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Simple Models of Complex Phenomena: The Case of Cultural Evolution

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A great deal of the progress in evolutionary biology has resulted from the deployment of relatively simple theoretical models. Staddon's, Smith's, and Maynard Smith's contributions to this volume illustrate this point. Despite their success, simple models have been subjected to a steady stream of criticism. Emlen's, Sober's, and Kitcher's papers here are good examples. The complexity of real social and biological phenomena is compared to the toylike quality of the simple models used to analyze them, and their users charged with unwarranted reductionism or plain simplemindedness.

This critique is intuitively appealing—complex phenomena would seem to require complex theories to understand them—but misleading. In this paper we argue that the study of complex, diverse phenomena like organic evolution requires complex, multilevel theories, but that such theories are best built from toolkits made up of a diverse collection of simple models. Because individual models in the toolkit are designed to provide insight into only selected aspects of the more complex whole, they are necessarily incomplete. Nevertheless, students of complex phenomena aim for a reasonably complete theory by studying many related simple models. The neo-Darwinian theory of evolution provides a good example: fitness optimizing models, one and multiple locus genetic models, and quantitative genetic models all emphasize certain details of the evolutionary process at the expense of others. While any given model is simple, the theory as a whole is much more comprehensive than any one of them.

Our argument is not very original; the conscious use of the strategy of using simple models to study complex phenomena goes back at least as far as Weber's (1949) use of "ideal types" to study human societies. Good modern expositions include those by Levins (1966, 1968), Liebenstein (1976), Wimsatt (1980), and Quinn and Dunham (1983). If we can contribute anything useful to the case for simple models, it is because our work has involved extending standard evolutionary theory to a particularly

troublesome complexity, cultural inheritance of humans (and in rudimentary form, of some other organisms). This work makes a variety of uses of starkly simple evolutionary models, including models based on the assumption of fitness optimization. Yet one of our concerns has been to determine the conditions under which fitness optimization models will fail to account for human behavior. Perhaps we have acquired a self-conscious awareness of some of the tactical details of the simple-model strategy that will be of some use to others.

1 The Complexity and Diversity of Evolutionary Processes

Evolutionary processes are both extremely complex and extremely diverse. On this count, those who are skeptical of simple models are certainly on solid ground. Every evolving population has a complex history in which many processes have contributed to its evolution, including perhaps drift, migration, mutation, and many other things besides selection. Further, each of these processes can be broken down into a series of interacting subprocesses, each encompassing many varieties. Take selection. There is selection on genes with large effects, selection on quantitative characters, selection on correlated characters and pleiotropic genes, frequency and density dependent selection, selection on sex-limited and sex-linked characters, sexual selection of a couple of kinds, and so on. Aside from viruses, all organisms have an intimidatingly large number of interacting genes and phenotypic characters. Environments vary in space and time with large effects on migration and selection. Age, sex, and social organization structure populations and affect their response to evolutionary processes. Developmental processes are complex, although poorly understood, and perhaps affect evolution in fundamentally important ways. Organisms affect their environments as they evolve. In the case of cultural evolution, additional complexities are introduced. We must understand the details of how individuals acquire and modify attitudes and beliefs, how different attitudes and beliefs interact with genes and environment to produce behavior, and how behavior and environment interact to produce consequences for individual lives. Obviously, the study of evolutionary processes must somehow cope with this complexity.

Evolutionary processes are diverse because different populations are quite different from one another in terms of their biology and the environments to which they are and have been exposed. Discoveries about the concatenation of processes affecting the evolution of one population or species do not necessarily say very much about those in others. In the case of cultural evolution, the details of the cultural transmission process vary appreciably from culture to culture. In some, fathers are more important in childhood socialization; in others, less. Modern societies depend on formal

teachers, in traditional societies members of the extended family are often important, and so on. Our models of cultural evolution suggest that such structural differences can be quite important to understanding what cultural traits might evolve.

2 Culture and the Evolutionary Process

In this section, in order to provide a body of detailed examples for use in the later sections, we shall sketch some theoretical results from our own work on the complexities in the evolutionary process caused by culture. Other kinds of complexities of the evolutionary process could be used instead, but we know this one best.

In the last few years, a number of scholars have attempted to understand the processes of cultural evolution in Darwinian terms. Social scientists (Campbell, 1965, 1975; Cloak, 1975; Durham, 1976; Ruyle, 1973) have argued that the analogy between genetic and cultural transmission is the best basis for a general theory of culture. Several biologists have considered how culturally transmitted behavior fits into the framework of neo-Darwinism (Pulliam and Dunford, 1980; Lumsden and Wilson, 1981; Boyd and Richerson, 1983). Other biologists and psychologists have used the formal similarities between genetic and cultural transmission to develop theory describing the dynamics of cultural transmission (Cavalli-Sforza and Feldman, 1973, 1981; Cloninger, Rice, and Reich, 1979; Eaves et al., 1978).

The idea that unifies all this work is that social learning or cultural transmission can be modeled as a system of inheritance; to understand the macroscopic patterns of cultural change we must understand the microscopic processes that increase the frequency of some culturally transmitted variants and reduce the frequency of others. Put another way, to understand cultural evolution we must account for all of the processes by which cultural variation is transmitted and modified. This is the essence of the Darwinian approach to evolution. We (Boyd and Richerson, 1985) have been particularly interested in the question of the origin of cultural transmission. Under what circumstances might selection on genes favor the existence of a second system of inheritance based on the principle of the inheritance of acquired variation?

Cultural and genetic transmission are similar in some respects. For example, the skills and dispositions transmitted during enculturation of children by parents create patterns of behavior that are very difficult to distinguish empirically from patterns resulting from genetic influences.

In other respects, cultural and genetic transmission differ sharply. First, culture is transmitted by an individual observing the behavior of others or by the naive being taught by the experienced. This means that behavior modified by trial-and-error learning can subsequently be transmitted; cul-

ture is a system for the inheritance of acquired variation. Second, patterns of cultural transmission are quite different from patterns of genetic transmission. Models other than biological parents are often imitated, including peers, grandparents, and so forth. The cultural analogues of generation length and the mating system are different from, and more variable than, the genetic case. Finally, the naive individual acquiring an item of culture is a more or less active decision-making participant in the transmission process. To some extent, we choose what traits we learn from others, but a zygote cannot choose its genes.

The goal of the Darwinian approach to cultural evolution is to understand cultural change in terms of the forces that act on cultural variation as individuals acquire cultural traits, use the acquired information to guide behavior, and act as models for others. What processes increase or decrease the proportion of people in a society who hold particular ideas about how to behave? We thus seek to understand the cultural analogues of the forces of natural selection, mutation, and drift that drive genetic evolution. These are divisible into three classes: random forces, decision-making forces, and natural selection operating directly on cultural variation.

The random forces are the cultural analogues of mutation and drift in genetic transmission. Intuitively, it seems likely that random errors, individual idiosyncracies, and chance transmission play a role in behavior and social learning. For example, linguists have documented a good deal of individual variation in speech, some of which is probably random individual variation (Labov, 1972). Similarly, small populations might well lose rare skills or knowledge by chance, for example due to the premature death of the only individuals who acquired them (Diamond, 1978).

Decision-making forces result when naive individuals evaluate alternative behavioral variants and preferentially adopt some variants relative to others. Naive individuals may be exposed to a variety of models and preferentially imitate some rather than others. We call this force biased transmission. Alternatively, individuals may modify existing behaviors or invent new ones by individual learning. If the modified behavior is then transmitted, the resulting force is much like the guided, nonrandom variation of classical "Lamarckian" transmission.

The decision-making forces are derived forces (Campbell, 1965). Decisions require rules for making them, and ultimately the rules must derive from the action of other forces. These decision-making rules may be acquired during an earlier episode of cultural transmission, or they may be genetically transmitted traits that control the neurological machinery for acquisition and retention of cultural traits. The latter possibility is the basis of the various sociobiological hypotheses about cultural evolution (Alexander, 1979; Lumsden and Wilson, 1981). These authors, among others, argue that the course of cultural evolution is determined by natural

selection operating indirectly on cultural variation via the decision-making forces.

Natural selection may also operate directly on cultural variation. Selection is an extremely general evolutionary process (Campbell, 1965). Darwin was able to formulate a clear statement of natural selection in the absence of a correct understanding of genetic inheritance because it is a force that will operate on any system of inheritance with a few key properties. There must be heritable variation, the variants must affect phenotype, and the phenotypic differences must affect individuals' chances of transmitting the variants they carry. That variants are transmitted by imitation rather than sexual or asexual reproduction does not affect the basic argument, nor does the possibility that some of the variants were originally acquired under the guidance of individual decisions. Darwin had no problem in imagining that random variation, acquired variation, and natural selection all acted together as forces in organic evolution. In the case of cultural evolution, we see none either.

We have attempted to construct a series of models that represent all of the processes sketched in the previous section. One interesting general result is that the processes of cultural evolution can easily lead to the evolution of behaviors that reduce Darwinian fitness, especially when nonparental individuals are important in cultural transmission. In the simplest model we have analyzed (Richerson and Boyd, 1984) natural selection acting on cultural variation transmitted by a parent and a "teacher" may cause the trait favoring transmission via teachers to go to fixation at a cost in terms of the number of children produced by parents. Some Darwinian students of humans (Alexander, 1979; Lumsden and Wilson, 1981; Durham, 1976) argue that such effects are unlikely to be important because a system of cultural inheritance with such properties would not be favored by selection on genes. Selection, the argument would run, ought to have acted to prevent such distorted cultural adaptations by either (1) the creation of decision-making forces that counteract the effect of selection on nonparentally transmitted cultural variation or (2) preventing nonparental individuals from becoming important in cultural transmission.

We believe this argument is incomplete because it ignores the fact that individual decision-making may be costly compared to social learning. If the costs of using individual decision-making processes are high, selection may not favor decision-making forces that would completely compensate for the maladaptive effects of nonparental transmission. Similarly, if nonparental pattern of cultural transmission offer advantages to individuals of economy in information acquisition, selection on the genes that underlie a capacity for asymmetric transmission may be favored.

For example, nonparental individuals may be more useful models than parents because they may be more skilled or knowledgeable than parents.

The effort in decision-making required to discriminate exactly among the adaptive skills and maladaptive inclinations of teachers and other non-parental models may require extensive, costly, empirical checks of each element of the teacher's behavior. In contrast, the use of relatively simple, low-cost decision-making rules to bias the choice of models or which of their behaviors to imitate may substantially increase a naive person's skills at a tolerable cost of imitating some maladaptive behaviors. We have analyzed the evolutionary consequences of a variety of simple bias rules. These models suggest that nonparental transmission may often be adaptive despite the cost of selection, especially in spatially variable environments (Boyd and Richerson, 1982, 1985—chapters 7 and 8). In essence, humans may accept the cost of imitating maladaptive cultural traits because the alternatives are a high frequency of random errors or extreme decision-making costs. Even when a cultural system of inheritance optimizes genetic fitness when averaged over all the traits it transmits, many traits taken individually may be quite far from those that would optimize fitness.

Even more extreme violations of the genetic fitness optimizing model are conceivable. For example, if rules of mate choice are transmitted culturally, human genes might be "domesticated" to serve cultural functions. On the other hand, perhaps the critics of these models are correct, and the abstract possibilities demonstrated by such models are empirically unimportant. The essential point is that, like many bits of genetic realism, adding culture to the evolutionary process might make a qualitative difference in the behavior we expect to observe compared to that expected from the simple fitness optimizing caricature of evolution.

3 Why Families of Simple Models

Disadvantages of Complex Models

In the face of the complexity of evolutionary processes, the appropriate strategy may seem obvious: to be useful models must be realistic; they should incorporate all factors that scientists studying the phenomena know to be important. This reasoning is certainly plausible, and many scientists, particularly in economics (e.g., Hudson and Jorgenson, 1974) and ecology (Watt, 1968), have constructed such models, despite their complexity. On this view, simple models are primitive, things to be replaced as our sophistication about evolution grows.

Nevertheless, theorists in such disciplines as evolutionary biology and economics stubbornly continue to use simple models even though improvements in empirical knowledge, analytical mathematics, and computing now enable them to create extremely elaborate models if they care to do so. Theorists of this persuasion eschew more detailed models because

(1) they are hard to understand, (2) they are difficult to analyze, and (3) they are often no more useful for prediction than simple models. Let us now consider each of these points in turn.

(1) Complex, detailed models are usually extremely difficult to understand. As more realism is added, the myriad interactions within the model become almost as opaque as the real world we wish to understand. When a set of not-so-complex parts is linked into an interacting complex, it is often impossible to understand why the results behave as they do. To substitute an ill-understood model of the world for the ill-understood world is not progress. In the end, the only way to understand how such a model works is to abstract pieces from it or study simplified cases where its behavior is more transparent. Even when complex models are useful, they are so because we understand how they work in terms of simple models abstracted from them.

Costly, complex models are most likely to be scientifically justified when phenomena are complex but not diverse. It is worth studying the complexities of atoms in great detail because there are only a few kinds, and they all obey the same basic laws. The generality of such laws makes them worth knowing even if the task is difficult. The equivalent sophistication in a model of the evolution of a given society or species is possible, perhaps, but unlikely to be justified on scientific grounds because of limited generalizability to other species or societies.

(2) The analysis of complex models is also expensive and time consuming. The complexity of a recursion model is roughly measured by the number of independent variables that must be kept track of from generation to generation. It usually is not possible to analyze nonlinear recursions involving more than a handful of variables without resorting to numerical techniques. Until the advent of digital computers, obtaining numerical solutions was impractical. Since then, however, there have been many attempts to make computer simulation models of complex social and biological processes. These projects have generally been quite costly. As the number of variables in a model increases, the number of interactions between variables increases even faster. This means that even with the fastest computers, it is not practical to explore the sensitivity of a model to changes in assumptions about very many of its constituent interactions. Considerations of economy of effort in scientific practice dictate that we should be satisfied with much simpler models than we could build in principle.

Complex, realistic models are sometimes employed when prediction rather than understanding is the main goal. Numerical weather prediction models and economic forecasting models come to mind. In both cases the gains in *understanding* of atmospheric and economic phenomena are mostly attributable to the constituent simple submodels of particular processes that

are individually not much good for prediction. The marginal increase in understanding relative to cost in the large predictive models is so small that only their practical application justifies their expense; scientific discovery would be better served by more attention to the simpler models. As Dupré observes in his introduction, explanation differs from prediction in being easier to achieve (leaving aside statistical models that make no pretentions to explanation). We would argue in addition that explanation or understanding is scientifically far more fundamental than prediction as well. This is most clearly evident in examples such as the simple deterministic models of economic and population processes that can exhibit chaotic behavior (Day, 1982; May, 1976). If these models prove to apply in the real world, they will guarantee that only short-range predictions are possible with less than perfect specification of initial conditions, but they also give a quite satisfactory explanation of why this is so. The problem is well understood in the context of a purely physical problem, weather prediction (Smagorinsky, 1969).

(3) Detailed models of complex social or biological systems are often not much more useful for prediction than are simple models. Detailed models usually require very large amounts of data to determine the various parameter values in the model. Such data are rarely available. Moreover, small inaccuracies or errors in the formulation of the model can produce quite erroneous predictions. The temptation is to "tune" the model, making small changes, perhaps well within the error of available data, so that the model produces reasonable answers. When this is done, any predictive power that the model might have is due more to statistical fitting than to the fact that it accurately represents actual causal processes. It is easy to make large sacrifices of understanding for small gains in predictive power. Contrariwise, although evolutionary processes are inherently complex and diverse, models with a few variables may capture enough of the really important processes in a given case or class of cases both to explain and to predict with tolerable accuracy, as Smith's, Staddon's, and Maynard Smith's papers in this volume show.

The Utility of Simple Models

In the face of these difficulties, the most useful strategy will usually be to build a variety of simple models that can be completely understood but that still capture the important properties of the processes of interest. Liebenstein (1976—chapter 2) calls such simple models "sample theories." Students of complex and diverse subject matters develop a large body of models from which "samples" can be drawn for the purpose at hand. Useful sample theories result from attempts to satisfy two competing desiderata: They should be simple enough to be clearly and completely grasped, and

at the same time they should reflect how real processes actually do work, at least to some approximation. A systematically constructed population of sample theories and combinations of them constitutes the theory of how the whole complex process works.

The synthetic theory of evolution provides a good example. Each of the basic processes (e.g., selection, mutation, drift) is represented by a large variety of simple models, some specific to a particular population, and others quite general. These models are combined in different ways to represent interesting phenomena, (e.g., sexual selection, speciation). This whole family of models, together with a knowledge of which models are appropriate for what kinds of situations, constitutes the theoretical system of population biology.

A theoretical system so constituted from simple sample models is a complicated and diverse collection of knowledge; it cannot be legitimately labeled simpleminded. Still, every tactical deployment of models to study a question of interest will be quite simple compared to the phenomena that they are intended to represent. The sample models are caricatures. If they are well designed, they are like good caricatures, capturing a few essential features of the problem in a recognizable but stylized manner, and with no attempt to represent features not of immediate interest.

Wimsatt (1980, 1981) provides good general discussions of tactical considerations in the deployment of simple models. To Wimsatt, all sample models of evolutionary phenomena should be viewed as "heuristics" rather than universally applicable laws. This terminology has the virtue of emphasizing that all sample models have defects. They usefully apply only over a limited range of phenomena, and even over the range where they are useful they are almost certain to have biases. Even the very best scientific heuristic (or sample model) will fail and possibly mislead if pushed too far or in the wrong direction. It is in attention to details of the use of simple sample theories that these problems are minimized and the maximum understanding gained. The user attempts to discover "robust" results, conclusions that are at least qualitatively correct, at least for some range of situations, despite the complexity and diversity of the phenomena they attempt to describe.

Note that simple models can often be tested for their scientific content via their predictions even when the situation is too complicated to make practical predictions. Experimental or statistical controls often make it possible to expose the variation due to the processes modeled, against the background of "noise" due to other ones, thus allowing a ceteris paribus prediction for purposes of empirical testing. Simple models, in other words, are the formal theoretical parallel of the experimental and comparative methods so widely used in biology and the social sciences.

Generalized Sample Theories

Generalized sample theories are an important subset of the simple sample theories used to understand complex, diverse problems. They are designed to capture the qualitative properties of the whole class of processes that they are used to represent, while more specialized ones are used for closer approximations to narrower classes of cases. Generalized sample theories are useful because we do not seem to be able to construct models of social and biological phenomena that are general, realistic, and precisely predictive (Levins, 1966, 1968). That is, evolutionary biologists and social scientists have not been able to satisfy the epistemological norm derived from the physical sciences that holds that theory be in the form of universal laws that can be tested by the detailed predictions they make about the phenomena considered by the law. This failure is probably a consequence of the complexity and diversity of living things. Basic theoretical constructs like natural selection are not universal laws like gravitation; rather they are taxonomic entities, general classes of similar processes that nonetheless have a good deal of diversity within the class. A theoretical construct designed to represent the general properties of the class of processes labeled natural selection must sacrifice many of the details of particular examples of selection. On the other hand, a model tailored to the details of a particular case is unlikely to have much relevance beyond that case. Further, the most precise predictions may be obtained by statistical models that sacrifice realism and hence are useless as explanatory devices.

One might agree with the case for a diverse toolkit of simple models, but still doubt the utility of *generalized* sample theories. Fitness maximizing calculations are often used as a simple caricature of how selection ought to work most of the time in most organisms to produce adaptations. Does such a generalized sample theory have any serious scientific purpose? Some might argue that their qualitative kind of understanding is, at best, useful for giving nonspecialists a simplified overview of complicated topics and that real scientific progress still occurs entirely in the construction of specialized sample theories that actually predict. A sterner critic might characterize the attempt to construct generalized models as loose speculation that actually inhibits the real work of discovering predictable relationships in particular systems.

These kinds of objections implicitly assume that it is possible to do science without any kind of general model. All scientists have mental models of the world. The part of the model that deals with their disciplinary specialty is more detailed than the parts that represent related areas of science. Many aspects of a scientist's mental model are likely to be vague and never expressed. The real choice is between an intuitive, perhaps covert, general theory and an explicit, often mathematical, one.

It seems to us that generalized sample models such as fitness optimizing models do play an important role. Well chosen to represent the stripped-down essence of a much larger set of more specialized models, generalized sample theories serve important functions in scientists' cognitive organization of complex-diverse subject matters and in communication between specialists. For example, we are concerned with the details of how cultural transmission occurs, a subject studied by psychologists (Boyd and Richerson, 1985—chapter 3). Social learning theorists have made many, but not all, of the kinds of measurements that are necessary for specifying good sample theories of cultural transmission. Crucial unknowns include the mechanisms by which variation and covariation are maintained in cultural traits. These properties have important implications for the process of cultural evolution because the selection and bias forces depend on the maintenance of variation for their effectiveness. These deficiencies of social learning theory are not at all apparent in the absence of a theory linking the psychology of enculturation with the macroscopic phenomena of social institutions and long-run outcomes. It seems unlikely that a sensible psychologist would be motivated to make the arduous and costly experiments necessary to determine such processes without a general theoretical argument justifying their importance. This is an example of a common situation: constructing models that make such links, even if they are simple caricatures, often shows that processes with small, relatively hard to measure, effects can produce major results.

The relationship between a generalized sample theory and empirical test or prediction is a subtle one. To insist upon empirical science in the style of physics is to insist upon the impossible. However, to give up on empirical tests and prediction would be to abandon science and retreat to speculative philosophy. Generalized sample theories normally make only limited qualitative predictions. The logistic model of population growth is a good elementary example. At best, it is an accurate model only of microbial growth in the laboratory. However, it captures something of the biology of population growth in more complex cases. Moreover, its simplicity makes it a handy general model to incorporate into models that must also represent other processes such as selection, and intra- and inter-specific competition. If some sample theory is consistently at variance with the data, then it must be modified. The accumulation of these kinds of modifications can eventually alter general theory, either by compelling the abandonment of some sample models or by systematizing knowledge about the variation of processes. In extreme cases, major discoveries in some of the components of a general theory can compel the reorganization of the entire edifice, as exemplified by the impact of Mendelian genetics on Darwinian theory in biology. No one nowadays would think of using Karl Pearson's models of the inheritance of acquired variation as a sample

theory of genetic inheritance, although they might have some specialized uses in the study of cultural evolution.

A generalized model is useful so long as its predictions are qualitatively correct, roughly conforming to the majority of cases. It is helpful if the inevitable limits of the model are understood. It is not necessarily an embarrassment if more than one alternative formulation of a general theory, built from different sample models, is more or less equally correct. In this case, the comparison of theories that are empirically equivalent makes clearer what is at stake in scientific controversies and may suggest empirical and theoretical steps toward a resolution.

4 Some Remarks on the Strategy of Building Simple Models

One of the main points of the preceding discussion is that the analysis of evolutionary problems using simple models depends very much on the appropriate choice of those models. How does one go about making such choices? Evolutionary biologists and social scientists use a variety of methods to accomplish this task that, we believe, can be collected under three main headings, corresponding to idealized analytical steps: (1) the choice of problem, (2) the modularization of analysis, and (3) the construction of synthetic hypotheses that we shall call "plausibility arguments."

Choice of Problem

When one uses simple models to understand complex and diverse problems, the choice of the problem to be analyzed exerts a strong influence on the kinds of simplifications one chooses. The idea is to simplify most drastically those aspects that are not centrally related to the problem at hand in order to retain the maximum feasible detail in the features of most direct interest. In the case of our models of cultural evolution, we have been concerned with the evolution of cultural organisms from acultural ancestors. This required us to represent the processes of ordinary organic evolution in most of our modeling efforts. Still, we were also interested in trying to develop preliminary general models of the important structural features and forces that affect cultural evolution. Given this choice of problem, it seemed advisable to use very simple models of genetic processes to represent the evolution of genetic capacities for culture in order that the models of cultural transmission could be made a bit more elaborate. Thus, we frequently asked what parameter value of a model controlling the propensity to acquire culture in a certain way would cause fitness to be optimized. Those models that included specific genetics used only the simplest haploid one locus or quantitative models of genetic transmission.

Models emphasizing cultural detail at the expense of genetic detail accept the risk that some particular complexity of the human genetic

system plays a direct role in the coevolution of genes and culture. For example, if genes affecting the behavior toward relatives are transmitted on the Y chromosome, as Hartung (1976) suggested, the models we constructed might turn out to be seriously misleading. The opposite risk, however, seemed more serious to us in the context of the problem; in models that are too complex the important details of culture itself might be obscured or lost. Several commentators (Maynard Smith and Warren, 1982; Boyd and Richerson, 1983; Kitcher, 1985) have remarked that the analysis that led Lumsden and Wilson (1981) to their "thousand year rule" is dubious because key properties of culture disappear as a result of simplifying assumptions. The general formulation of their model is conceptually satisfactory, but its complexity appears to have dictated misleading simplifications in the interests of successful analysis.

Modularization of Analysis

Most interesting evolutionary problems involve the interaction of evolutionary processes and a particular pattern of genetic transmission and gene expression. For example, the interaction of selection and mutation at a diploid locus is a classic problem of the synthetic theory. The sample models of the parts of this problem are less interesting than the combination of them in a model that can help us understand how the two basic forces interact with genetically inherited variation. Similar problems are of interest in cultural evolution. How does learning, acting as an evolutionary force because learned variants can be imitated, interact with selection, both selection on the cultural variants and on the underlying senses of reward and punishment that guide learning? Such combinations of processes inevitably make for relatively complex models. To make any headway, relatively difficult mathematical and experimental procedures have to be introduced, and many simplifying assumptions have to be made. Difficult choices between analytical tractability, comprehensibility, generality, and realism have to be made. Is a fitness optimization representation of the genetic process a reasonable simplification, or can some additional genetic realism be usefully retained in the context of the problem?

The answers to such questions are sought by breaking the problem down first into its constituent sample models and then reassembling them step by step into more complex combinations. This tactic is obvious, but easily misunderstood and misused. In the long run, the simple models strategy leads to large families of well understood sample models, some of which will be relatively complex, specialized, and difficult to understand. Also, relatively complex combinations of models are often useful. However, such relatively complicated models depend on a thorough understanding of the simplest models of each family and of the constituent submodels of compound models. The possibility for artifactual results in-

creases with the complexity of the analysis unless one can be reasonably confident that the constituent sample models are empirically reasonable and mathematically well behaved. It is relatively much easier to conduct experiments and detailed mathematical analysis on processes when they are isolated than when they are imbedded in a complex system. In population biology, both history and pedagogic practice suggest that one must begin with an understanding of the elementary constituents of the theory.

While building models of complex processes composed of simpler modules may be second nature to evolutionary biologists, in our experience it sometimes confuses social scientists who read the present body of theory in cultural evolution. The modularization of complex problems seems reductionistic; even after the parts are reassembled it seems to some readers as if the models are attempting to deduce the properties of wholes from properties of parts. The tactical "reductionism" used to understand a problem does not imply that the interaction of parts might not produce irreducible effects. For example, some models of culture built using this tactic suggest that group selection might be especially likely under some plausible forms of cultural transmission (Boyd and Richerson, 1985— chapter 7).

Sometimes, evolutionary biologists (and social scientists who use similar methods, such as economists) contribute to the confusion by failing to distinguish between the heuristic use of tactical reductionism from a real belief that some particular simple model is true description of a complex process. Indeed, the relative ease with which interesting, even approximately correct, results can be obtained for intrinsically rather complex processes with simple models can lead the unwary to conclude that successful tactical reduction implies the adequacy of a philosophical reductionist stance. Those who are so tempted should consult the papers of Wimsatt cited above. Most users of simple models know better. For example, Dawkins (1982), a prototypical genetic reductionist by some accounts (Sober, 1984), begins his discussion (pp. 1–2) by asking the reader to take his idea of selfish genes with extended phenotypes as a heuristic model. Later (by p. 7), Dawkins does express the hope that it may prove more fundamental than a mere heuristic, but the distinction between the two interpretations is clear, and the reader is left the choice.

The development of a formal theory of cultural evolution is in its infancy, and attention has properly concentrated on quite elementary models. This means that the theory to date appears quite reductionistic. For example, most models consider only one cultural trait. On the one hand, an overenthusiast might claim that these models are relatively successful in explaining human behavior and hence that human cultures really can be atomized into traits. On the other hand, a critic might complain that they are completely bankrupt because they do not take account of the fact that

cultural traits must interact in complex ways. The fact is that such preliminary models are silent about what complexities might flow from the interaction of multiple traits. That is a difficult question in its own right, but one whose analysis must be deferred until we understand the simpler theoretical elements we might use in such an analysis.

The thorough study of simple models includes pressing them to their extreme limits. This is especially useful at the second step of development, where simple models of basic processes are combined into a candidate generalized model of an interesting question. There are two related purposes in this exercise.

First, it is helpful to have all the implications of a given simple model exposed for comparative purposes, if nothing else. A well understood simple sample theory serves as a useful point of comparison for the results of more complex alternatives, even when some conclusions are utterly ridiculous.

Second, models do not usually just fail; they fail for particular reasons that are often very informative. Just what kinds of modifications are required to make the initially ridiculous results more nearly reasonable? For example, the failures of the logistic model of population growth suggest the amendments needed to make better models. In the case of culture, models that include only faithful cultural transmission suggest that culture is generally inferior to genes as a mode of inheritance (Cavalli-Sforza and Feldman, 1983). If the evolution of culture in the hominid line was favored by natural selection, there must be more to the story than just the acquisition of behavior by imitation. We have suggested that the ability of culture to couple individual learning to a transmission mechanism, thus to generate a system for the inheritance of acquired variation, could cause capacities for culture to evolve (Boyd and Richerson, 1983a, 1985—chapter 4). However, this analysis also fails because it suggests that the advantages of culture are quite general, and hence that many organisms ought to have "Lamarckian" systems of inheritance. This failure in turn suggests that there are other costs to the inheritance of acquired variation that must be accounted for.

In both of these respects, human sociobiology has made a major contribution by showing what must be true if the genetic fitness optimizing model generally holds when behavioral variation is proximally transmitted by culture. For example, Alexander (1979; see also Flinn and Alexander, 1982) argues that decision-making forces are powerful enough to constrain cultural variation to maximize fitness in most circumstances. Important qualitative predictions flow from this argument. If strong, accurate decision-making is possible, then humans need not depend on relatively passive imitation; they can easily invent or choose those behaviors appropriate to the environments they find themselves in. If so, culture will

behave more like ordinary mechanisms of phenotypic flexibility than like an inheritance system. Empirically, behavioral variation will be largely explicable, even in the short run, in terms of environmental variation rather than the variation in what traits are available for imitation. This argument also implies that costs of making decisions are low relative to any economies that might result from imitation. In our judgment (Boyd and Richerson, 1985—chapter 5), theory and the available data suggest that Alexander's argument is incorrect in general, although it may well be roughly correct for those traits for which accurate decision-making is easy. Regardless of whether we or Alexander ultimately prove more nearly correct, his contribution is substantial; work on the complexities of culture is much aided by having the implications of the simplest genetic fitness maximizing model incorporating culture cogently developed.

The exhaustive analysis of many sample models in various combinations is also the main means of seeking robust results (Wimsatt, 1981). One way to gain confidence in simple models is to build several models embodying different characterizations of the problem of interest and different simplifying assumptions. If the results of a model are robust, the same qualitative results ought to obtain for a whole family of related models in which the supposedly extraneous details differ. Although he makes a slightly different point, Maynard Smith's discussion in this volume of the use of multiple models of the same general process is a good example. The fact that genetic and game theoretic models of altruism usually lead to similar conclusions reassures us that general results like Hamilton's $k = 1/r$ rule are robust. Similarly, as more complex considerations are introduced into the family of models, simple model results can be considered robust only if it seems that the qualitative conclusion holds for some reasonable range of plausible conditions. Thus, quantitative genetic (Boyd and Richerson, 1982) and multiple-locus models (Uyenoyama and Feldman, 1980) suggest that Hamilton's rule is approximately correct when a variety of complications are introduced. Complications substantially affect the exact form of the rule, but do preserve the qualitative result that kin cooperation can evolve and the propensity to cooperate should be a function of relatedness under most circumstances that seem empirically reasonable. Nevertheless, it is slow and difficult work to make reasonably certain that particular results can be treated as robust (Wimsatt, 1980).

In the case of cultural evolution, we make the tentative claim that the costly information argument is a robust result. In all of the models we have constructed of the novel structural properties of culture and the evolutionary forces that result from them, it seems that optimizing the genetic fitness of a capacity for culture generally leads to a situation in which many individual cultural traits can easily evolve to values quite distant from those that would maximize fitness, so long as decision-making is costly. These

results do not depend on whether cultural traits are imagined to be discrete characters or continuous quantitative variables, for example. The tentativeness of the claim must be emphasized because the whole corpus of models of cultural evolution is still so small.

Plausibility Arguments

We believe that "plausibility argument" is a useful term for a scientific construct that plays much the same role in the study of complex, diverse phenomena that mutually exclusive hypotheses are supposed to play in the investigation of simpler subject matters. A plausibility argument is a hypothetical explanation having three features in common with a traditional hypothesis: (1) a claim of deductive soundness, of in-principle logical sufficiency to explain a body of data, (2) sufficient support from the existing body of empirical data to suggest that it might actually be able to explain a body of data as well as or better than competing plausibility arguments, and (3) a program of research that might distinguish between the claims of competing plausibility arguments. The differences are that competing plausibility arguments (1) are seldom mutually exclusive, (2) can seldom be rejected by a single sharp experimental test (or small set of them), and (3) often end up being revised, limited in their generality or domain of applicability, or combined with competing arguments rather than being rejected. In other words, competing plausibility arguments are based on the claims that a different set of submodels is needed to achieve a given degree of realism and generality, that different parameter values of common submodels are required, or that a given model is correct as far as it goes, but applies with less generality, realism, or predictive power than its proponents claim. Most frequently, the empirical program suggested by competing plausibility arguments is an arduous series of measurements of the relative strengths of several known processes in a wide range of organisms.

The reason for these differences is that quantitative questions are at the crux of debates about evolutionary processes. For example: How strong is selection among individuals relative to selection among groups? Theoretical analysis suggests that selection among groups must be commonplace, and laboratory experiments (Wade, 1977) demonstrate that it could have important effects. However, it is not at all clear whether selection among groups is important in nature. Sex ratio provides another example. Clear examples of sex ratio distortion exist (Hamilton, 1967), and theory suggests that it should be favored under a wide variety of ecological conditions (Charnov, 1982). Yet this process seems to be relatively rare— at least weak enough to neglect in most cases. Even if we are willing to be content with qualitative knowledge of complex processes, the term "qualitative" must be taken in the sense of rough estimates of quan-

titative variables, not in the sense of simple acceptance or rejection of mutually exclusive hypotheses. This feature of evolutionary problems is the basis for Quinn and Dunham's (1983) rejection of Popperian falsification as a proper epistemological model in ecology and evolution (See also Rapoport's, 1967, claim that many scientific paradoxes have been resolved when the polar positions were shown to be only opposite ends of a continuum).

Human sociobiology provides a good example of a plausibility argument. The basic premise of human sociobiology is that fitness optimizing models drawn from evolutionary biology can be used to understand human behavior. Many social scientists have objected to this enterprise on the grounds that evolutionary theory does not account for the existence of culture. As we have already noted, Alexander (1979), Lumsden and Wilson (1981), Durham (1976), and others have defended the fitness optimizing approach not by denying the importance of culture but by proposing various means by which decision-making forces could evolve under the guidance of selection to constrain cultural evolution so as generally to produce fitness optimizing behavior. These authors have supported their plausibility argument by constructing an array of simple models that predict the details of human behavior in various circumstances—for example, patterns of adoption, unilineal descent, and child abuse—and compared the results of these simple models with empirical data.

The sociobiological explanations of human behavior and those derived from explicit models of cultural evolution provide an example of competing plausibility arguments. As Flinn and Alexander (1982) argue, there is wide agreement among Darwinian students of the problem of human evolution that culture is important, and that the processes of cultural evolution may sometimes fail to keep cultural variation "on track" of genetic fitness (e.g., Alexander, 1979—p. 142). Disagreements revolve around the relative strength of decision-making forces compared to natural selection on cultural variation, the degree to which cultural transmission acts like an inheritance system rather than an ordinary mechanism for phenotypic flexibility, the importance of nonparental transmission, and so forth. For example, we have argued that decision-making is frequently costly, and that this allows culture a certain autonomy, while Durham (1976) argues that cultural evolution will be constrained to produce behaviors that approximately maximize fitness most of the time.

We think that the clearest way to address the controversial questions raised by competing plausibility arguments is to try to formulate models with parameters such that for some values of the critical parameters the results approximate one of the polar positions in such debates, while for others the model approximates the other position. If the parameters that

produce these contrasting results capture some real features of the processes of cultural and genetic coevolution, it may be possible to understand at least what is at stake in the controversy. In the models we have constructed, several parameters control the extent to which a typical cultural trait will be at the fitness optimum. If decisions about what cultural behaviors to adopt or invent can be made easily and accurately, and the rules that guide choices are ultimately transmitted genetically and subject to selection, culture will be very strongly constrained to maximize genetic fitness. Similarly, if important cultural traits are transmitted mostly from biological parents to offspring, cultural variation will act much like an extra chromosome of a biochemically odd kind. Even if decision-making forces are weak, selection on cultural variation will favor individual (inclusive) reproductive success, subject only to the same kinds of qualifications that obtain for a genetic locus. This result seems to approximate Durham's (1976) argument. As decision-making costs and nonparental transmission are allowed to become more important, cultural evolution becomes less directly constrained by selection on genes that control culture and it is possible to approximate positions like the group-functionalism of many social scientists and the afunctional position of Sahlins (1976).

As primitive as our own models are in this regard (see also Pulliam and Dunford, 1980; Werren and Pulliam, 1981; Pulliam, 1982, 1983), we think they are a promising step. The costs of decision-making and the extent to which important items of culture are transmitted by nonparental individuals are empirical issues that can be resolved. Indeed, data already exist on these points (Boyd and Richerson, 1985 chapters 3 and 5). It would be overenthusiastic to claim that any of the controversial questions surrounding the application of Darwinism to human culture are resolved, but we do believe that the modest body of formal theory so far developed, and empirical argument derived from the theory, has clarified the issues to the extent that rapid progress is now possible.

A well developed plausibility argument differs sharply from another common type of argument that we call a programmatic claim. Most generally, a programmatic claim advocates a plan of research for addressing some outstanding problem without, however, attempting to construct a full plausibility argument. Programmatic claims can be exceedingly useful; the development of a Darwinian theory of culture was greatly stimulated by mostly programmatic essays such as those by Campbell (1965), Ruyle (1973), and Cloak (1975). However, they are useful only insofar as they indicate the possibility of, or need for, new plausibility arguments. An attack on an existing, often widely accepted, plausibility argument on the grounds that the plausibility argument is incomplete is a kind of programmatic claim. Critiques of human sociobiology are commonly of this type. Burden-of-proof claims are another variant. For example, sociobiologists

often seem to imply that the general success of adaptive reasoning in biology means that the existence of any prima facie plausible adaptive interpretation of human behavior is a sufficient counter to anything but a perfect case for a nonadaptive explanation.

Programmatic attacks and burden-of-proof claims can be positively harmful when taken, by themselves, as sufficient substitutes for a sound plausibility argument. We have argued that theory about complex-diverse phenomena is necessarily made up of simple models that omit many details of the phenomena under study. It is very easy to criticize theory of this kind on the grounds that it is incomplete (or defend it on the grounds that it one day will be much more complete). Such criticism and defense is not really very useful because all such models are incomplete in many ways and may be flawed because of it. What is required is a plausibility argument that shows that some factor that is omitted could be sufficiently important to require inclusion in the theory of the phenomenon under consideration, or a plausible case that it really can be neglected for most purposes. Thus, for example, it is not enough to attack a purportedly general plausibility argument with a few special cases, for it is (or ought to be) stipulated that generalized models are always likely to account more or less poorly for many special cases. Contrariwise, the success of genetic fitness maximizing theory in biology cannot be used to defend that generalized model in the face of plausible arguments that cultural evolution is a divergent special case.

It seems to us that until very recently, "nature-nurture" debates have been badly confused because plausibility arguments have often been taken to have been successfully countered by programmatic claims. It has proved relatively easy to construct reasonable and increasingly sophisticated Darwinian plausibility arguments about human behavior from the prevailing general theory. It is also relatively easy to spot the programmatic flaws in such arguments; conventional Darwinian models do not allow for human culture. The problem is that programmatic objections have not been taken to imply a promise to deliver a full plausibility claim. Rather, they have been taken as a kind of declaration of independence of the social sciences from biology. Having shown that the biological theory is in principle incomplete, the conclusion is drawn that it can safely be ignored. Sahlins's (1976) objections to human sociobiology seem to us to have been as much in this tradition as Tarde's (1903—pp. xxi–xxii) very early one. Both arguments ignore that Darwinian plausibility arguments ordinarily contain a serious rationale for accepting their claims despite the unique aspects of the human species. Certainly this is the case with contemporary human sociobiology, and explains why it has attracted support by social scientists like van den Berghe (1979, 1981) who cannot be accused of simpleminded hereditarianism.

5 The Importance of Scientific Pluralism

Jared Diamond (personal communication) has drawn the following useful lesson from his experience as both a physiologist and a community ecologist: In physiology, controversial issues are ordinarily settled quickly by definitive experiments. As a result, debate over contending hypotheses is quite restrained and polite. One or the other contending claim is almost certain to turn out wrong in short order, and any grandiose pronouncements, ad hominem attacks, or similar departures from polite scientific discourse can be held against the loser. As long as scientists know that they can easily be proven wrong by a few critical experiments in the next few years, they will refrain from such departures. In ecology, major controversies last much longer because the issues are more complex and testing contending plausibility arguments is a long-drawn-out affair. The result is that individual claimants are often unlikely to be proven cleanly right or wrong, at least during their own lifetimes. Rhetorical excesses thus cannot be clearly proven as such by the failure of the programmatic claim or plausibility argument to which they are attached, and consequently the motivation to avoid them is reduced.

Perhaps differences between these two disciplines can be understood in terms of Campbell's (1979) general discussion of scientific honesty (see also Beatty's contribution to this volume). According to Campbell, scientists are more honest in their occupational behavior than other professionals, but not because they are morally superior as individuals. Rather, they are careful to present honest work because other scientists are very discriminating consumers. Scientists frequently replicate crucial experiments, and can gain prestige by detecting errors. In a controversy, many members of the community will act as relatively unbiased judges of the acceptability of contending hypotheses because their own work depends on using the correct result—say, to make a more accurate measurement instrument. Such acceptors (to borrow Beatty's term) have an interest in the resolution of the controversy, but not a vested interest in any particular outcome. It seems likely that this mechanism will work much more effectively when controversial issues are resolved quickly, and consumer/acceptors can confidently use secure results in their own work. In the case of evolutionary and ecological problems, ambiguity lasts longer, and consumers may be forced to choose among plausibility arguments, thus coming to have a vested interest in the controversy. The extensive empirical program of the complex-diverse disciplines reduces the incentive to replicate individual experiments directly because they make so small a contribution to the total program.

Campbell (1969, 1986) contributed an insightful analysis of another potentially serious problem in the study of complex-diverse subject matters:

the social complexity of the sciences that study them. Specialization is obviously demanded by complexity and diversity. But there is no guarantee that disciplines will not evolve what Campbell characterized as parochial "tribal" norms and customs that impede scientific progress. His argument is illustrated with reference to the arbitrary disciplinary boundaries, schools within disciplines, and the resulting "ethnocentrism" within the social sciences. Our impression is that the scientific endeavor becomes more prone to "ethnocentrism" as problems become more complex and diverse; certainly evolutionary biology, despite the unifying value of Darwinism, is not immune. As the enforcement of the universalistic norms of scientific discourse weaken, very human motives, such as a desire for collegial relations within one's discipline, a tendency to find that one's extrascientific ideology can be squared one way or another with one's science, career considerations, and a need to economize on information, can easily lead the social structure of science in directions that reduce its collective ability to solve complex-diverse problems. The mental effort of keeping multiple, partly conflicting, plausibility arguments in mind, the ambiguous relationship of these to ideas and norms derived from other roles, and the need to have some knowledge of several unfamiliar disciplines might be psychological motivations that encourage the formation of independent disciplines and schools with little communication between them. Nevertheless, it seems inescapable that complex-diverse subjects demand free communication between specialists and a wide tolerance for the pursuit of temporarily divergent plausibility claims.

Deriving norms from this diagnosis is by no means straightforward. Perhaps new disciplines and new ideas need a measure of isolation, which the development of ethnocentric and sectarian attitudes affords (Campbell, 1985). Beatty's argument in this volume that the pursuit of hypotheses is a useful enterprise is very well taken. On the other hand, unchecked this process can result in a declaration of independence for a mature discipline, such as Sahlins offers for anthropology, which may be wholly harmful. There may be an optimal amount of disciplinary and research program "ethnocentrism" for maximizing scientific progress at any given time.

Nonetheless, we think that the following two norms would, if adopted, improve scientific debate surrounding complex, diverse subjects.

Ad hominem attacks on particular positions and the use of self-serving programmatic claims should be viewed as tacky. Given the deep importance of human behavior to humans, the weakness of the consumer/acceptor mechanism for regulating academic discourse, and the fact of the evolution of "ethnocentric" norms within disciplines, it is utopian to expect that the temptation to behave in such ways will always be resisted, particularly by those who are legitimately pursuing a position. Widespread agreement that

such behavior is moderately offensive is a practical norm perhaps, and might help to further productive debate over real issues.

Scientists should be encouraged to take a sophisticated attitude toward empirical testing of plausibility arguments (Quinn and Dunham, 1983; Diamond, 1986). Folk Popperism among scientists has had the very desirable result of reducing the amount of theory-free descriptive empiricism in many complex-diverse disciplines, but it has had the undesirable effect of encouraging a search for simple mutually exclusive hypotheses that can be accepted or rejected by single experiments. By our argument, very few important problems in evolutionary biology or the social sciences can be resolved in this way. Rather, individual empirical investigations should be viewed as weighing marginally for or against plausibility arguments. Often, empirical studies may themselves discover or suggest new plausibility arguments or reconcile old ones.

6 Conclusion

We confess to being somewhat puzzled by the debate between the "adaptationists" and their critics. We suspect that most evolutionary biologists and philosophers of biology on both sides of the dispute would pretty much agree with the defense of the simple models strategy presented here. To reject the strategy of building evolutionary theory from collections of simple models is to embrace a kind of scientific nihilism in which there is no hope of achieving an understanding of how evolution works. On the other hand, there is reason to treat any given model skeptically. As Kitcher puts it in his contribution to this volume, his criticisms of optimality arguments are not meant as "forlorn skepticism," but rather as helpful "in pinpointing strategies for improving hypotheses about selective pressures and functional significance" (p. 99). Kitcher quite properly and quite explicitly calls attention to the fact that because diversity and complexity are real, the tactics of seeking understanding via simple models is something that must be done with care. No one ought to disagree.

Unfortunately, the critics of "adaptationism" are not always as sophisticated as this; they sometimes seem to want to benefit rhetorically from a programmatic critique that implies scientific nihilism without having to face the real (and extremely unpleasant) consequences of actually adopting it. It may be possible to defend the proposition that the complexity and diversity of evolutionary phenomena make any scientific understanding of evolutionary processes impossible. Or, even if we can obtain a satisfactory understanding of particular cases of evolution, any attempt at a general, unified theory may be impossible. Some critics of adaptationism seem to invoke these arguments against adaptationism without fully embracing them. The problem is that alternatives to adaptationism must face the same

problem of diversity and complexity that Darwinians use the simple model strategy to finesse. The critics, when they come to construct plausibility arguments, will also have to use relatively simple models that are vulnerable to the same attack. If there is a vulgar sociobiology, there is also a vulgar criticism of sociobiology. Perhaps because we have devoted a considerable effort to building a plausibility argument for the novel and sometimes maladaptive role of culture in human evolution, we are very sensitive to the strength of the sociobiologists' plausibility arguments and the weakness of most of the objections to them.

In our opinion, human sociobiology has been a successful research.program because it has made rather good use of the simple models strategy. Its practitioners have taken care to construct sound plausibility arguments and, in the spirit of scientific pluralism, to use the work of social scientists. As pursuers of a somewhat narrow range of plausibility arguments, their work is not above criticism in detail or in general. As befits pursuers, they have usefully driven the fitness optimizing postulate to extremes that are not likely to be ultimately warranted. Less usefully, they have used a burden-of-proof claim to attempt to insulate sociobiology from counterarguments. On the other hand, the attacks on sociobiology are a good source of negative object lessons. The criticism of human sociobiology has far too frequently depended on mere programmatic claims (often invalid ones at that, as when sociobiologists are said to ignore the importance of culture and to depend on genetic variation to explain human differences). These claims are generally accompanied by dubious burden-of-proof arguments. Some critics also show little sense of the importance of scientific pluralism.

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