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Sociobiology and the Theory of Natural Selection

NATURAL SELECTION
AS STORYTELLING

Ludwig von Bertalanffy, a founder of general systems theory and a holdout against the neo-Darwinian tide, often argued that natural selection must fail as a comprehensive theory because it explains *too much*—a paradoxical, but perceptive statement. He wrote (1969: 24, 11):

If selection is taken as an axiomatic and *a priori* principle, it is always possible to imagine auxiliary hypotheses—unproved and by nature unprovable—to make it work in any special case. . . . Some adaptive value . . . can always be construed or imagined.

I think the fact that a theory so vague, so insufficiently verifiable and so far from the criteria otherwise applied in “hard” science, has become a dogma, can only be explained on sociological grounds. Society and science have been so steeped in the ideas of mechanism, utilitarianism, and the economic concept of free competition, that instead of God, Selection was enthroned as ultimate reality.

Similarly, the arguments of Christian fundamentalism used to frustrate me until I realized that there are, in principle, no counter cases and that, on this ground alone, literal bibliolatry is bankrupt. The theory of natural selection is, fortunately, in much better straits. It could be invalidated as a general cause of

evolutionary change. (If, for example, Lamarckian inheritance were true and general, then adaptation would arise so rapidly in the Lamarckian mode that natural selection would be powerless to create and would operate only to eliminate.) Moreover, its action and efficacy have been demonstrated experimentally by 60 years of manipulation within *Drosophila* bottles—not to mention several thousand years of success by plant and animal breeders.

Yet in one area, unfortunately a very large part of evolutionary theory and practice, natural selection has operated like the fundamentalist’s God—he who maketh *all* things. Rudyard Kipling asked how the leopard got its spots, the rhino its wrinkled skin. He called his answers “just-so-stories.” When evolutionists try to explain form and behavior, they also tell just-so stories—and the agent is natural selection. Virtuosity in invention replaces testability as the criterion for acceptance. This is the procedure that inspired von Bertalanffy’s complaint. It is also the practice that has given evolutionary biology a bad name among many experimental scientists in other disciplines. We should heed their disquiet, not dismiss it with a claim that they understand neither natural selection nor the special procedures of historical science.

This style of storytelling might yield acceptable answers if we could be sure of two things: 1) that all bits of morphology and behavior arise as direct results of natural selection, and 2) that only one selective explanation exists for each bit. But, as Darwin insisted vociferously, and contrary to the mythology about him, there is much more to evolution than natural selection. (Darwin was a consistent pluralist who viewed natural selection as the most important agent of evolutionary change, but who accepted a range of other agents and specified

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the conditions of their presumed effectiveness. In Chapter 7 of the *Origin* (6th ed.), for example, he attributed the cryptic coloration of a flat fish's upper surface to natural selection and the migration of its eyes to inheritance of acquired characters. He continually insisted that he wrote his 2-volume *Variation of Animals and Plants under Domestication* (1868), with its Lamarckian hypothesis of pangenesis, primarily to illustrate the effect of evolutionary factors other than natural selection. In a letter to *Nature* in 1880, he used the sharpest and most waspish language of his life to castigate Sir Wyville Thomson for caricaturing his theory by ascribing all evolutionary change to natural selection.)

Since God can be bent to support all theories, and since Darwin ranks closest to deification among evolutionary biologists, panselectionists of the modern synthesis tended to remake Darwin in their image. But we now reject this rigid version of natural selection and grant a major role to other evolutionary agents—genetic drift, fixation of neutral mutations, for example. We must also recognize that many features arise indirectly as developmental consequences of other features subject to natural selection—see classic (Huxley 1932) and modern (Gould 1966 and 1975; Cock 1966) work on allometry and the developmental consequences of size increase. Moreover, and perhaps most importantly, there are a multitude of potential selective explanations for each feature. There is no such thing in nature as a self-evident and unambiguous story.

When we examine the history of favored stories for any particular adaptation, we do not trace a tale of increasing truth as one story replaces the last, but rather a chronicle of shifting fads and fashions. When Newtonian mechanical explanations were riding high, G.G. Simpson wrote (1961: 1686):

The problem of the pelycosaur dorsal fin . . . seems essentially solved by Romer's demonstration that the regression relationship of fin area to body volume is appropriate to the functioning of the fin as a temperature regulating mechanism.

Simpson's firmness seems almost amusing since now—a mere 15 years later with behavioral stories in vogue—most paleontologists feel equally sure that the sail was primarily a device for sexual display. (Yes, I know the litany: It might have performed both functions. But this too is a story.)

On the other side of the same shift in fashion, a recent article on functional endothermy in some large beetles had this to say about the why of it all (Bartholomew and Casey 1977: 883):

It is possible that the increased power and speed of terrestrial locomotion associated with a modest elevation of body temperatures may offer reproductive advantages by increasing the effectiveness of intraspecific aggressive behavior, particularly between males.

This conjecture reflects no evidence drawn from the beetles themselves, only the current fashion in selective stories. We may be confident that the same data, collected 15 years ago, would have inspired a speculation about improved design and mechanical advantage.

SOCIOBIOLOGICAL STORIES

Most work in sociobiology has been done in the mode of adaptive storytelling based upon the optimizing character and pervasive power of natural selection. As such, its weaknesses of methodology are those that have plagued so much of evolutionary theory for more than a century. Sociobiologists have anchored their stories in the basic Darwinian notion of selection as individual reproductive success. Though previously underemphasized by students of behavior, this insistence on selection as individual success is fundamental to Darwinism. It arises directly from Darwin's construction of natural selection as a conscious analog to the laissez-faire economics of Adam Smith with its central notion that order and harmony arise from the natural interaction of individuals pursuing their own advantages (see Schweber 1977).

Sociobiologists have broadened their range of selective stories by invoking concepts of inclusive fitness and kin selection to solve (successfully I think) the vexatious problem of altruism—previously the greatest stumbling block to a Darwinian theory of social behavior. Altruistic acts are the cement of stable societies. Until we could explain apparent acts of self-sacrifice as potentially beneficial to the genetic fitness of sacrificers themselves—propagation of genes through enhanced survival of kin, for example—the prevalence of altruism blocked any Darwinian theory of social behavior.

Thus, kin selection has broadened the range of permissible stories, but it has not alleviated any methodological difficulties in the process of storytelling itself. Von Bertalanffy's objections still apply, if anything with greater force because behavior is generally more plastic and more difficult to specify and homologize than morphology. Sociobiologists are still telling speculative stories, still hitching without evidence to one potential star among many, still using mere consistency with natural selection as a criterion of acceptance.

David Barash (1976), for example, tells the following story about mountain bluebirds. (It is, by the way, a perfectly plausible story that may well be true. I only wish to criticize its assertion without evidence or test, using consistency with natural selection as the sole criterion for useful speculation.) Barash reasoned that a male bird might be more sensitive to intrusion of other males before eggs are laid than after (when he can be certain that his genes are inside). So Barash studied two nests, making three observations at 10-day intervals, the first before the eggs were laid, the last two after. For each period of observation, he mounted a stuffed male near the nest while the male occupant was out foraging. When the male returned he counted aggressive encounters with both model and female. At time one, males in both nests were aggressive toward the model and less, but still substantially, aggressive toward the female as well. At time two, after eggs had been laid, males were less aggressive to models and scarcely aggressive to females at all. At time three, males were still less aggressive toward models, and not aggressive at all toward females. Barash concludes that he has established consistency with natural selection and need do no more (1976: 1099–1100):

These results are consistent with the expectations of evolutionary theory. Thus aggression toward an intruding male (the model) would clearly be especially advantageous early in the breeding season, when territories and nests are normally defended. . . . The initial, aggressive response to the mated female is also adaptive in that, given a situation suggesting a high probability of adultery (i.e., the presence of the model near the female) and assuming that replacement females are available, obtaining a new mate would enhance the fitness of males. . . . The decline in male-female aggressiveness during incubation and fledgling stages could

be attributed to the impossibility of being cuckolded after the eggs have been laid. . . . The results are consistent with an evolutionary interpretation. In addition, the term "adultery" is unblushingly employed in this letter without quotation marks, as I believe it reflects a true analogy to the human concept, in the sense of Lorenz. It may also be prophesied that continued application of a similar evolutionary approach will eventually shed considerable light on various human foibles as well.

Consistent, yes. But what about the obvious alternative, dismissed without test in a line by Barash: male returns at times two and three, approaches the model a few times, encounters no reaction, mutters to himself the avian equivalent of "it's that damned stuffed bird again," and ceases to bother. And why not the evident test: expose a male to the model for the *first time after* the eggs are laid.

We have been deluged in recent years with sociobiological stories. Some, like Barash's, are plausible, if unsupported. For many others, I can only confess my intuition of extreme unlikeliness, to say the least—for adaptive and genetic arguments about why fellatio and cunnilingus are more common among the upper classes (Weinrich 1977), or why male panhandlers are more successful with females and people who are eating than with males and people who are not eating (Lockard et al. 1976).

Not all of sociobiology proceeds in the mode of storytelling for individual cases. It rests on firmer methodological ground when it seeks broad correlations across taxonomic lines, as between reproductive strategy and distribution of resources, for example (Wilson 1975), or when it can make testable, quantitative predictions as in Trivers and Hare's work on haplodiploidy and eusociality in Hymenoptera (Trivers and Hare 1976). Here sociobiology has had and will continue to have success. And here I wish it well. For it represents an extension of basic Darwinism to a realm where it should apply.

SPECIAL PROBLEMS FOR HUMAN SOCIOBIOLOGY

Sociobiological explanations of human behavior encounter two major difficulties, suggesting that a Darwinian model may be generally inapplicable in this case.

Limited Evidence and Political Clout

We have little direct evidence about the genetics of behavior in humans; and we do not know how to obtain it for the specific behaviors that figure most prominently in sociobiological speculation—aggression, conformity, etc. With our long generations, it is difficult to amass much data on heritability. More important, we cannot (ethically, that is) perform the kind of breeding experiments, in standardized environments, that would yield the required information. Thus, in dealing with humans, sociobiologists rely even more heavily than usual upon speculative storytelling.

At this point, the political debate engendered by sociobiology comes appropriately to the fore. For these speculative stories about human behavior have broad implications and proscriptions for social policy—and this is true quite apart from the intent or personal politics of the storyteller. Intent and usage are different things; the latter marks political and social influence, the former is gossip or, at best, sociology.

The common political character and effect of these stories lies in the direction historically taken by innatist arguments about human behavior and capabilities—a defense of existing social arrangements as part of our biology.

In raising this point, I do not act to suppress truth for fear of its political consequences. Truth, as we understand it, must always be our primary criterion. We live, because we must, with all manner of unpleasant biological truth—death being the most pervasive and ineluctable. I complain because sociobiological stories are not truth but unsupported speculations with political clout (again, I must emphasize, quite apart from the intent of the storyteller). All science is embedded in cultural contexts, and the lower the ratio of data to social importance, the more science reflects the context.

In stating that there is politics in sociobiology, I do not criticize the scientists involved in it by claiming that unconscious politics has intruded into a supposedly objective enterprise. For they are behaving like all good scientists—as human beings in a cultural context. I only ask for a more explicit recognition of the context and, specifically, for more attention to the evident impact of speculative sociobiological stories. For example, when the *New York Times* runs a weeklong front page series on women and their ris-

ing achievements and expectations, spends the first four days documenting progress toward social equality, devotes the last day to potential limits upon this progress, and advances sociobiological stories as the only argument for potential limits—then we know that these are stories with consequences:

Sociologists believe that women will continue for some years to achieve greater parity with men, both in the work place and in the home. But an uneasy sense of frustration and pessimism is growing among some advocates of full female equality in the face of mounting conservative opposition. Moreover, even some staunch feminists are reluctantly reaching the conclusion that women's aspirations may ultimately be limited by inherent biological differences that will forever leave men the dominant sex (*New York Times*, Nov. 30, 1977).

The article then quotes two social scientists, each with a story.

If you define dominance as who occupies formal roles of responsibility, then there is no society where males are not dominant. When something is so universal, the probability is—as reluctant as I am to say it—that there is some quality of the organism that leads to this condition.

It may mean that there never will be full parity in jobs, that women will always predominate in the caring tasks like teaching and social work and in the life sciences, while men will prevail in those requiring more aggression—business and politics, for example—and in the 'dead' sciences like physics.

Adaptation in Humans Need Not Be Genetic and Darwinian

The standard foundation of Darwinian just-so stories does not apply to humans. That foundation is the implication: if adaptive, then genetic—for the inference of adaptation is usually the only basis of a genetic story, and Darwinism is a theory of genetic change and variation in populations.

Much of human behavior is clearly adaptive, but the problem for sociobiology is that humans have so far surpassed all other species in developing an

alternative, non-genetic system to support and transmit adaptive behavior—cultural evolution. An adaptive behavior does not require genetic input and Darwinian selection for its origin and maintenance in humans; it may arise by trial and error in a few individuals that do not differ genetically from their groupmates, spread by learning and imitation, and stabilize across generations by value, custom and tradition. Moreover, cultural transmission is far more powerful in potential speed and spread than natural selection—for cultural evolution operates in the “Lamarckian” mode by inheritance through custom, writing and technology of characteristics acquired by human activity in each generation.

Thus, the existence of adaptive behavior in humans says nothing about the probability of a genetic basis for it, or about the operation of natural selection. Take, for example, Trivers’ (1971) concept of “reciprocal altruism.” The phenomenon exists, to be sure, and it is clearly adaptive. In honest moments, we all acknowledge that many of our altruistic acts are performed in the hope and expectation of future reward. Can anyone imagine a stable society without bonds of reciprocal obligation? But structural necessities do not imply direct genetic coding. (All human behaviors are, of course, part of the potential range permitted by our genotype—but sociobiological speculations posit direct natural selection for specific behavioral traits.) As Benjamin Franklin said: “We must all hang together, or assuredly we shall all hang separately.”

FAILURE OF THE RESEARCH PROGRAM FOR HUMAN SOCIOBIOLOGY

The grandest goal—I do not say the only goal—of human sociobiology must fail in the face of these difficulties. That goal is no less than the reduction of the behavioral (indeed most of the social) sciences to Darwinian theory. Wilson (1975) presents a vision of the human sciences shrinking in their independent domain, absorbed on one side by neurobiology and on the other by sociobiology.

But this vision cannot be fulfilled, for the reason cited above. Although we can identify adaptive behavior in humans, we cannot tell thereby if it is genetically

based (while much of it must arise by fairly pure cultural evolution). Yet the reduction of the human sciences to Darwinism requires the genetic argument, for Darwinism is a theory about genetic change in populations. All else is analogy and metaphor.

My crystal ball shows the human sociobiologists retreating to a fallback position—indeed it is happening already. They will argue that this fallback is as powerful as their original position, though it actually represents the unravelling of their fondest hopes. They will argue: yes, indeed, we cannot tell whether an adaptive behavior is genetically coded or not. But it doesn’t matter. The same adaptive constraints apply whether the behavior evolved by cultural or Darwinian routes, and biologists have identified and explicated the adaptive constraints. (Steve Emlen [1980] reports, for example, that some Indian peoples gather food in accordance with predictions of optimal foraging strategy, a theory developed by ecologists. This is an exciting and promising result within an anthropological domain—for it establishes a fruitful path of analogical illumination between biological theory and non-genetic cultural adaptation. But it prevents the assimilation of one discipline by the other and frustrates any hope of incorporating the human sciences under the Darwinian paradigm.)

But it does matter. It makes all the difference in the world whether human behaviors develop and stabilize by cultural evolution or by direct Darwinian selection for genes influencing specific adaptive actions. Cultural and Darwinian evolution differ profoundly in the three major areas that embody what evolution, at least as a quantitative science, is all about:

1. Rate. Cultural evolution, as a “Lamarckian” process, can proceed orders of magnitude more rapidly than Darwinian evolution. Natural selection continues its work within *Homo sapiens*, probably at characteristic rates for change in large, fairly stable populations, but the power of cultural evolution has dwarfed its influence (alteration in frequency of the sickling gene vs. changes in modes of communication and transportation). Consider what we have done with ourselves in the past 3000 years, all without the slightest evidence for any biological change in the size or power of the human brain.

2. Modifiability. Complex traits of cultural evolution can be altered profoundly all at once (social revolution, for example). Darwinian change is much slower and more piecemeal.
3. Diffusibility. Since traits of cultural evolution can be transmitted by imitation and inculcation, evolutionary patterns include frequent and complex anastomosis among branches. Darwinian evolution in sexually reproducing animals is a process of continuous divergence and ramification with few opportunities for coming together (hybridization or parallel modification of the same genes in independent groups).

I believe that the future will bring mutual illumination between two vigorous, independent disciplines—Darwinian theory and cultural history. This is a good thing, joyously to be welcomed. But there will be no reduction of the human sciences to Darwinian theory, and the research program of human sociobiology will fail. The name, of course, may survive. It is an irony of history that movements are judged successful if their label sticks, even though the emerging content of a discipline may lie closer to what opponents originally advocated. Modern geology, for example, is an even blend of Lyell's strict uniformitarianism and the claims of catastrophists (Rudwick 1972; Gould 1977). But we call the hybrid doctrine by Lyell's name, and he has become the conventional hero of geology.

I welcome the coming failure of reductionistic hopes because it will lead us to recognize human complexity at its proper level. For consumption by *Time's* millions, my colleague Bob Trivers maintained: "Sooner or later, political science, law, economics, psychology, psychiatry, and anthropology will all be branches of sociobiology" (*Time*, Aug. 1, 1977: 54). It is one thing to conjecture, as I would allow, that common features among independently developed legal systems might reflect adaptive constraints and might be explicated usefully with some biological analogies. It is quite another to state, as Trivers did, that the mores of the entire legal profession will be subsumed, along with a motley group of other disciplines, as mere epiphenomena of Darwinian processes.

I read Trivers' statement the day after I had sung in a full production of Berlioz' *Requiem*. And I re-

membered the visceral reaction I had experienced upon hearing the 4 brass choirs, finally amalgamated with the 10 tympani in the massive din preceding the great *Tuba mirum*—the spine tingling and the involuntary tears that almost prevented me from singing. I tried to analyze it in the terms of Wilson's conjecture—reduction of behavior to neurobiology on the one hand and sociobiology on the other. And I realized that this conjecture might apply to my experience. My reaction had been physiological and, as a good mechanist, I do not doubt that its neurological foundation can be ascertained. I will also not be surprised to learn that the reaction has something to do with adaptation (emotional overwhelming to cement group coherence in the face of danger, to tell a story). But I also realized that these explanations, however "true," could never capture anything of importance about the meaning of that experience.

And I say this not to espouse mysticism or incomprehensibility, but merely to assert that the world of human behavior is too complex and multifarious to be unlocked by any simple key. I say this to maintain that this richness—if anything—is both our hope and our essence.

SUMMARY

Even since Darwin proposed it, the theory of natural selection has been marred by an uncritical style of speculative application to the study of individual adaptations: one simply constructs a story to explain how a shape, function, or behavior might benefit its possessor. Virtuosity in invention replaces testability, and mere consistency with evolutionary theory becomes the primary criterion of acceptance. Although this dubious procedure has been used throughout evolutionary biology, it has recently become the primary style of explanation in sociobiology.

Human sociobiology presents two major problems related to this tradition. First, evidence is so poor or lacking that speculative storytelling assumes even greater importance than usual. Secondly, the existence of behavioral adaptation does not imply the operation of Darwinian processes at all—for non-genetic cultural evolution, working in the Lamarckian mode, dwarfs by its rapidity the importance of slower Darwinian change. The sociobiological vision of a reduction of the

human sciences to biology via Darwinism and natural selection will fail. Instead, I anticipate fruitful, mutual illumination by analogy between independent theories of the human and biological sciences.

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