Special issue on: Evolved Constraints of Cultural Evolution

Evolutionary Psychology and the Generation of Culture, Part I

Theoretical Considerations

John Tooby and Leda Cosmides
Department of Psychology, Stanford University, Stanford, California

Culture is the ongoing product of the evolved psyches of individual humans living in groups. Progress in our understanding of culture as a phenomenon depends on progress in uncovering the nature of the evolved mechanisms that comprise the human psyche, including but not limited to those responsible for learning. Actual attempts to specify information processing mechanisms that could, in fact, perform tasks humans routinely perform have demonstrated that the human psyche cannot, even in principle, be comprised only of a general purpose learning mechanism or any other general purpose mechanism, such as an inclusive fitness maximizer. Instead, the human psyche appears to consist of a large number of mechanisms, many or most of which are special purpose and domain-specific. The output of these mechanisms taken together constitutes the "private culture" of each individual, and the interactions of these private cultures lead to the cross-individual patterns of similarity that have led anthropologists to think typologically of social groups as having "a" culture. The construction of a scientific theory of culture requires as its building blocks specific models of these psychological mechanisms, and so evolutionary anthropology depends on the forging of an evolutionary psychology. The most productive application of evolutionary biology is, therefore, in the study of the psychological mechanisms that generate and shape culture, rather than in the attempt to impose on cultural change too close a parallel to population genetics and organic evolution.

KEY WORDS: Learning; Culture; Sociobiology; Gene-culture coevolution; Mental organs; Evolutionary psychology; Darwinian psychology.

1. INTRODUCTION

The most productive application of evolutionary biology to the question of culture will not ultimately lie in framing cultural change as an evolutionary process parallel to organic evolution. Although there are some parallels, there are many more differences that render the processes nonanalogous (Daly 1982; see also Flinn and Alexander

Received April 1, 1987; revised October 27, 1987.

Address reprint requests to: John Tooby, Department of Psychology, Bldg. 420, Stanford University, Stanford, CA 94305.

Ethology and Sociobiology 10: 29–49 (1989)

655 Avenue of the Americas, New York, NY 10010
0162-3095/89/$03.50

1982). Such interpretive frameworks, while they have produced valuable and provocative results (e.g., Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981; Dawkins 1976, 1982; Durham 1979; Lumsden and Wilson 1981), will be limited in their future development by the far-reaching nature of the differences between cultural and population genetics processes. Nor does it seem most productive to us to consider culture to be an autonomous inclusive fitness-seeking adaptative system, guided by some kind of invisible hand (such as "learning") to embody collections of behavioral "strategies" for maximizing inclusive fitness under present-day conditions (e.g., Irons 1979; Borgerhoff Mulder 1987). We will argue that the promise of the evolutionary perspective lies instead in its power to assist in the discovery, inventory, and analysis of innate psychological mechanisms (for similar, congenial views, see Barkow 1978, 1980, 1984; this issue; Symons 1979, 1987, this issue; Blurton Jones 1976; also, Cosmides and Tooby 1987; Cosmides 1985; Tooby 1985; Tooby and DeVore 1986). By directly regulating individual behavior and learning, these mechanisms directly govern cultural dynamics; the key to understanding cultural processes must therefore lie in the discovery and subsequent mapping of the properties of these complex and specialized psychological mechanisms.

Evolutionary biology provides the crucial missing element that will allow psychologists to discover the design of the innate psychological mechanisms that exist in humans (Tooby 1985; Cosmides, 1985; Cosmides and Tooby 1987). In our view, evolutionary biology is best used as an heuristic, providing models of the adaptive problems the psyche had to be able to solve, and providing models of the conditions within which these mechanisms had to solve these adaptive problems: Pleistocene conditions. The evolutionary approach thus has implicit within it a new and more powerful method for psychologists, which dovetails smoothly with methods forged within an increasingly sophisticated cognitive psychology: Natural selection defines information processing problems the organism must be able to solve (in a given adaptive context), and cognitive psychology now has methods available to assist in discovering what algorithms exist in the psyche to solve these problems. Application of these methods will allow the exploration of the design features of innate human psychological mechanisms, including the design features of those learning mechanisms that create and maintain cultural phenomena, as well as those mechanisms that by shaping behavior must be accommodated by cultural phenomena. Until this mapping is done, both "learning" and "culture" will remain what they are now: phenomena to be explained, instead of (as many social scientists hostile to evolutionary approaches suppose) alternative explanations to evolutionary hypotheses.

2. THE EMERGING OUTLINES OF EVOLUTIONARY PSYCHOLOGY

After several false starts in the century following Darwin (Ghiselin 1973), there are signs that a truly evolutionary psychology is finally beginning to

coalesce. A small but growing minority of psychologists have been applying an evolutionary perspective to psychological problems with increasing success, based on the Darwinian premise that psychological phenomena are, above all, biological phenomena, and, as products of the evolutionary process are explicable using the same conceptual tools that have illuminated the other branches of evolutionary biology. Among many others, psychologists whose research has been informed by modern evolutionary considerations include Bowlby, Blurton Jones, Buss, Daly and Wilson, Erickson, Garcia, Rozin, Shepard, and Staddon (see, e.g., Blurton Jones 1976; Bowlby 1969; Buss 1985; Daly and Wilson 1984; Erickson and Zenone 1976; Garcia et al. 1973; Rozin 1976; Rozin, in press; Shepard 1984, 1987; Seligman 1972; Staddon 1979).

Although for many years psychology has made at least marginal use of Darwinian insights, until recently several obstacles (aside from unfamiliarity with evolutionary biology) have prevented psychologists from implementing a fully Darwinian research program. These obstacles have been the absence of several necessary elements, all of which must be present and combined systematically for an evolutionarily oriented psychology (or, in fact, any psychology) to succeed. Several recent developments in evolutionary biology and psychology, however, lead us to believe that all of the elements are now available and can be assembled into a powerful research program for psychology, and are in fact often nascently present in the work of those listed above, as well as many others working in allied fields, such as Symons (1979, 1987) and Chomsky (1957, 1959, 1975, 1980).

In our view, the indispensable elements of a successful psychological research paradigm—the centerpiece of any biological approach to human behavior—include a recognition of the following:

> 1. In addition to whatever domain-general mechanisms may exist, the psyche is almost certainly comprised of a multitude of domain-specific, special-purpose adaptative mechanisms, organized into a coevolved, highly intricate architecture. Despite a widespread prejudice among psychologists to the contrary, evolutionary considerations render it highly implausible that the psyche consists of a single or small number of domain-general general purpose mechanisms or processes (Cosmides and Tooby 1987). Even where lip service is paid to the concept of special purpose mechanisms, it is difficult to find much actual research into them. In order to make progress, psychologists must discard the unrealistic assumption that every act, capacity, or phenomenon is governed by or is the expression of a few underlying general laws, processes, or mechanisms. This search for unity of psychological process, borrowed from physics, is wholly inappropriate to biological phenomena, and has led psychologists to impose artificial categories on and seek unified explanations for wildly disparate phenomena. To the extent that the demands of different adaptive tasks are different in nature, and more efficiently solved using different means, psychological mechanisms will tend, over evolutionary time, to multiply in number and differentiate in procedure. Not only have social scientists been all too inclined to think of the mind as a general purpose computer, but even evo-

lutionarily informed scholars have been susceptible to a similar species of error: Instead of a general learning mechanism, evolutionary biologists have used the concept of the psyche which operates "as if" it were an inclusive fitness maximizer. Not only is this hypothetical entity impossible even in principle (Cosmides and Tooby 1987), but as a conceptual tool it has interfered with productive research directions (Symons, this issue; Kitcher 1985; Cosmides and Tooby 1987).

2. Psychological research needs to pay attention to function. Although this is surely uncontroversial, it is surprising how often serious inquiry into functional significance and functional design is neglected. The advances in modern evolutionary biology can give rich and specific content to the concept of function for psychologists. Although the functional significance of various systems is sometimes relatively straightforward (e.g., visual perception), in other cases it is not, and all too often the theories and evidence concerning the structure of Pleistocene selection pressures (which define functionality for humans) are completely unfamiliar to psychologists. Considerations drawn from evolutionary biology can be used to carve the world along "natural" lines into functional subsets or adaptive problems, which can then be matched to the domain-specific mechanisms that evolved to solve them.

3. Research emphasis needs to shift away from the description and analysis of behavior—even in adaptive terms—to the discovery and characterization of psychological mechanisms as adaptations. Although the study of behavior is essential, because it is the consequences of behavior that selection acts on, the study of behavior is only a first step, useful as a means to a more important goal: the investigation and characterization of the innate psychological mechanisms that generate and regulate behavior (Tooby 1985; Cosmides and Tooby 1987; Daly and Wilson 1984; see especially, Symons, this issue).

4. Models of psychological phenomena need to be expressed in an algorithmic, procedural form, or at least as structured and well-specified "cause and effect" models, instead of in vague, qualitative descriptions, or as patterns found in behavior. Fortunately, the rise of cognitive science has provided a host of powerful new modeling tools. Because the adaptive regulation of behavior so often depends on information, it appears likely that cognitive and information processing models will be the most natural and convenient level of explanation for evolutionary psychology (Cosmides and Tooby 1987). The language of cognition provides an economical and powerful language for describing the design of proximate mechanisms viewed as adaptations—that is, for describing in precise terms what such mechanisms do in solving adaptive problems, and how they operate procedurally—without becoming entangled in the immensely intricate and largely unknown area of their neurological and physiological basis. When researchers appreciate that effective functional description of mechanisms need not require physiological research, or await advances in neuroscience, the widespread reluctance to describe proximate mechanisms (in favor of noting adaptive patterns in behavior) may begin to evaporate.

5. Finally, evolutionary biology provides the missing framework to weave these elements together: It gives a precise meaning to function (fitness promotion); it indicates what functions (adaptive problems) must be solved by the psyche to promote fitness; through identifying adaptive problems, it carves the universe of tasks into functional subsets, thereby defining the domain each psychological mechanism is adaptively specialized to deal with; it weights the relative importance of the accomplishment of various tasks; it provides comparative information allowing investigations of phylogenetic constraint; it can often provide some information on how long and how strongly selection pressures of a certain kind have been operating on a species; it identifies the biological (and hence functional) meaning of various stimuli, events, and situations; and so on. Recognizing that the psyche is the product of evolution, and that it represents a collection of solutions to adaptive problems, allows the belated identification of psychology as a branch of evolutionary biology.

Because all of these necessary elements have been brought together only rarely, progress in psychology has been fitful. It is interesting to note that, where genuine progress has been achieved, it has been achieved in proportion to how closely the research strategy used has corresponded to the program outlined here. Although detailed knowledge of evolutionary biology has been rare among psychologists, psychologists (and allied researchers) who have attacked problems from a functional, cognitive, and domain-specific perspective have done well. Where function is relatively straightforward, as in language and perception, the lack of a strong evolutionary orientation is not a serious handicap. In fact, these two fields can be differentiated from much of the rest of psychology by their relative success. Behavioristic attempts to assimilate verbal behavior into general laws of learning proved to be a failure, while Chomsky's emphasis on the necessary existence of innate, special purpose mechanisms with their own unique and functional characteristics revolutionized psycholinguistics (Chomsky 1957, 1959, 1975, 1980). Similarly, the field of perception has been peculiarly successful throughout the history of psychology because early investigators established a research tradition with a clear-cut notion of function, clear-cut domains of special purpose functionality (color perception, depth perception, boundary perception, location of sound sources, etc.), and no urge to impose on their models of the various perceptual processes the constraint that the individual mechanisms operate only according to general laws of mind. Both fields have especially progressed since the emergence of cognitive models, sometimes with striking results, such as Marr's work on vision (1982). It is also not accidental that influential researchers in these fields, such as Chomsky (1975, 1980), Shepard (1984, 1987), and Marr (1982), have been sympathetic to evolutionary considerations.

Although evolutionary psychology is in its embryonic stages, we hope and expect that its growth will eventually replace the welter of conflicting middle-range psychological theories and the wealth of descriptive information with a series of models of the innate mechanisms that comprise the human psyche.

In doing so, it will clearly have to accommodate cultural phenomena. The assorted phenomena grouped under the single term "culture" lie at the center of human life, and hence any comprehensive psychology will have as its centerpiece models of the mechanisms that create, sustain, and modify culture or cultural phenomena. Even though evolutionary psychology is in

its infancy, however, some conclusions can be drawn about the contributions that evolutionary psychology might make to a theory of culture.

3. HUMAN PSYCHOLOGICAL MECHANISMS ARE COMPLEX AND FREQUENTLY SPECIAL PURPOSE, AND HENCE EVOLVE SLOWLY COMPARED TO CULTURAL CHANGE

Recent research in artificial intelligence has revealed that mechanisms to solve even supposedly simple cognitive tasks require very complex "innate" or pre-specified procedures and/or information to be effective (for review, see Boden 1977; also, on the "frame problem," see Fodor 1983; Brown 1987). Thus, most or all innate psychological mechanisms (dubbed "mental organs" by Chomsky [1975, 1980]) can be expected to be quite complex in their properties and "design." Clinical and experimental neuroscience, despite initial theoretical biases to the contrary, has not been able to avoid the flood of evidence that the human nervous system is comprised of a very large number of complex special purpose mechanisms (e.g., Gardner 1975).

In consequence, it is not plausible to expect mental mechanisms to evolve very quickly (though simple single-step modifications in their operation could evolve reasonably quickly). It is no more plausible to believe that whole new mental organs could evolve since the Pleistocene—i.e., over historical time—than it is to believe that whole new physical organs such as eyes would evolve over brief spans. It is easily imaginable that such things as the population mean retinal sensitivity might modestly shift over historical time, and similarly minor modifications might have been made in various psychological mechanisms. However, major and intricate changes in innately specified information-processing procedures present in human psychological mechanisms do not seem likely to have taken place over brief spans of historical time.

4. HUMAN PSYCHOLOGICAL MECHANISMS ASSUMED THEIR PRESENT FORM ADAPTING TO PLEISTOCENE CIRCUMSTANCES, NOT MODERN CONDITIONS

For these and other reasons, the complex architecture of the human psyche can be expected to have assumed approximately modern form during the Pleistocene, in the process of adapting to Pleistocene conditions, and to have undergone only minor modifications since then. The hominid penetration into the "cognitive niche" involved the evolution of some psychological mechanisms that turned out to be relatively general solutions to problems

posed by "local" conditions (Tooby and DeVore 1987). The evolution of the psychological mechanisms that underlie culture turned out to be so powerful that they created a historical process, cultural change, which (beginning at least as early as the Neolithic) changed conditions far faster than organic evolution could track, given its inherent limitations on rates of successive substitution. Thus, there is no *a priori* reason to suppose that any specific modern cultural or behavioral practice is "adaptive" (Symons 1979, 1986, this issue; Barkow 1978, this issue) or that modern cultural dynamics will necessarily return cultures to adaptive trajectories if perturbed away. Adaptive tracking must, of course, have characterized the psychological mechanisms governing culture during the Pleistocene, or such mechanisms could never have evolved; however, once human cultures were propelled beyond those Pleistocene conditions to which they were adapted at high enough rates, the formerly necessary connection between adaptive tracking and cultural dynamics was broken. Thus, adaptive tracking need no longer characterize modern cultural dynamics, though it seems probable that there has been enough continuity that many components of modern cultural dynamics do function to modify cultures in adaptive directions. Although post-Neolithic human population growth indicates that at least some dimensions of adaptation have been extremely successful over historical time (such as food production and disease prevention), there is no reason to suppose that this is generally true for all or even most domains of adaptation, including such important aspects as optimizing number of offspring, kin-directed assistance, or participation in coalitional competition for resources—social phenomena of central theoretical interest. A wide variety of modern practices suggest that many human psychological mechanisms have been pushed by rapidly changing circumstances outside the envelope of Pleistocene conditions within which they evolved and could be expected to produce adaptive results. Human behavior can be meaningfully divided into a series of domains functionally defined by the psychological mechanisms that govern them, and modern human behavior within many of these domains appears to be widely at variance with what is fitness-promoting under modern conditions (see especially the discussion in Symons [n.d.] on how a world composed of true inclusive fitness maximizers would be unrecognizably different from the world we inhabit). Examples are easy to multiply: The initiation or voluntary participation in modern war by Germans, Japanese, Russians, North Koreans, Cambodians, Argentinians, Iraqis, or Americans, or their elites, do not seem to have enhanced the fitness of those involved). Although natural selection should slowly tend to act to correct these deviations, there are many reasons to believe that these "corrective" selective forces are far too slow in their operation and weak in their magnitude to significantly reduce these shifting disparities: History and modern cultural change are simply too fast, compared to the evolutionary process.

5. EVOLUTIONARY PSYCHOLOGY PROVIDES THE NEEDED CAUSAL AND EXPLANATORY BRIDGE FROM EVOLUTIONARY THEORY TO MANIFEST BEHAVIOR

There has been a trend among evolutionarily sophisticated behavioral scientists (who are making otherwise very valuable contributions, such as Alexander [1977, 1979]; Irons [1979]; Dickemann [1979], and many others) towards viewing the evolutionary approach as consisting of the direct leap from adaptive expectation to modern manifest behavior (e.g., are humans in Idaho maximizing their inclusive fitness?). Not only does this narrowly limit the scientific program to the cataloguing of correspondences between evolutionary theory and observed behavior, but even this circumscribed program goes astray to the extent that our innate psychological mechanisms are tuned to our ancestral conditions and not to our modern world.

However, one does not have to believe that natural selection is powerful enough to keep modern human culture and behavior tightly adaptive, to believe that the evolutionary approach provides the crucial elements necessary to forge an authentically scientific behavioral science. The hope of those who would leap from evolutionary expectation to modern behavior is that evolutionary theory itself provides the necessary powerful generalizations about human behavior (e.g., humans display kin selected altruism towards kin): that evolutionary theory constitutes the theory of human behavior. The evolutionary psychological program suggests, instead, that human universals and powerful generalizations exist at the level of the functionally described psychological mechanism, and that evolutionary theory and patterns discerned in modern behavior are important primarily because they are sources of information about the functional structure of these mechanisms, shaped as they were by the evolutionary process. *In short, evolutionary theory does not itself constitute a theory of human nature: Instead, it is a theory of how human nature came to be, and an invaluable tool in the campaign to discover what human nature actually is.*

Thus, an example of research that has, in our judgment, taken the first few steps down the right road is Wolf's (1970) and Shepher's (1971, 1983) work on the negative sexual imprinting mechanism that leads to sexual avoidance between individuals who were raised together as children. Rather than stopping with the generalization drawn from evolutionary expectation that humans should avoid mating with close kin, and matching expectation to observed conduct (do people avoid incest?), it is more powerful to discover the approximate functional outlines of the various psychological mechanisms that contribute to incest avoidance (e.g., determining types of exposure; necessary duration; age of exposure; strength of the effect, sex differences, principles of categorization and generalization). Just as in studies of the acquisition of grammar, errors (maladaptive behaviors such as avoiding sex with non-kin from the same Kibbutz creche) can be as informative or more

informative than adaptive behaviors in deducing the properties of psychological mechanisms.

Evolutionary psychology provides the missing link between evolutionary theory and manifest behavior (Cosmides and Tooby 1987). Evolutionary processes are what have shaped the innate psychological mechanisms that are inherited from one generation to the next, whereas the resulting structure of these mechanisms governs manifest behavior within a generation. Innate psychological mechanisms are, after all, what actually causally link evolutionary processes and observed behavior, and are therefore—implicitly or explicitly—necessarily the focal point of any evolutionary analysis of behavior. Expectations of adaptation predict behavior only approximately and do not appear to lead further than the characterization of modern behavior as either adaptive or maladaptive, i.e., as consistent with expectations derived from fitness maximization models or inconsistent with them. On the other hand, knowledge of the innate psychological mechanisms that actually produce behavior should predict behavior far more closely, even in modern cultures, and would provide a unified core of models that could assimilate into common regularities phenomena drawn from anthropology, history, social psychology, sociology, and so on. Such a set of models would constitute a genuine knowledge of human nature.

Attempts to finesse a precise characterization of this functional level have led to a series of roadblocks in the application of evolutionary biology to behavior (Cosmides and Tooby 1987). For example, because the causal chain by which evolution influenced behavior was left vague and unspecified, this approach led to the widespread confusion that hypotheses about economics, culture, consciousness, learning, rationality, social forces, and so on, necessarily constituted distinct alternative hypotheses to evolutionary or "biological" explanations (see Harris 1979; Sahlins 1976a,b). This kind of confusion has persisted even among many within the evolutionary community, but more importantly, it has left most of those outside of the evolutionary community convinced of the primacy of nonevolutionary explanations and with the impression that evolutionary explanations are *ad hoc*, uninformative, "just so" stories with little of value to contribute to their own research.

Using evolutionarily informed methods to recover properties of psychological mechanisms (what we call elsewhere "Darwinian algorithms"; Cosmides 1985; Cosmides and Tooby 1987) allows a powerful new level of validated modeling—one that is not confounded by post-Pleistocene circumstances. Once the structure of these innate mechanisms is elucidated, modern behavior can be analyzed. By feeding modern conditions (economic, cultural, social, etc.) as parameters into these algorithms, modern behavior can then be both predicted and understood—not simply as adaptive or maladaptive, but as a consequence of the structure of the mechanisms that regulate behavior and the modern conditions that are their input.

Although specific modern behavior may or may not be *adaptively pat-*

terned, both modern and past behavior is *evolutionarily patterned*, and can only be understood by being placed in an evolutionary framework. Adaptive patterning and evolutionary patterning are only synonymous within Pleistocene conditions, and so it is the modeling of evolutionary processes within Pleistocene conditions that constitutes the framework within which human psychological mechanisms—both those that create culture and those that are relatively independent of culture—can be meaningfully investigated.

6. THE DISCOVERY AND MODELING OF INNATE HUMAN PSYCHOLOGICAL MECHANISMS REQUIRES THE DEVELOPMENT OF "COMPUTATIONAL THEORIES"

Discovering the structure of complex cognitive programs requires a great deal of theoretical guidance. In their pioneering studies of visual perception, Marr and Nishihara (1978; Marr 1982) argued that "computational theories" of each information processing problem must be developed before progress can be made in experimentally investigating the cognitive programs that solve them. A computational theory specifies the nature of an information processing problem. It does this by incorporating "constraints on the way the world is structured—constraints that provide sufficient information to allow the processing to succeed" (Marr and Nishihara 1978, p. 41). A computational theory is an answer to the question: What must happen if a particular function is to be accomplished?

For example, the information processing problem that Marr and Nishihara wanted to understand was how an organism reconstructs three-dimensional objects in the world from a two-dimensional retinal display. To do this, they first examined relevant constraints and relationships that exist in the world, such as the reflectant properties of surfaces, because these constraints must somehow be used by and embodied in any cognitive mechanism capable of solving this particular problem. The specification of such constraints, together with their deductive implications, constitutes the "computational theory" of an information processing problem.

Note that it does not contribute materially to an understanding of either visual perception or any larger issues to either invoke "learning," or to state that human perception operates "as if" perception were maximizing inclusive fitness, or even to show that blinded animals have lower fitness than healthy ones. Instead, evolutionary concepts play a far more useful role through assisting in the construction of a model of the adaptive mechanism: We know that the ability to recover such three-dimensional information about the world from the retina is the product of evolution, and hence must depend on relationships between features of the world and the visual properties of objects *that have been stably associated during the evolution of the visual system*. Thus, to begin with, evolutionary considerations allow

the researcher to identify and isolate the relevant evolutionary recurrent features of the social or physical environment, investigate their interrelationships, and to link these to the goal or function of the processing.

Natural selection theory, when applied to behavior, defines information processing problems. That is exactly what a computational theory is: the definition of an information processing problem. Natural selection theory allows one to develop computational theories for adaptive information processing problems, because for humans, an evolved species, natural selection in a particular ecological situation defines and constitutes "valid constraints on the way the world is structured." The instantiation of these constraints is a cognitive program's adaptive function.

For example, the cognitive programs of an organism that confers benefits on kin evolves within the [Cost to self $<$ (Benefit to kin member) $\times$ (relatedness to kin member)] constraint of kin selection theory. Cognitive programs regulating behavior towards kin that significantly and systematically violate this constraint cannot be selected for. Cognitive programs that instantiate this constraint can be selected for. A species may lack the ability to confer benefits discriminatively on kin, but if it has this ability, then it has it by virtue of cognitive programs that respect this constraint.

The specification of constraints imposed by the evolutionary process does not, in itself, constitute a complete computational theory. These constraints only define what counts as adaptive behavior. Cognitive programs are the means by which behavior—adaptive or otherwise—is produced. The important question for a computational theory to address is: What kind of cognitive programs must an organism have if it is to behave adaptively?

An organism's behavior cannot fall within the bounds of the constraints imposed by evolutionary theory unless it is guided by cognitive programs that can solve certain information processing problems that are highly specific. For example, an organism cannot confer benefits on kin in accordance with the constraints of kin selection theory unless it has cognitive programs that allow it to extract certain specific information from its environment: What are reliable cues indicating who its relatives are? Which kin are close and which distant? What are the costs and benefits of an action to itself? To its kin? What is the proper "coefficient of altruism" to use in judging when to incur a cost to self to confer a benefit on kin? The organism's behavior will be random with respect to the constraints of kin selection theory unless 1) it has some means of extracting this information from its environment, and 2) it has well-defined decision rules that use this information in ways that instantiate the theory's constraints. It is the ability to perform these specific information processing tasks that ties the organism's behavior to the vicissitudes of the real world; it is the ability to perform these specific information processing tasks that generates adaptive behavior.

The specific information processing problems entailed by the constraints of natural selection theory are the most essential part of the computational theory. They should be made explicit, for they are the building blocks of

psychological theories. Knowing, for example, that an organism must have some means of distinguishing kin from non-kin may not uniquely determine the structure of a cognitive program, but it does help narrow hypotheses. The cognitive program responsible must be sensitive to environmental cues that correlate with kin, but do not correlate with non-kin. In most cases, the researcher will find that very few cues from the species environment of evolutionary adaptedness would adequately specify this information. Second, *a hypothesized system of cognitive programs must be powerful enough to realize the computational theory*. In other words, it must be powerful enough to produce adaptive behaviors while *not* simultaneously producing maladaptive behaviors. Not just any cognitive program will do: Our cognitive programs must be constructed such that they somehow lead to the adaptive results specified by evolutionary theory.

For example, most traditional models of learning used in anthropology and psychology (e.g., operant conditioning, domain general cognitive mechanisms [Rindos 1986], Sahlins' "symbolic logic" [1976a] or symbol manipulation constrained only by syntactic rules, or "generalized" learning capacity—whatever that may mean) are not powerful enough to guide behavior efficiently along adaptive paths, and so can be ruled out as candidate hypotheses governing, among other things, cultural learning. Perhaps the most famous example of using a computational theory to rule out hypotheses took place in the early days of cognitive science, when Chomsky (1957, 1959), through formal analysis, demonstrated that operant conditioning as a "finite state grammar" could not, in principle, account for human language learning, because it did not have the necessary power.

7. THE METHOD OF EVOLUTIONARY PSYCHOLOGY

The emergence of a method for evolutionary psychology has been made possible by the simultaneous maturation of evolutionary biology, our knowledge of Pleistocene conditions, and cognitive psychology, and these taken together allow the principled investigation of the innate mechanisms of the human psyche. We propose that they be combined according to the following guidelines:

1. Use evolutionary theory as a starting point to develop models of adaptive problems the human psyche had to solve.

2. Attempt to determine how these adaptive problems manifested themselves in Pleistocene conditions, insofar as this is possible. Recurrent environmental features relevant to the adaptive problem, including constraints and relationships that existed in the social, ecological, genetic, and physical situation of early hominids should be specified; these constitute the conditions in which the adaptive problem arose, and indicate the informational resources available to solve the problem. Such features and relationships constitute the only environmental information available to whatever cognitive program evolved to solve the adaptive problem. The structure of the cognitive program must be such that it can guide behavior along adaptive paths given only the information available to it in these Pleistocene conditions.

3. Integrate the model of the adaptive problem with available knowledge of the relevant Pleistocene conditions, drawing whatever valid and useful implications can be derived from this set of constraints. Catalog the specific information processing problems that must be solved if the adaptive function is to be accomplished.

This constitutes a computational theory of the adaptive information processing problem. The computational theory is then used as an heuristic for generating testable hypotheses about the structure of the cognitive programs that solve the adaptive problem in question.

4. Use the computational theory to a) determine whether there are design features that *any* cognitive program capable of solving the adaptive problem must have, and b) develop candidate models of the structure of the cognitive programs that humans might have evolved to solve the adaptive problem. Be sure the model proposed is, in principle, powerful enough to realize the computational theory.

5. Eliminate alternative candidate models with experiments and field observation. Cognitive psychologists have already developed an impressive array of concepts and experimental methods for tracking complex information processing systems—these should be used to full advantage. The end result is a validated model of the cognitive programs in question, together with a model of what environmental information, and other factors, these programs take as input.

6. Finally, compare the model against the patterns of manifest behavior that are produced by modern conditions. Informational inputs from modern environments should produce the patterns of manifest behavior predicted by the model of the cognitive programs already developed.

The desire to leapfrog directly from step one to step six must be resisted if evolutionary biology is to have any enduring impact on the social sciences.

For one example of the application of this method, see Cosmides (1985) and Cosmides and Tooby (this issue).

8. NEGLECTING EVOLUTIONARY PSYCHOLOGY IN FAVOR OF TRADITIONAL ANTHROPOLOGICAL APPROACHES TO CULTURE RESULTS IN OVERDRAWN PARALLELS BETWEEN POPULATION GENETICS AND CULTURAL DYNAMICS

Traditional anthropology has operated on the usually implicit assumption that there is a single global learning process responsible for culture, and this metatheoretical assumption has been imported, unexamined, into some of

the evolutionary approaches to culture that have appeared. A simple transmission dynamics for culture depends for its validity on the existence of such a single general learning mechanism. Ignoring the complex structure of human learning mechanisms, and believing learning to be a simple and straightforward process, the details of which can be safely neglected, has resulted in too much autonomy being attributed to the cultural transmission process.

The maintenance and widespread acceptance of the idea that culture "learning" is a unitary phenomenon is a consequence of the scientific void that has existed at the center of traditional anthropology; this void is the failure to develop an adequate model of the psychological mechanisms that create, shape, maintain, and modify culture. Anthropology has been left in the position of studying the results of a process, without ever focusing on the causal process responsible for the properties of their objects of study. Given the clear nature of the scientific problem that confronted them, it is difficult to account for this failure to investigate what is, in causal terms, the structural center of anthropological phenomena. Although it is not addressed in quite these terms, this neglect has constituted a consciously articulated and, in fact, dominant position that has been vigorously defended from the inception of anthropology and sociology by many of its most influential scholars, such as Durkheim (1938) and Kroeber (1917). Unluckily for the emerging community of social scientists, Durkheim had only a hazy layman's grasp of how the natural sciences were actually conducted, and he was not sophisticated in his understanding of the philosophy of science. In his *Rules of the Sociological Method*, he argued that just as chemistry was purportedly unconnected with physics, sociological phenomena were causally unconnected to psychological phenomena, and that accordingly sociological phenomena should be studied independently of and without reference to human psychology. This and related arguments about the insulated and "superorganic" nature of culture are widely taught and repeated as basic principles of the standard anthropological outlook.

Because the study of culture until recently has been the exclusive domain of anthropologists, evolutionarily oriented researchers wishing to examine the same phenomena have been forced to adopt standard anthropological terminology and perspectives. This process has been inevitable, yet has resulted in the inclusion of an entire array of unexamined or little examined assumptions, which have sometimes guided evolutionary approaches to culture in inappropriate directions. Often, even when these assumptions are explicitly examined and explicitly rejected, they have so deeply interpenetrated the study of culture that they remain tacitly influential in setting the terms of discussion. Ironically, some of these assumptions have tended to exaggerate the parallels between cultural dynamics and population genetics.

A few of the most important of these assumptions are listed below. We would claim that although there are elements of truth in them, they are all in serious need of restatement and amendment.

1. Particular human groups are properly characterized typologically as having "a" culture, which consists of nearly universal behavioral practices. (Although "deviation" from the "norm" and other acknowledgments of variation do exist, nevertheless, the common anthropological method of getting an informant to describe what "the" custom "is" is an indicator of how deeply rooted typological thinking is when applied to culture.)
2. These common practices are maintained and transmitted "by the group."
3. Unless other factors intervene, the culture, like the gene pool, is accurately replicated from generation to generation.
4. This process is maintained through learning, a well-understood and unitary process, which acts to make the child like the adult of his culture.
5. This process of socialization is imposed by the group on the child.
6. The individual is the passive recipient of his culture, and is the product of his culture.
7. The features of a particular culture are the result of emergent group level processes, whose determinants arise at the group level and function as a superorganic process divorced from the psychology of individuals.
8. In discussing culture, one can safely neglect consideration of the psychological basis of the capacity for culture as anything other than the nondescript "black box" of learning. Learning is a sufficiently specified and powerful explanation, and is the proper investigation of psychologists rather than anthropologists anyway.
9. Innate aspects of human behavior are negligible, having been superseded by the capacity for culture, leading to a flexibility in human behavior that belies any significant "instinctual" or innate component (e.g., Montagu 1968, p. 11; Sahlins 1976a,b). As Rindos (1986, p. 315) puts this view, "the specifics that we learn are in no sense predetermined by our genes."

Although evolutionarily sophisticated readers at once recognize that many of these ideas, when they are made explicit, are wrong or at least suspect, some aspects of these traditional anthropological ideas are congenial to a population genetics analogy, and hence have not been as fully scrutinized as they might be. Space prevents a detailed discussion of each of these assumptions, so discussion will be restricted to those that have contributed to the analogy between culture and population genetics.

In genetic transmission, the simple Mendelian laws have their origin in the tightly structured system of cytogenetic and sexual processes: linear DNA organized into chromosomes in a diploid system with meiotic division and sexual recombination. These simple and elegant features of the diploid genetic system give population genetics its clear analytic structure. Cultural transmission, when it is analogized to genetic transmission, has not been so firmly grounded in the procedurally far more complex psychological mech-

anisms that underlie it, and instead many of the standard anthropological beliefs about cultural transmission and social learning have been adopted.

An individual is the "passive recipient" of his genes—the often random sample of his deme. When the gametes fuse, the resulting individual has a fixed and unchanging genotype for his entire life, equally constraining his phenotype and his contribution to the genotypes of his offspring. The human is not, however, the passive recipient of his culture, and his individual behavior is not a passive collection of elements randomly combined out of elements maintained in the group. The psychological mechanisms of an individual choose which behaviors observed in surrounding individuals will be adopted, which will be rejected, which will be newly created to fill a need, and they additionally determine how these elements of different origin will be integrated. These choices will be made according to the evolved algorithms of the relevant psychological mechanisms (as activated by personal circumstances and available information). Genes, on the other hand, cannot be filtered, cannot be chosen, cannot be discarded, and cannot be repeatedly changed during the course of one's life. One cannot drop one's own genotype and instead construct a wholly new genotype when circumstances make it necessary.

In cultural processes there is no single, clearly structured parallel to the cytogenetic processes that create Mendelian patterns of transmission; what functions in their stead is a collection of a large number of mechanisms with separate, sometimes overlapping domains, which interact, and which are also integrated into a self-organizing architecture. A hypothetical genetic system whereby genes were created and destroyed, and where genes at different loci were adapted or transmitted in different fashions, at different times, with different probabilities, and in a complex dependency with the particular genes that happened to exist at different loci, would be simple in comparison.

Three of the traditional anthropological outlooks listed above have in particular led to an overemphasis on the parallels between cultural change and genetic evolution: 1) the individual is the passive receptacle of fixed culture traits, 2) culture is a group level phenomenon and process, and 3) the nature of the mechanisms in individuals that underlie culture can be safely neglected. In contrast, an evolutionary psychological approach would suggest that:

1. *Evolution could not have produced a psyche that functioned as the passive receptacle of information transmitted from the social group, because (among other reasons) many members of the social group have antagonistic interests.* Instead, the psyche evolved to generate adaptive rather than repetitive behavior, and hence critically analyzes the behavior of those surrounding it in highly structured and patterned ways, to be used as a rich (but by no means the only) source of information out of which to construct a "private culture" or individually tailored adaptive system; in consequence, this system may or may not mirror the behavior of others in any given respect.

2. *The individual is primary:* Patterns of shared behavior and interindividual influence (i.e., "culture"), while they clearly exist, themselves require explanation in individual-level and evolutionary terms. Group level cultural and social phenomena, while they have some emergent properties, are the consequence of the operation of evolved psychological (and morphological) mechanisms functioning in individuals who evolved to live in groups. The group and properties of the group are themselves evolved consequences, rather than prior phenomena that require no explanation. In marked departure from commonplace anthropological thought, an evolutionary perspective indicates that the group level of characterization (e.g., customs, social solidarity, social structure, etc.) does not have explanatory priority or ontological primacy. For example, constructing group level phenomena out of individual links in a social network allows the integration of the principles of conflict and cooperation that the evolutionarily oriented are already comfortable with and knowledgeable about, e.g.:

- Because individuals are not clonally related, social groups will be arenas of conflict and cooperation.
- Where interests conflict, there is no "best solution" or adaptive culture for all.
- The shared features of culture are the outcome of negotiating individuals.
- Differential power or the ability to influence shared or common cultural elements is not just the property of ruling classes, but is rather a constant feature of almost every interaction between individuals (e.g., even infants have influence over parents [Trivers 1974]). Psychological mechanisms have evolved to shape and shade social outcomes in what would have been in the Pleistocene self-interested directions (in the biological sense), and accordingly all individuals present will contribute in some measure to the outcome.
- Different social contexts will manifest different arrays of individuals, and so different social contexts will tend to have different local or situation-specific "cultures" (the home or family will have its culture, the unsupervised children of a family will have their characteristic culture, the peer group will have its culture, the male band its culture, the female group its culture, particular friendship groups will have their culture, etc.).

3. *In contrast to "the sociological method," specific characterization of the mechanisms underlying culture cannot be ignored or neglected. Culture and cultural dynamics cannot be understood apart from the evolved psychological mechanisms that create, shape, and maintain culture.* As Symons (this issue) argues, valid psychology is essential to a successful evolutionary anthropology.

9. LEARNING

Despite widespread belief in the social sciences to the contrary, neither "learning" nor "culture" are explanations for phenomena, let alone alter-

native hypotheses. To claim that a behavior was "learned" or "cultural" is not to make reference to a well-worked out and highly specified theory of how that behavior came to be. Instead, these are minimal claims about the behavior. To say something is learned is solely to make the claim that one input influencing the resultant behavior is some kind of environmental influence. That is all. To claim that behavior is "cultural" is to make the slightly more specific claim that surrounding or preceding individuals constitute an environmental factor that has influenced the behavior under discussion in some way. Both characterizations have no more necessary content to them than that, regardless of the fact that most social scientists believe they are invoking a powerful explanatory principle when they claim that a behavior is "learned" or "cultural." As hypotheses to account for mental or behavioral phenomena, they are remarkably devoid of meaning. At this point in the study of human behavior, learning and culture are phenomena to be explained, and not explanations themselves.

10. THE EVOLVED CONSTRAINTS ON CULTURE ARE THE DESIGN FEATURES OF HUMAN INNATE PSYCHOLOGICAL MECHANISMS

The richest source of information about local adaptation is the behavior of other members of one's social group. Learning mechanisms have evolved allowing humans to make use of this valuable source of information, creating the social and cross-generational interactions anthropologists lump together as "culture." Although these numerous mechanisms are responsible for the existence of culture, virtually every other psychological mechanism also participates in shaping the particular features of local culture (or an individual's private culture) as well. In consequence, it is neither accurate nor useful to approach culture as if it were a homogeneous process, whose contents are passed on according to the structural dynamics of a single general learning system. Instead, the scientific task involved is the discovery of the information processing structure of each of these psychological mechanisms.

This scientific program is neither hopelessly complex nor hopelessly particularistic. Understanding how human learning mechanisms operate will uncover many useful generalizations; moreover, inventorying and elucidating the different psychological mechanisms will allow domain-specific rules about important adaptive areas to be developed (e.g., what are the mechanisms governing coalition formation and maintenance? What cues are used to judge biologically relevant kinship categories? How are reciprocation relationships enforced?).

Cognitive psychology and evolutionary biology are sister disciplines. The goal of evolutionary theory is to define the adaptive problems that organisms must be able to solve. The goal of psychological theory is to discover the information processing mechanisms that have evolved to solve them.

Alone, each is incomplete for the understanding of human nature. Together, they are powerful: Understanding the adaptive problems the human mind was designed to solve is a great aid to discovering how it works. And discovering how the mind works is the necessary groundwork for understanding the resulting social and cultural dynamics.

We are very indebted to Jerome Barkow, Martin Daly, Irven DeVore, Roger Shepard, Donald Symons, and Margo Wilson for many stimulating discussions of the issues explored in this paper. We are especially grateful to Jerome Barkow, Nicholas Blurton Jones, Michael McGuire, and an anonymous reviewer for their comments on the various drafts, and to Jason Banfield and Lisa Bork for their help with the manuscript. We would also like to thank Jeff Wine and Roger Shepard for their support.

REFERENCES

Alexander, R.D. Evolution and culture. In *Evolutionary Biology and Human Social Behavior*, Napoleon Chagnon and William Irons (Eds.). North Scituate, Mass.: Duxbury Press, 1979, pp. 59–78.

—— Evolution, culture, and human behavior: Some general considerations. In *Natural Selection and Social Behavior*, R.D. Alexander and D.W. Tinkle (Eds.). New York: Chiron Press, 1981, pp. 509–520.

Barkow, J.H. Culture and sociobiology. *American Anthropologist* 80: 5–20, 1978.

—— Sociobiology: Is this the new theory of human behavior?, in *Sociobiology Examined*, A. Montagu (Ed.). New York: Oxford University Press, 1980.

—— The distance between genes and culture. *Journal of Anthropological Research*, 37: 367–379, 1984.

Blurton Jones, N.G. Growing points in human ethology: another link between ethology and the social sciences? In *Growing Points in Ethology*, P.P.G. Bateson and R.A. Hinde (Eds.). Cambridge: Cambridge University Press, 1976, pp. 427–450.

Boden, M. *Artificial Intelligence and Natural Man*, New York: Basic Books, 1977.

Borgerhoff Mulder, M. On cultural and reproductive success: Kipsigis evidence. *American Anthropologist* 89: 617–634, 1987.

Bowlby, J. *Attachment*, New York: Basic Books, 1969.

Boyd, R., and P.J. Richerson. *Culture and the Evolutionary Process*, Chicago: University of Chicago Press, 1985.

Brown, F.M. *The Frame Problem in Artificial Intelligence*, Los Altos, Calif.: Morgan Kaufman, 1987.

Buss, D.M. Human mate selection. *American Scientist* 73: 47–51, 1985.

Cavalli-Sforza, L.L., and M.W. Feldman. *Cultural Transmission and Evolution: A Quantitative Approach*, Princeton, N.J.: Princeton University Press, 1981.

Chomsky, N. *Syntactic Structures*, The Hague: Mouton & Co., 1957.

—— Review of Skinner's "Verbal Behavior." *Language* 35: 26–58, 1959.

—— *Reflections on Language*, New York: Random House, 1975.

—— *Rules and Representations*, New York: Columbia University Press, 1980.

Cosmides, L. Deduction or Darwinian algorithms?: An explanation of the "elusive" content effect on the Wason selection task. Ph.D. diss., Department of Psychology and Social Relations, Harvard University, 1985.

——, and Tooby, J. From evolution to behavior: Evolutionary psychology as the missing link. In *The Latest on the Best: Essays on Evolution and Optimality*, J. Dupre (Ed.). Cambridge, Mass.: The MIT Press, 1987.

——, and Tooby, J. Evolutionary psychology and the generation of culture. Part II: A computational theory of social exchange. *Ethology and Sociobiology* 10: 51–97, 1989.

Daly, M. Some caveats about cultural transmission models. *Human Ecology* 10: 401–408, 1982.
——, and M. Wilson. A sociobiological analysis of human infanticide. In *Infanticide*, G. Hausfater and S.B. Hrdy (Eds.). New York: Aldine, 1984.
Dawkins, R. *The Selfish Gene*, New York: Oxford University Press, 1976.
—— *The Extended Phenotype*, San Francisco: W.H. Freeman, 1982.
Dickemann, M. Female infanticide, reproductive strategies, and social stratification: A preliminary model. In *Evolutionary Biology and Human Social Behavior*, Napoleon Chagnon and William Irons (Eds.). North Scituate, Mass.: Duxbury Press, 1979, pp. 4–39.
Durham, W. The adaptive significance of cultural behavior. *Human Ecology* 4: 89–121, 1979.
Durkheim, E. *The Rules of the Sociological Method*, Glencoe, Ill.: Free Press, 1938.
Erickson, C.J., and Zenone, P.G. Courtship differences in male ring doves: Avoidance of cuckoldry? *Science* 192: 1353–1354, 1976.
Flinn, M.V., and Alexander, R.D. Culture theory: The developing synthesis from biology. *Human Ecology* 10: 383–400, 1982.
Fodor, J.A. *The Modularity of Mind*, Cambridge, Mass.: The MIT Press, 1983.
Garcia, J., Clarke, J., and Hankins, W.G. Natural responses to scheduled rewards. In *Perspectives in Ethology*, P.P.G. Bateson and P. Klopfer (Eds.). New York: Plenum Press, 1973.
Gardner, Howard. *The Shattered Mind*, Cambridge, Mass.: MIT Press, 1975.
Ghiselin, M.T. Darwin and evolutionary psychology. *Science* 179: 964–968, 1973.
Harris, M. *Cultural Materialism: The Struggle for a Science of Culture*, New York: Random House, 1979.
Kitcher, P. *Vaulting Ambition*, Cambridge, Mass.: MIT Press, 1985.
Kroeber, Alfred L. The Superorganic. *American Anthropologist* 19: 163–213, 1917.
Irons, W. Natural selection, adaptation, and human social behavior. In *Evolutionary Biology and Human Social Behavior*, Napoleon Chagnon and William Irons (Eds.). North Scituate, Mass.: Duxbury Press, 1979, pp. 4–39.
Lumsden, C., and E.O. Wilson. *Genes, Mind, and Culture*, Cambridge, Mass.: Harvard University Press, 1981.
Marr, D. *Vision: A Computational Investigation Into the Human Representation and Processing of Visual Information*, San Francisco: Freeman, 1982.
——, and Nishihara, H.K. Visual information processing: Artificial intelligence and the sensorium of sight. *Technology Review* (October), 28–49, 1978.
Montagu, M.F.A. *Man and Aggression*, New York: Oxford University Press, 1968.
Rindos, D. The evolution of the capacity for culture. *Current Anthropology* 27: 315–332, 1986.
Rozin, P. The evolution of intelligence and access to the cognitive unconscious. In *Progress in Psychobiology and Physiological Psychology*, J.M. Sprague and A.N. Epstein (Eds.). New York: Academic Press, 1976.
——, and Schull, J. The adaptive-evolutionary point of view in experimental psychology. In *Handbook of Experimental Psychology*, R.C. Atkinson, R.J. Herrnstein, G. Lindsey, and R.D. Luce (Eds.). 1987.
Sahlins, M.D. *The Use and Abuse of Biology: An Anthropological Critique of Sociobiology*, Ann Arbor: University of Michigan Press, 1976a.
—— *Cultural and Practical Reason*, Ann Arbor: University of Michigan Press, 1976b.
Seligman, M.E.P. Phobias and preparedness. In *The Biological Boundaries of Learning*, M. Seligman and J. Hager (Eds.). New York: Appleton-Century Crofts, 1972.
Shepard, R.N. Ecological constraints on internal representation: Resonant kinematics of perceiving, imagining, thinking, and dreaming. *Psychological Review* 91: 417–447, 1984.
—— Evolution of a mesh between principles of the mind and regularities of the world. In *The Latest on the Best*, J. Dupre (Ed.). Cambridge, Mass.: The MIT Press, 1987.
Shepher, J. Mate selection among second generation kibbutz adolescents and adults; incest avoidance and negative imprinting. *Archives of Sexual Behavior* 1: 293–307, 1971.
—— *Incest: A Biosocial Approach*, New York: Academic Press, 1983.
Staddon, J.E.R. Operant behavior as adaptation to constraint. *Journal of Experimental Psychology: General* 108: 48–67, 1979.
Symons, D. *The Evolution of Human Sexuality*, Oxford University Press: New York, 1979.
—— Sociobiology and Darwinism. *Behavioral and Brain Sciences* 9: 208–209, 1986.
—— If we're all Darwinians, what's the fuss about? In *Sociobiology and Psychology*, C.B. Crawford, M.F. Smith, and D.L. Krebs (Eds.). Hillsdale, N.J.: Lawrence Erlbaum Associates, 1987.
—— A critique of Darwinian anthropology. *Ethology and Sociobiology* 10: 131–144, 1989.
—— Further comment on Vining's "Social versus Reproductive Success," no date.
Tooby, J. The emergence of evolutionary psychology. In *Emerging Syntheses in Science*, D. Pines (Ed.). Santa Fe: Rio Grande Institute, 1985.
——, and DeVore, I. Man, beast, and mind: Evolutionary psychology and the maturation of the biological sciences. Paper presented at "Man and Beast Revisited" conference, The Smithsonian Institution, May 6–9, 1986.
——, and DeVore, I. The reconstruction of hominid behavioral evolution through strategic modeling. In *The Evolution of Human Behavior: Primate Models*, W.G. Kinzey (Ed.). Albany: SUNY Press, 1987.
Trivers, R.L. Parent-offspring conflict. *American Zoologist* 14: 249–264, 1974.
Williams, G.C. *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought*, Princeton, N.J.: Princeton University Press, 1966.
Wolf, A.P. Childhood association and sexual attraction: A further test of the Westermarck hypothesis. *American Anthropologist* 72: 503–515, 1970.