Sociobiology and the Semantic View of Theories

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The semantic view of scientific theories has been defended as more adequate than the "received" view, especially with respect to biological theories (Beatty 1980, 1981; Thompson 1983). However, the semantic view has not been evaluated on its own terms. In this paper I first show how the theory of sociobiology propounded by E.O. Wilson (1975) can be understood on the semantic approach. I then discuss the criticism that Wilson's theory is beset by the problem of unreliable generalizations. I suggest that this problem results from the use of the model-building strategy in theory. I conclude that the problem is pressing enough to impugn the semantic view as an adequate account of sociobiological theory.

According to proponents of the semantic view of theories, scientific theories function to specify a class of "models," interpretations, or representations of their postulates. The most interesting models are, of course, those that describe actual empirical phenomena, but the task of assessing the adequacy of the specified models to empirical phenomena is separate from, and subsequent to, the specification of the models themselves. By contrast, advocates of the "received" view of theories, a view that emerged from the logical empiricist tradition and that held sway for decades, maintain that a scientific theory should be first understood syntactically, as a set of formal axioms constructed according to a specific set of rules from a well-defined vocabulary of uninterpreted primitive terms, and a set of theorems that could be deduced from the basic axioms. Once the syntactic characterization of a theory had been completed, a semantic interpretation of the syntactic system could be given. This consisted in an assignment of meanings to the non-logical terms that occurred in the axiomatization of the theory. Again, the most interesting interpretations or models of the theory were those that described actual empirical phenomena. Because most scientific theories found in standard scientific textbooks are not presented as interpreted formal calculi, and because it may be doubted that every scientific theory can be formalized (within first order logic), proponents of the semantic view have suggested that the "extrinsic" or semantic characterization of theories is logically prior to their "intrinsic" or axiomatic characterization (Suppes 1967). That is, if we can ask about a given scientific theory, whether or not it can

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be given a standard formalization, we must already have some understanding of what kinds of systems the theory describes. Thus, it is argued, a syntactic characterization of scientific theories is unnecessary; we need only concern ourselves with the theory's semantics, i.e., with the models it specifies.

Theoretical model-building in biology exemplifies the methodology of theory construction advocated by proponents of the semantic view. For example, the optimal sex-ratio theory suggested by MacArthur (1965) and Leigh (1971) proposes a model to account for the nearly universal 50:50 ratio of males and females in natural populations. The model attempts to explain this fact in terms of the relationship between individual fitness and the number of male and female offspring the individual produces, subject to a constraint on the number of offspring an individual can produce. The model consists in the statement that individual fitness varies directly with the product of the number of male offspring, x, and the number of female offspring, y, subject to the constraint that $x + y = k$ (the upper limit to the number of offspring one individual can produce). In this model individual fitness is maximized when $x = y = k/2$, i.e., when equal numbers of male and female offspring are produced. The 50:50 sex ratio is explained as that ratio of offspring that maximizes parental fitness.

The model building approach is fundamental to E.O. Wilson's account of sociobiology. Wilson states that the ultimate goal of sociobiological theory is a "stoichiometry of social evolution...an interlocking set of models that permit the quantitative prediction of the qualities of social organization...from a knowledge of the prime movers of social evolution." (Wilson 1975, p. 63). There are two prime movers of social evolution: phylogenetic inertia and ecological pressure. Phylogenetic inertia includes both the degree of genetic variability of a population and the particular genetic characteristics of its members that predispose them to (or preclude them from) developing a particular trait. The haplo-diploid mode of inheritance of Hymenopterans has been held to have pre-adapted some species of ants, wasps, and bees to eusociality (Hamilton 1972), and is an example of phylogenetic inertia influencing the evolution of social behavior. Ecological pressures are imposed on individuals in the form of biotic and abiotic factors. The most important ecological pressures on the evolution of social behavior include the type and distribution of food sources, and the nature and intensity of predation (Crook 1965).

Once we have information about phylogenetic inertia and ecological pressures provided by research in evolutionary ecology, we can proceed to the construction of the "interlocking set of models" that Wilson regards as the ultimate goal of sociobiology. These models fall within the province of population biology. For example, theoretical population ecology provides quantitative models that describe population growth, survivorship and fertility schedules, age distributions, reproductive effort, the dynamics of population fluctuation and competition, and density-dependent effects on population size, on fertility, and on the spread of disease. Likewise, theoretical population genetics introduces models describing the effects of selection, migration, mutation, genetic drift, linkage, segregation distortion, and random and assortative mating on the genetic structure of an interbreeding group.

The semantic view of theories does accurately describe Wilson's account of sociobiological theory. The models of theoretical population ecology and theoretical population genetics specify the kinds of systems to be studied. Information about the phylogenetic inertia and ecological pressures on particular interbreeding populations constitute the empirical claims that those populations are instances of the kind of system specified by the models.

Predictions about the social organization flow from this interrelated set of models. For example, one model assumes constant rates of birth, immigration, death, and emigration, and predicts patterns of distribution of group size in primate troops (Cohen 1969, cited in Wilson 1975). On Wilson's view group size may be incorporated into a model that predicts the amount or pattern of "connectedness", i.e., the extent to which different kinds of signals are preferentially directed at certain group members. Similarly, patterns of immigration and emigration determine group "permeability", the extent to which members of one society communicate with members of other conspecific societies. Ergonomic theory predicts an optimum mix of individuals of different "castes" or "roles".

A common theme in the critical literature on sociobiology is the failure of the theory to produce reliable generalizations about the evolution of social behavior (numerous authors in Caplan 1978; Kitcher 1985). Indeed, Wilson's strategy for arriving at sociobiological "laws" is to start with the model of social organization developed in connection with his study of insect societies and generalize to a model for the social organization displayed by all social species. "I have been increasingly impressed," he wrote, "with the functional similarities between invertebrate and vertebrate societies and less so with the structural differences that seem, at first glance, to constitute such an immense gulf between them... . This comparison may seem facile, but it is out of such deliberate oversimplification that the beginnings of a general theory are made." (Wilson 1975, p. 5).

This strategy has drawn criticism most frequently when the generalizations are extended to the human species. For example, in discussing the hypertensive, hypersexual, homosexual, and cannibalistic behavior displayed in overcrowded laboratory populations of Norway rats Wilson comments, "Such behavior is obviously abnormal. It has its close parallels in certain of the more dreadful aspects of human behavior... . We must not be misled, however, into thinking that because aggression is twisted into bizarre forms under conditions of abnormally high density, it is therefore nonadaptive." (Wilson 1975, p. 255). Although this flawed methodology is most apparent in such generalizations to human social behavior, it pervades most of Wilson's comparisons among nonhuman species as well. For example, he remarks that caste structure, long recognized as a major feature of social insect colonies, has at last been admitted to characterize nonhuman vertebrate groups as well; "typical" vertebrate qualities, such as improved communication, personal recognition, and increased behavioral modification make the formation of selfish sub-groups within a society possible; the significance of synchronous breeding in African wild dogs is revealed by comparison with a similar phenomenon in army ants -- individuals of both species are forced to be nomadic in search of new food sources, a pattern the least constrained by synchronous development of young.

Such generalizations are likely to be unreliable predictors, because they ignore the possibility that similar consequences may be the result of diverse causes. They will therefore usually fail to be applicable across diverse taxa, whose members experience different ecological constraints, and whose morphology and physiology limit available behavioral responses. Synchronous breeding (spawning) in oysters is keyed to the spring tide; in lions it permits communal suckling, which has been shown to increase the survival rate of cubs; female wild dogs are closely related to the puppies in their pack and thus benefit through increased inclusive fitness from sharing food with young of other individuals; in army ants the necessity of renewing food sources makes a short stationary period -- and thus synchronous breeding -- desirable. Generalizations about synchronous breeding based similar effects, e.g., increased group mobility, are likely to be unreliable unless the morphological, physiological, developmental, genetic, and ecological details of each species in which it occurs are given serious consideration (Horan 1985, 1986).

Wilson's incautious claims about human social behavior have been the target of much of the critical literature on sociobiology. However, I believe that the problem of arriving at reliable sociobiological laws is more profitably located in the model-building approach itself. Let us first see what is involved in a sophisticated model-building approach to scientific theories.

In their searching discussion of the model-building as a tool for understanding complex phenomena such as social evolution Richerson and Boyd (forthcoming) suggest that complex and diverse phenomena, such as those found in the biological world, are better studied through the construction of a large number of simple, rather unrealistic models than by attempts to construct one large model that is complex but realistic. They argue correctly that complex models are often so complex that they are difficult to understand and provide little understanding of complex systems. Complex models are often made to agree with observations by statistical fitting techniques, and so gain predictive success at the cost of explanatory power. The increase in predictive power gained through the use of complex rather than simple models often is too small to justify the enormous increase in time and expense required for their analysis. Unlike populations of atoms, whose behavior is complex but uniform, populations of organisms exhibit behaviors that are complex and diverse. The difficulty of analyzing complex models in physics is usually more than compensated by the robustness of the results; this payoff is not available to the biologist, who must study complex processes in specific populations that are likely to vary significantly in other groups. The best strategy for biologists, they urge, is to construct a variety of simple models that can be completely understood, that focus on the "important" properties of the process under study, and that "reflect how the world actually does work, at least to some approximation." A good simple model will be "robust", that is, it will incorporate enough of the important properties of the phenomenon to enable predictions "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."

The use of simple as opposed to complex models of biological processes does not preclude the formulation of general theory.

Richerson and Boyd argue that from a set of simple models describing specialized cases a "general sample theory" can be culled. A general sample theory is a collection of general models, each of which abstracts the most important features of the larger set of simple models that describes a particular process. The synthetic theory of evolution is, on their view, a good example of a general sample theory. This theory consists of a number of general models, e.g., of natural selection, mutation, migration, and drift, together with models of the interaction of these processes, e.g., of speciation. Each of these general models is itself an abstraction from the collection of simple models that describe particular cases, for example, the operation of natural selection in a particular population subject to specific ecological constraints. The general model of natural selection would attempt to capture the most important features of the operation of natural selection, perhaps the effects of selection on change in gene frequency in Mendelian populations, by neglecting the details of how natural selection acts in this or that particular population. An underlying presumption here is that the complexity and diversity of biological phenomena make concepts like natural selection, mutation, migration, and drift, umbrella-terms, terms that refer not to unitary processes, but to a large number of processes that are similar, yet diverse. A general model of natural selection would thus attempt to capture the common elements of the selective processes reflected in each of the simple models. The general sample theory would combine the elements of each of the general models into a unified predictive and explanatory system.

The elegance and power of sophisticated model-building is indeed appealing. However, I shall argue that the appeal is superficial: the model-building approach to theory formulation cannot guarantee, or even make likely, the attainment of reliable generalizations. The construction of a simple model of the evolution of a trait is a process of abstracting from a complex set of processes a small number of factors regarded as "important", yet also simple enough to be completely understood, both individually and in interaction with other factors of the model. The choice of "important" factors is constrained by the desire that the model be realistic: we would like to pick out the factors that we believe have in fact led to the evolution of a particular trait in a given species. At the same time we would like the model to be robust: it should enable us to predict the presence of the trait in other species. But these two goals are in conflict. For the more realistic (and hence complex) the model becomes, the more tied it will be to the particular case from which it was fashioned. As a consequence of this increased realism, the less robust it will be, since its predictions are likely to be false when applied to other cases.

This tension is well illustrated by hitherto unsuccessful attempts to develop a general sample model of cooperative breeding in birds. As two researchers on this topic have remarked, "More than 100 species of birds share...this pattern of cooperative breeding, but no single set of factors can explain why one species displays the behavior pattern and an apparently similar species does not." (Ligon and Ligon 1982, p. 126). Green woodhoopoes (Phoeniculus purpureus) are east African birds that inhabit acacia woodlands and roost communally at night inside cavities of the acacia trees. A flock of woodhoopoes usually consists of a single breeding pair, and from one to sixteen sexually mature but nonbreeding "helpers", who feed and protect the breeding female and her offspring. Helpers are sometimes, but not always, either siblings of one of the breeders, or offspring of one or both breeding individuals. Annual mortality rate among woodhoopoes can be as great as 40%, with breeding males at substantially greater risk than nonbreeding males and females. Individuals of the same sex usually roost together at night. This means that it is possible for a predator to eliminate most or all of the members of one sex on a territory, and thus for a territory to be recolonized by solitary individuals or by flocks from adjacent territories. Migration to a new territory is dangerous; colonization of a new territory is almost always accomplished by "teams" of two or more individuals of the same sex, sometimes (but not always) by flock mates, but owing to strong antagonism between nest mates, never by siblings of the same brood. Owing to the great mortality rate, "subordinates" in the emigration team almost always have the opportunity to become breeders following the death of the "dominant" member of the team.

Compare this with the breeding biology of Florida scrub jays (Aphelocoma coerulescens), which nest in oak scrub. Scrub jay groups consist of a single breeding pair and the young of one or more previous broods. The breeding female is fed by her mate alone; all others are driven away. Most helpers are close relatives of the breeding pair, being offspring of one or both breeding individuals. The scrub jay habitat is fairly stable, and life span of individual scrub jays is long. Nonbreeding males gain their own breeding territories by subdividing expanded parental territories; colonization of abandoned territories or takeover of territories held by other breeding pairs is rare. Females are not permitted to breed on the parental territory; hence, mortality is greater among females than among males.

How would we go about formulating a general sample theory of cooperative breeding in birds, to say nothing of an even more general theory about cooperative breeding in all species? Woodhoopoes and scrub jays differ in significant respects. According to the model building strategy of Richerson and Boyd, we must begin with the social-ecological correlates peculiar to one species and abstract some general factors that we might regard as capturing the important features of their cooperative breeding behavior. Which of the factors important to scrub jay biology, for example, should we pick out in a simple model? Perhaps, as Emlen (1978) has done, we would say that cooperative breeding occurs in species experiencing severe limitations of roosting or nesting sites and in species inhabiting tropical or neotropical, relatively stable habitats. A model with this assumption would then lead us to predict the absence of cooperative breeding in species inhabiting unstable habitats. But in its attempt to capture the most important factors influencing evolution of cooperative breeding of one species the model would have lead us to a false prediction. For cooperative breeding does occur in woodhoopoes, and their environment is highly variable, owing to fluctuation in timing and amount of rainfall, which in turn has often quite dramatic effects on the moth populations that provide woodhoopoes with their food supply.

Thus, on the one hand, models of cooperative breeding that attempt to be realistic tend to compromise robustness. On the other hand, simple models, because they abstract from the details of the cases they are intended to describe may yield robust results, but to gain robustness is often to sacrifice realism. This problem of loss of predictive power with increasing realism only worsens with the construction of general sample theories from large sets of simple models, for the method advocated by Richerson and Boyd is to continue the process of abstraction, simplification, and neglect of details. Wilson's attempts to suggest general models that would explain homosexuality, aggression, territoriality, and caste systems might indeed be robust enough to reflect patterns of social behavior in species as phylogenetically diverse as insects and human beings. But few think that such robustness by itself indicates that Wilson's explanations are true. Again, the problem is that coincidence of effects is not sufficient warrant for inferring identity of causes.

The model-building approach to theory construction in sociobiology forces us to choose between realism, or explanatory strength, and robustness, or predictive power. Richerson and Boyd acknowledge this dilemma, and opt for explanation: "We would argue...that explanation or understanding is far more fundamental than prediction... ." (Richerson and Boyd forthcoming). But the main goals of sociobiological theory are both to explain the patterns of social behavior that occur in each species and to derive a set of general laws that will predict the evolution of social behaviors across a wide range of taxa. If the model-building approach cannot accommodate these goals, then it must be admitted that the model-building approach is not by itself an adequate method of theory construction. And if this is admitted, it must be acknowledged that the semantic view, which advocates the model-building approach to theory construction, is not an adequate account of the structure and function of sociobiological theory.

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