. Rather than attacking one another, they interact solely through the "externality" of resource depletion. (In the economy, this is equivalent to bidding up prices of factors ~~or~~ driving down prices of products.) As would be expected, "hold-back" strategies tend to evolve where resource limitations are less severe, as in the case of organisms occupying unfilled environments.

The second, more positive and far-reaching kind of cooperative strategy is suggested by that famous phrase, the division of labor. Since competition is most intense when organisms are attempting all to do the same thing, a way out is for individuals to do different things, cooperatively!

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 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, 1974). 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 individuals, the division of labor with its concomitant of social exchange must become compensatingly productive as the force of altruism is diluted.^{55/} 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]) went beyond this to credit the division of labor with the emergence of 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).^{56/} As is so often the case in social analysis, however, Durkheim is (I believe) 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. The division of labor does not create solidarity. Rather, it is simply a strategic choice that, by reducing the intensity of inter-individual competition, allows fuller sway to the element of altruism already latent in genetic relationships.

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. (For example, mimic cleaner fish are, with some probability, detected and punished by being eaten!) Even emotional

^{55/} Forms of association also exist without division of labor, such as bird flocks or fish schools. But these are mere evanescent congregations, rather than social units in any organized sense.

^{56/} Durkheim (1933 [1893]), especially Introduction and Book 1.

supports for exchange, like the sense of justice ("moralistic aggression") may represent genetically evolved characters (Trivers, 1971). On the other hand, human culture has evolved institutional supports for exchange and the division of labor -- property, law and government.

Leaving aside the strategic choices involved in the "Dilemma of Sociality," a number of other choice options have been explored by biologists. One 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.^{57/} Their inclination is to produce a smaller number of more carefully optimized offspring.^{58/}

^{57/} See Wilson (1975), p. 101.

^{58/} Compare the discussion of "high-quality" and "lower-quality" children in Becker (1960) and Nerlove (1974).

Analogues 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.^{59/} Even today it seems likely that a suitable comparison of populations in environments like Alaska on the one hand and New York City on the other would reveal differential genetic (over and beyond merely cultural) adaptations.^{60/}

^{59/} See Wilson (1975), pp. 107-08.

^{60/} Many such associations of human genetic types with historical and geographical determinants are elaborated in Huntington (1945). While 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 Eskimos) is evident.

Another strategic dimension in biology is the degree of competitive specialization in the use of resources. This is not the kind of specialization involved in the division of labor for mutual benefit, but rather is akin to product differentiation in the economy (as in monopolistic competition). In this type of specialization, participants in no way rely upon one another. Indeed, each would be better off if the others were to vanish, in which case the survivor would broaden his use of resources in adopting a "generalist" strategy. The introduction of close interspecific competition tends to force each species away from the zone of overlap -- a process called "character displacement" leading to an equilibrium "separation distance."^{61/} But there is also the possibility that a single generalist of intermediate character might outcompete the two specialist types (Cody, 1974). Relative abundance and certainty of resources favors specialists; relative scarcity and unpredictability requires generalists.^{62/}

Biologists, having developed a more subtle and elaborate approach to this question of specialization than economists, recognize a variety of different "generalist" strategies. 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

^{61/} A result seemingly in conflict with Hotelling's famous proposition of locational convergence under duopoly (1929). His result is achieved only under rather peculiar assumptions, however (absolutely inelastic demands). More reasonable demand assumptions, equivalent to recognizing diminishing returns, would dictate the minimum separation distance outcome of the biologists.

^{62/} This rather suggests a parallel with Adam Smith's dictum "That the Division of Labor is Limited by the Extent of the Market," Wealth of Nations, Chapter 3. The analogy is imperfect, as we are not dealing here with specialization for mutual benefit as in the division of labor. The determinants of cooperative specialization and of the kind of competitive specialization represented by product differentiation do, however, have some points in common.

generalization is plasticity, whereby the species is enabled to change its character in response to environmental shifts.^{63/} 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.

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 well 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?

^{63/} Compare the discussion of "adaptability" in Stigler (1966), pp. 129ff.

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.^{64/}

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^{65/} and Lanchester's equations of combat.^{66/} Economists will of course recognize the duopoly solutions associated with Cournot.^{67/}

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.^{68/}

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

^{64/} See McNaughton and Wolf (1973), Ch. 10.

^{65/} 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.

^{66/} See Lanchester (1916), Morse and Kimbell (1951).

^{67/} See Allen (1938), pp. 200-04.

^{68/} 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.^{69/}

"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.^{70/} A human population might increase fitness by "mutations"

^{69/} Wilson and Bossert (1971), pp. 68-70.

^{70/} 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.^{71/} 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.^{72/} 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.^{73/} 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.^{74/}

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

^{71/} 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 or organization is not so vital.

^{72/} Wilson and Bossert (1971), pp. 106-08.

^{73/} Ibid., pp. 156-58.

^{74/} 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 the 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 sentences 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."^{75/}

The alternative mechanistic view, that evolution is an entirely undirected process, is almost universally postulated by modern biologists.^{76/} But it has been contended that hidden teleology lurks wherever adaptation is explained in such terms as "the good of the species" or "the good of the community" (Ghiselin, 1974).

As to hidden teleology, I do not believe the accusation is warranted. The question, as seen above in the discussion of altruism, 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 to kin 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 --

^{75/} Quoted in Himmelfarb (1959), 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).

^{76/} Mechanism is not, any more than its opposite (the postulate of design or purposiveness) a scientifically provable proposition. It is a working hypothesis.

from sexual combats within species to predation between species -- preclude any inference of a universal harmonious adaptation to the non-living environment (Tullock, 1971). Still, it seems that there may be at least some slow long-run pressure in this direction.^{77/}

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.^{78/}

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,^{79/} 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

^{77/} One possible instance is the tendency to reduced virulence in disease parasites (Wilson, 1975, p. 116). It is sometimes contended that the beneficial bacteria living within our bodies have evolved from what were originally harmful ones.

^{78/} See Alland (1967), p. 171; Wilson (1975), p. 560.

^{79/} "By pursuing his own interest he frequently promotes that of the society more effectually than when he really intends to promote it." (Wealth of Nations, Book IV, Ch. 2).

individual (in his own eyes) without harming one or several other 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 possible failure of Pareto-optimality -- natural monopoly, oligopoly, externalities, and public goods being leading examples.

The failure of Nature (below the human level, at any rate) to evolve the institution of property -- which is founded, in turn, upon the larger institutions of law and government -- 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.^{80/} 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 for

^{80/} 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 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.

IV. 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 each discipline. 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. Needless to say, 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 (Trivers, 1972 and 1974). 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"

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 genotypes
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

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. To the extent that this is the case 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 do different things, so as to complement one another; the participants in competitive clusters are each trying to do the same thing -- 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 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" cooperative groupings of organisms 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, into genotype-pairs, and other assemblages whose prospects for reproduction are linked 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 niches of different species at least potentially 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 genotype-pairs, 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. (Other social sciences have recognized the great importance of the provenance of preferences, and this question is bound to receive more attention with the progress of economic imperialism.) 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 force of Nature. (The thrust of the "satisficing" argument 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 the 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.

In this Section relatively little has been said about the social sciences other than economics. Unfortunately, too little is known about the principles of selection, equilibrium, or progressive change in these areas to permit even the very limited amount of systematization required by the Table. Economic imperialists hope to fill in all these blanks.

V. 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.^{81/} Considerable light has been cast, 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, where general biological laws will have only negligible relevance or have even been absolved by "unique" developmental advances achieved by mankind. Some comment on a number of these allegedly unique advances follow.

1. Cultural evolution: While far from unknown among animals, cultural evolution represents the primary response mechanism of the human species. Man has been able to penetrate new environments (recently, the air, underwater, space) even without

^{81/} Compare Wilson (1975), Ch. 27.

significant genetic adjustments. Language and writing have provided means of communication and memory that far transcend any genetically evolved mechanisms serving those functions. And since cultural evolution is so rapid and flexible, the human species has been led to try a far greater variety of adaptive experiments than any other. (But recently, it seems, this has been reversed thanks to increasing integration -- see below.)

2. Intelligence and awareness: Man is not only intelligent, but he is conscious of his abilities. Individual and group adaptive responses are therefore to a greater and greater extent subject to deliberate choice (optimization) rather than merely arrived at by chance so as to provide raw material for blind natural selection. In particular, man has become aware of evolution itself, and of the possibility of modifying it for his purposes. Even the genetic process may, it seems likely, in the very near future become highly subject to man's control in designing human types for normal and abnormal environments.

3. Moral, esthetic, and spiritual values: Moral consciousness can be regarded pragmatically as a group-selected character that reinforces genetically-based altruism (see Trivers 1971, Kurz 1975) beyond the limits of kin selection or reciprocal aid. In view of the inordinate advances in the capacity of the human species to compete through mutual injury, one can hardly understate the importance of this function. Whether this pragmatic view suffices to explain the origin or role of moral consciousness remains doubtful, however. Esthetic values and spiritual consciousness are at least equally mysterious, scientifically speaking.

4. Increasing integration: One aspect of cultural evolution has been the ever-increasing intensity of economic, political, and social interaction among humans all over the globe. To a greater and greater extent the human species is becoming a single unit for good or evil, e.g., in terms of exposure to environmental

hazards.^{82/} The most obvious instance is of course the threat of world-wide nuclear war.

Whether these advances -- cultural evolution for example -- are regarded as replacing biological mechanisms or rather as particular kinds of biological mechanisms or strategies, is perhaps only a matter of point of view.^{83/} But grounding all of social science upon an ultimate biological foundation is a programmatic challenge that seems bound to yield a world of important results.

^{82/} A nice example was the power failure of 1966 that blacked-out the entire U.S. Northeast, except for a few localities served by organizationally or technologically backward enterprises that had escaped or failed to qualify for integration in the regional network.

^{83/} Compare Waddington (1961), Ch. 5 with Alland (1967), Ch. 9.

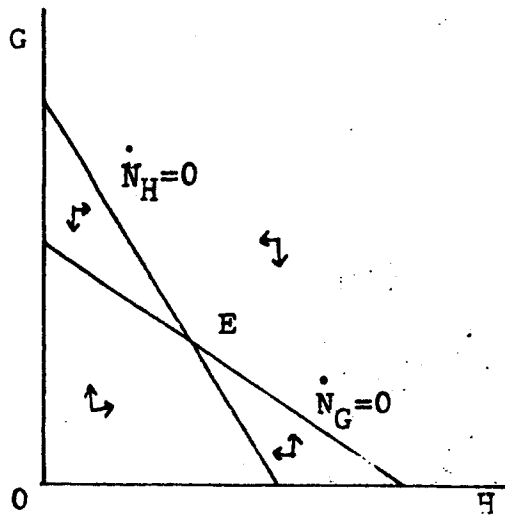


Figure 1

Two Competitive Populations
Stable Coexistence Equilibrium

Figure 2

Two Complementary Populations
Stable Coexistence
Equilibrium

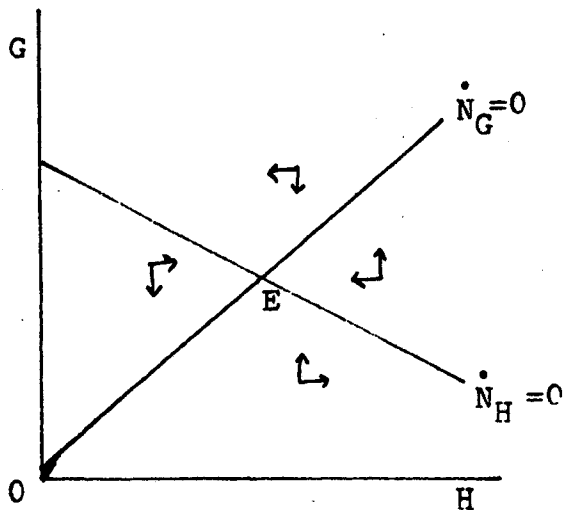
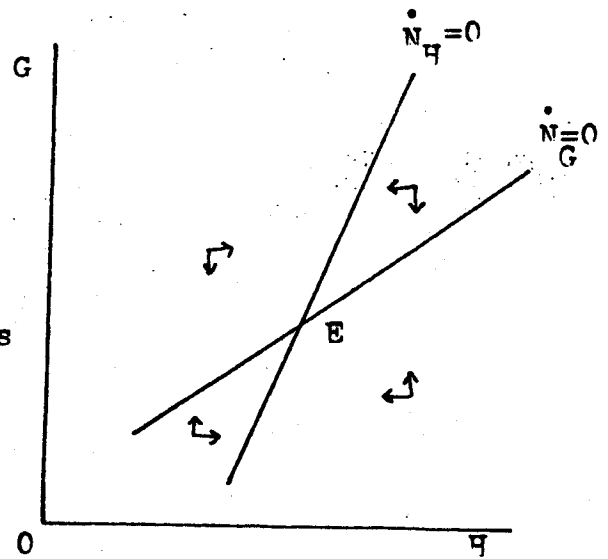


Figure 3

Predator-Prey Interaction

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