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EVOLUTIONARY PSYCHOLOGY: Toward a Unifying Theory and a Hybrid Science

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■ **Abstract** Although evolutionary psychology is typically associated with "selfish gene theory," numerous other approaches to the study of mind and behavior provide a wealth of concepts for theorizing about psychology, culture, and development. These include general evolutionary approaches and theories focused on sociality, dual inheritance, multilevel selection, and developmental systems. Most evolutionary accounts use the same methods as Darwin—the "fit among facts"—to use natural selection as an explanation for behavior. Scientific standards for constraining and evaluating such accounts, research into the mutual influence of science and society on the understanding of evolution, and computational technologies for modeling species-typical processes are important considerations. Coevolutionary theories and developmental systems theories may eventually give rise to unification in a broad and general sense. Such a unification would be interdisciplinary and problem centered rather than discipline centered.

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INTRODUCTION: What's in a Name?

Evolutionary psychology is a broad and eclectic topic. The evolutionary study of mind and behavior includes work on animal behavior (Boesch & Tomasello 1998, Heyes 1998, Waal & Lanting 1997), paleoanthropological studies of cognition (Mellars & Gibson 1996), neuropsychology (Deacon 1997, Edelman 1992), neurobehavioral genetics (Wahlsten 1999), and evolutionary theory (Depew & Weber 1996). If the fruitful alliance between cognitive science and philosophy (e.g. Bechtel 1998, Fodor 1983) is any indication, evolutionary psychology would also include the theoretical and conceptual contributions of philosophers of biology (e.g. Callebaut 1993, Sober 1994, Wimsatt 1980).

Recently, the term evolutionary psychology has become associated with a specific interpretation of evolution represented, for example, by the work of Buss (1999a), Symons (1979, 1992), and Tooby & Cosmides (1992), which is based on influential sociobiological theories from the 1970s (EO Wilson 1975). Sociobiology and evolutionary psychology are based on inclusive fitness theory and the "selfish gene." As this perspective is but one of many, the term evolutionary psychology is used here to accommodate a variety of theoretical approaches and research traditions from animal studies to neurobehavioral genetics. The term inclusive fitness evolutionary psychology is used to refer to studies of human nature drawing from the sociobiological tradition (see Jones 1999 for a review). This article focuses primarily on human social behavior and takes inclusive fitness evolutionary psychology as a starting point to discuss a common aim among evolutionary psychologists: the search for a unifying theory of behavior. It concludes that such a theory would be broadly conceived and include culture and development in its portfolio. Evolutionary psychology by necessity is an interdisciplinary hybrid science informed by a postmodern reflexivity; that is, a keen awareness of the ongoing interchanges between science and society.

INCLUSIVE FITNESS EVOLUTIONARY PSYCHOLOGY

Theory and Research

Theoretical population biologists define evolution as changes in population gene frequencies. The primary factors of interest are genes and their transmission generation-to-generation. Environment and development are secondary factors, subsumed in coefficients of selection, which with various population parameters are manipulated in mathematical models. The dependent variables in such models

are changes in frequencies (or fitness, loosely speaking) of alternative alleles (versions of a gene, e.g. "altruistic" or "selfish" alleles). Hamilton (1964) showed that the average fitness of a gene could be influenced by interactions among organisms. In particular, benefiting kin, even at the cost of individual reproduction, could cause the increase of altruistic genes because related individuals share genes. The inclusive fitness of a gene refers to the number of copies of it passed on to the next generation by an individual plus the number of genes passed on by relatives as a result of behavior toward them. Trivers (1971, 1972, 1974) built on Hamilton's insight, showing how other types of social interactions such as reciprocal altruism, parent-offspring and sibling conflict, sexual selection, and parental investment could influence changes in gene frequencies. Hamilton's and Trivers' work, widely disseminated by EO Wilson (1975) and Dawkins (1976), became the foundation for sociobiology and introduced the "gene's eye view" of quantitative population biology to the human sciences. The gene's eye view is an anthropomorphic metaphor or heuristic device: What decisions would a gene make to facilitate its survival and reproduction (Buss 1999a)?

Cosmides & Tooby (1987) adapted sociobiology, arguing that evolved psychological mechanisms were the missing links between inclusive fitness theory and the evolutionary analysis of behavior. These views were elaborated by Tooby & Cosmides (1992), who also emphasized the designed features of evolved psychological mechanisms or modules and the environment of evolutionary adaptedness (Bowlby 1969) in which such mechanisms evolved. Buss (1995) organized the foundation work on inclusive fitness into a level-of-analysis framework, in which he equates Hamilton's (1964) inclusive fitness theory with "general evolutionary theory." Trivers' work (1971, 1972, 1974) is identified as middle-level or motivating theories, which provide the basis for general hypotheses and specific predictions about behavior.

Inclusive fitness evolutionary psychologists have conducted research on a range of topics (Crawford & Krebs 1998; see also Crawford et al 1987, Simpson & Kenrick 1997). These include mating preferences (Buss & Schmitt 1993, Buss 1990), rape (Thornhill & Palmer 2000), Judaism as an evolutionary group strategy (MacDonald 1994), cheater detection mechanisms (Cosmides 1989), mind (Pinker 1997), "killer sperm" (Baker & Bellis 1995), female inhibition mechanisms (Bjorklund & Kipp 1996), judgments of attractiveness (Singh 1993), and effects of family on pubertal timing (Ellis et al 1999). Inclusive fitness evolutionary psychologists have been charged with proposing untestable hypotheses (Kenrick 1995), but in fact, several hypotheses have been disconfirmed. For example, there is no evidence of human killer sperm (Moore et al 1999); hip-to-waist ratio judgments of attractiveness have been shown to be artifacts of a limited range of stimuli (Tassinary & Hansen 1998), and judgments of attractiveness do not predict health status (Kalick et al 1998).

Alternative explanations have been proposed for other findings. For example, Miller & Fishkin (1997) argue that large mean differences in number of desired mates reported by Buss & Schmitt (1993) were an artifact of highly skewed data

(i.e. a few outliers desiring a large number of mates). Using median measures, Miller & Fishkin (1997) found that both men and women reported wanting a relatively small number of long-term partnerships. Sex differences predicted for males by Buss and Schmitt, such as jealousy and desiring a large number of partners, were reported by anxious-ambivalent males as predicted by attachment fertility theory. Eagly & Wood (1999), in a reanalysis of data reported in Buss et al (1990), correlated social structural conditions with mate preferences. They found that males' preference for younger females and a good cook and housekeeper (found to be significant sex differences in the original study) and females' preference for older males with good earning potential was associated with gender equality as provided by United Nations indices. Differences in preferences were greatest in cultures with the least gender equality. These results indicate that social structural variables can account for sex differences in mating preferences.

Limitations: Psychological Mechanisms or Interpretive Lens

Inclusive fitness evolutionary psychology has produced large numbers of empirical studies; however, there are concerns about their relationship to evolutionary theory and what they actually contribute to psychological understanding (Lloyd 1999, Smith 2000). The scientific critiques of sociobiology are well known, extensive, and apply directly to evolutionary psychology (Gould & Lewontin 1979, Kitcher 1985, Lloyd 1999, Rose & Rose 2000; see also Commentary on Buss 1995). These concern the inability to demonstrate a correlation between phenotypic variation and reproductive variation (a *sine qua non* for evolutionary biology research), the difficulty of identifying a history of adaptation, and the lack of detail (analogous to the detail available for artificial selection in plants and animals) that would enable understanding of possible sources of variation. Without a theoretical vocabulary for development and culture, genetic determinism is an almost inevitable consequence of inclusive fitness theory.

For example, the most common concept of gene-environment interaction requires that all possible phenotypic possibilities be preformed in the genes, to be triggered by appropriate environmental stimuli. The environment fills in gaps in "open programs," "shapes" innate proclivities, or "shunts" behavior from one option to another (e.g. Buss 1999b, Crawford & Anderson 1989, Tooby & Cosmides 1992). Genetic determinism is also part of inclusive fitness evolutionary psychology's cultural theory, which assumes that cultural differences are "evoked" from a panhuman genome. Different environmental conditions shared within groups evoke the same individual psychological mechanisms differentially across groups (Buss 1999a). Thus, interaction in inclusive fitness evolutionary psychology usually refers to selection among pre-existing genetic possibilities, all of which are coded in all humans (the panhuman genome). An alternative view sees gene-environment interaction as chains of contingent events composed of reciprocal influences at multiple levels of organization, including genes and various features of the environment (Gottlieb 1992, Wimsatt 1999).

Many constructs in inclusive fitness evolutionary psychology present challenges to the boundaries between culture and science (Caporael & Brewer 1991, Maynard Smith 1987; cf Buss 1994). For example, kinship, neighborliness, divorce, and sibling rivalry are familiar features of everyday life. It is not clear in the absence of genetic data that theories of inclusive fitness, reciprocal altruism, parental investment, and parent-offspring conflict explain their corresponding everyday categories or redescribe them. Other topics parallel old and familiar aphorisms: women as gold diggers and men sowing their wild oats (Buss 1987) or the madonna-whore dichotomy (Gangestad & Simpson 1990). Thiessen (1996) argues that everyday life makes sense when viewed through an evolutionary lens. However, it can be just as well argued that selfish gene theory was created in the image of common beliefs about everyday life (Caporael 1994). The influence of culture on theory, problem choice, methods, and interpretation is a scientific issue—not a political or ideological one. First, science is a human practice well worth understanding, and second, to the extent that culture holds science on a leash (e.g. through media attention, needs to appeal to mass markets, and funding opportunities), traditional canons of scientific objectivity can be undermined.

Although evolutionary theory, broadly conceived, still holds promise for the study of mind and behavior, it seems likely that inclusive fitness theory is too narrow to serve a unifying theoretical role. The heuristic device of a selfish gene may have simplified the work of theoretical population biologists (Dawkins 1976). However, imbuing genes with fictional psychological characteristics (e.g. preferences, intentionality, agency) eliminated the complexities of development and environment, including social interaction and culture. These complexities are recognized to be important by evolutionary biologists (Endler 1986) and central to the concerns of psychologists generally.

OTHER EVOLUTIONARY PSYCHOLOGIES

This section illustrates some approaches to evolutionary psychology at other levels of analysis than that offered by inclusive fitness evolutionary psychology. These other approaches also focus more on culture or development. The categorization below is neither mutually exclusive nor the only one possible.

General Selection Theories

Natural selection is a powerful general principle in the world of living things. What makes a theory "evolutionary" or "Darwinian" is not that it is based in biology, but rather the integration of three interacting principles of change: variation, selection and retention. What varies, what are the conditions for selection, and what are the mechanisms for retention may differ: neuronal selection, selection in the immune system, and learning are all examples of selection (Cziko 1995). Cultural artifacts, practices, and even scientific theories may be selected (Campbell 1997). Most

evolutionary psychologies can be classified as general selection theories in at least a minimal sense of invoking natural selection to explain change over time. They may take the form of a unifying theory of the evolution of mind and behavior, or they may focus on a specific feature. Implicitly, there is at least one alternative variant (the absence of the focal trait), and an account is derived showing how the focal trait could have been an adaptive advantage.

Donald (1991) is a fine example of the unifying theory approach. He proposes three major phases in the evolution of human cognition. The first is *episodic culture*, where memory is dependent on environmental cues; second is *mimetic culture*, which enabled using the body for representation and memory, and the third is *mythic culture*, where lexical invention becomes the basis for language and narrative. Donald (1991) argues that a fourth phase, based on the external symbolic storage and symbol manipulation as in print and computers, is beginning. Examples of special-focus theories address the evolution of landscape preferences (Orians & Heerwagen 1992), egalitarianism, (Boehm 2000), and handedness (Corballis 1997). Studies on the evolution of language (Bickerton 1990, Deacon 1997, Pinker 1997) illustrate just how diverse special-focus theories can be.

Following Darwin (1965), ethologists traced the evolution of a trait such as smiling through its primate antecedents, developmental sequence, cross-cultural communicative competence and cultural specific contexts in which smiling could take on different meanings (Eibl-Eibesfeldt 1971, 1989). The emphasis in these studies is on progression, from a simpler to a more complex expression. Recent research on emotional expression follows similar trajectories, but with greater methodological and conceptual sophistication including a more complex selection account (Ekman & Rosenberg 1997, Griffiths 1997). Research has also addressed how evolved characteristics also may be exapted for use in other contexts. (In contrast to an adaptation, defined in terms of a history of use for a particular function, an exaptation evolved for one use and is used, or exapted, for another; feathers were adaptations for thermal control and then exapted for flight.) For example, expressions of disgust have different communicative values, and through processes of development and cultural evolution, may be co-opted for use in a broader system of cultural meanings including expression of moral responses (Rozin et al 1994). As Rozin et al (1994) point out, disgust may be an excellent system for studying the connections between evolution, cultural evolution and development because the facial markers are reliably observable and communicative.

An area where more research is needed concerns artifacts in the study of mind and behavior. The earliest stone tools, associated with *Homo habilis* ("handy man"), are about 2.4 million years old, indicating that artifacts are as much a part of the evolution of human mind and behavior as group living. Tools mediate the reciprocal exchange between organisms and environment; today, satisfying the human fascination with the artifactual world threatens ecological disaster. Artifacts function in the coordination of behavior by entraining human activity and accumulating knowledge over generations (Caporael & Baron 1997, Hutchins 1996). Yet surprisingly few psychological studies focus on tools (Kipnis 1997).

An exception has been in the important area of tools and language (Calvin & Bickerton 2000, Gibson & Ingold 1993, Greenfield 1991), largely because speech and the manipulation of objects appear to share common developmental, cognitive and neural substrates.

Roughly speaking, general selection theories are the most common form of evolutionary psychology. They vary in quality from informal adaptive story-telling drawing on common knowledge to well-done theorizing unifying research results in two or more scientific areas.

Sociality Theories

Sociality theories are midway between inclusive fitness evolutionary psychology and multilevel evolutionary theories (below). They center on the evolution of "social intelligence" or "Machiavellian intelligence" (Byrne & Whiten 1988). For decades, the standard assumption has been that animal and human intelligence evolved for interacting with concrete nonsocial objects for subsistence. Social intelligence theorists (Humphrey 1976, Jolly 1966) proposed that social objects offered a different order of complexity compared to physical ones. Physical objects are more or less stable compared to conspecifics, which are much more labile and unpredictable. Consequently, the requirements for intelligence as members of group-living animals would have been much higher than what would have been required to simply find food or make tools. Machiavellian theorists, such as Byrne and Whiten (1988), married social intelligence to inclusive fitness theory. They proposed a model for an actor (human as well as non-human) with highly developed faculties to manipulate other individuals by tactical deception so as to serve the actor's inclusive-fitness interests. Apparent cooperation among individuals is interpreted as behavior in the service of genetic self-interest or an expression of competition within and between groups (Alexander 1989).

Dunbar (1993) built on the Machiavellian hypothesis in his proposition that language evolved as part of increasing group size and neocortical expansion. Maintaining and manipulating social relationships in large groups required an ability that could fulfill the same functions as social grooming, but service a larger number of relationships. Time budgets limit the number of relationships that can be serviced by grooming; however, language—and specifically gossip—allows a much larger number of relationships to be maintained as well as a corresponding increase in group size. Dunbar's hypothesis reverses a conventional wisdom. He sees language as having evolved for social relationships, and abilities for referring to objects and coordinating activities such as hunting as emerging as a by-product, or exaptation, from the social function of language.

Although Machiavellian theorists locate their origins in Humphrey (1976), his paper suggests a radically different view of human intelligence. Humphrey rejected the common view that human intelligence evolved for surviving on the savannah by developing tools. Rather, creative intellect evolved for holding society together so that subsistence skills and knowledge of the habitat could be passed on in a

protective environment. Although there were benefits to group living, it posed a challenge because each individual's priority would be the survival of his own genes. Escalating within-group competition would result in a high level of social intelligence. However, this social intelligence was not just deceptive and manipulative. It was "truly social" (Caporael 1997) in the sense that "technical intelligence" was not just a different kind of intelligence, but rather an application of social intelligence to other objects. The result could be a "mistaken" proto-social exchange; that is, humans would anthropomorphize non-living systems and from these misapplications of social intelligence, scientific and technological discoveries would emerge—or cognitive limitations would be apparent (Caporael 1986, Cheney et al 1986). In other words, Humphrey proposed a "general purpose" mind, but its purpose was social transactions with conspecifics.

Sociality theories opened new possibilities for conceptions of mind and behavior although these remain insufficiently developed. Where inclusive fitness evolutionary psychology drew on a familiar model of "economic man" or exchange theory using the currency of genetic success, sociality theories suggested a framework that was neither economic nor folk psychological. Instead, they focused on the social origins of human nature and the attributes necessary for group living (Brewer 1997). Unfortunately, the idea of "selection by the group" seemed too close to group selection, which is re-emerging as part of multilevel evolutionary theory.

Multilevel Evolutionary Theories

A persistent debate among evolutionary theorists has been whether the gene was the sole level of selection or whether selection operated at multiple levels. With the publication of Leo Buss' book, *The Evolution of Individuality* (1987), scientists have begun exploring alternatives to selfish gene theory (Jablonka 1994, Maynard Smith & Szathmáry 1995). Unlike inclusive fitness theories, which identify genes as the level of selection, multievolutionary theories incorporate other levels where selection can occur (e.g. chromosomes, individuals, groups). Different levels of selection provide opportunities for conflict and synergisms between levels. For example, in the evolution of multicellularity, some cells "gave up" reproductive autonomy to become body cells as others eventually became reproducing gametes (Buss 1987). Similar conflicts and opportunities obtain for humans in the relationship between the individual and the group. Individual advantage may be curtailed at the level of the group, sometimes resulting in cooperative groups better adapted to the habitat than are other groups (Caporael et al 1989).

The question of how group structure can influence the evolution of altruistic genes has received much attention from group selection theorists (Sober & Wilson 1998, DS Wilson 1975, 1997). This interest has been driven by the observation that altruistic behavior should be self-limiting; the reproductive advantage afforded non-altruistic genes should drive out altruistic variants. In Wilson's (1983) models, subgroups ("trait groups") of a larger group vary in the proportion of altruists

and non-altruists. Some groups will have low ratios of altruists to non-altruists; other groups will have high ratios. Within all the groups, the nonaltruists increase relative to the altruists. However, if groups with higher proportions of altruists also produce more offspring, then the total number of altruists in the global population will increase. In other words, within-group selection favors the evolution of self-interest whereas between-group selection favors the evolution of cooperation (because altruists benefit themselves as well as others).

Multilevel selection has always been implicit in theories incorporating culture as part of human evolution. In coevolutionary theories, genes and culture are two distinct modes of inheritance that nevertheless influence the distribution of each other (Janicki 1998). For example, lactose tolerance is believed to be a trait that has probably coevolved with dairy practices, including food-processing techniques such as cheese and yogurt manufacture, which reduce lactose concentrations and thereby increase digestibility. There are several approaches to coevolutionary theory.

Research in evolutionary ecology assumes culture is an adaptive behavioral system and actors behave "as if" they are rational decision makers with respect to a genetic currency (e.g. Smith & Winterhalder 1992). Evolutionary ecologists (once called sociobiologists, now also called "Darwinian anthropologists") do not invoke specific psychological mechanisms. They assume that behavior is fitness-maximizing and study differences in reproductive output as a result of variations in ecological and cultural factors such as marriage system, hunting prowess, or status.

Boyd and Richerson (1985) propose a dual inheritance of culture and genes. They are distinctive in their effort to bridge research in psychology with group-level cultural processes. Boyd and Richerson propose a theory of forces to describe the Darwinian evolution of cultural creatures. Some of the forces are random, analogs of genetic drift and mutation; others are the outcome of individual decision making and choice, and finally, there is natural selection of cultural variation. They do not assume the rational decision maker of neoclassical economics or of evolutionary ecology. Instead, they assume that human decision making is imperfect, and trial-and-error learning expensive. One of the advantages of culture, then, is to attenuate the inherent limitations of fallible human cognition, and at the individual level, the advantage is realized through social learning—copying the behavior of other people. Boyd and Richerson provide one of the few theories about human sociality that is explicitly developmental, concerned with variations in socialization patterns (e.g., "lateral" transmission from peers or "vertical" transmission from parents).

Durham (1991) emphasizes the ideational aspects of culture, drawing on Dawkins' (1976) term, memes, for units of culture. Genes specify primary values, sensations experienced as intrinsically pleasurable or unpleasant. Memes provide "secondary values," or rules-of-thumb, scripts, or other guides to behavior. Cultural selection, guided by secondary values, is a function of choices made by individuals or groups and/or imposed by individuals or groups on others (e.g. marital forms).

Durham (1991) proposes that there are at least five modes of gene-culture interaction. In two modes, genes and culture act as the selection environment

for each other. In the other three modes, secondary value selection favor cultural variants that can reduce, improve, or have no effect at all on individual reproductive fitness. By affecting the phenotype, culture influences the genotypic distribution in the population.

In contrast, Fiske's complementarity theory (2000) assumes that genes specify particular and highly structured social proclivities that become functional when combined with different features of cultural paradigms. The results are rituals, institutions, artifacts, etc that enable people to use four basic models of relationships. Fiske (1991) calls these communal sharing, authority ranking, equality matching, and market pricing. These are not strictly cognitive models; rather, they are relational models that span the public-private and external-internal dichotomies generally used to differentiate culture and cognition.

Multilevel evolutionary theories provide a conceptual embarrassment of riches, although connecting these to current scientific knowledge about human psychology is a formidable task. An important difference from selfish gene theory is the recognition that organisms shape their own niches, which in turn affect the evolution of "organism-in-system" (Levins & Lewontin 1985). Work such as that by Laland et al (2000) suggests that coevolutionary theories could eventually combine with systems approaches like those in the next section.

Systems Theories

Systems theories are a different breed of evolutionary psychology altogether (Gottlieb 1992, 1998; Griffiths & Gray 1994, Hejl et al 1997, Ho 1991, Lewontin 1982, Wimsatt 1999). The gene is not viewed as a privileged source of information containing blueprints or programs for phenotypic formation. Rather, the information emerges through the reliable recurrence of components (including the products of development itself) that in the past have produced a viable system in a specific environment (Oyama 1989, Oyama et al 2000). The concept of inheritance is also expanded to include not only genes but also items from cellular components to language environments to atmospheric constancies. Organisms are not designed to solve problems presented by an independent environment. Instead, organism and environment are coevolving and mutually defining (Brandon & Antonovics 1996, Levins & Lewontin 1985, Thelen 1992). The anthropomorphic metaphor of natural selection favoring or selecting some variants over others is de-emphasized because organism and environment are viewed as an interrelated, self-organizing system. One common metaphor for the organism, which is always undergoing development, is ecological succession: Activity at one phase alters conditions that become the basis for the next stage without any need for a priori specification. This "ontogeny of information" (Oyama 1985)—the recurrent developmental system itself–is the product and process of evolution. From the perspective of systems theorists, species-typical behavior is repeatedly constructed or emergent (rather than transmitted) in the history of the lineage, in ontogeny, and in the situated activity of organism-in-setting.

Systems approaches can be illustrated by infant walking, which is commonly considered to be a genetically programmed trait. From a more or less global view, walking demonstrates a sequence of irreversible stages that reliably recur in infants (Thelen & Smith 1994). The first stage in walking is marked by the loss, at about two months, of the coordinated steplike movements newborns make when held erect. Stepping movements appear again about nine months later, and at about one year, the final stage, intentional walking begins. But the sequence hardly seems programmed or designed when it is closely examined. For example, although newborn stepping disappears, the same kinematics and muscle activation continue when infants are in supine, prone, or sitting positions. Infants who "practice" stepping (e.g. are held on a slow-moving treadmill) retain the movement throughout the first year. Seemingly extraneous factors such as weight and arousal influence stepping. Infants who do not normally perform stepping movements may do so when they are held with their legs submerged in water.

From the closer view, the appearance of a unified and coherent progression vanishes. Thelan & Smith (1994) observed that walking is composed of multiple subcomponents such as responsiveness to backward leg-extension (which occurs when an infant is held on a treadmill), intentionality, the ability to support body weight on the legs, the ability to move the legs in alternating patterns of swing and stance, and so on. These capacities are modular: They develop over time at different rates and depend on context during the first year. The local variation is not just noise in the system; it is the process that engenders developmental change and provides the variation that potentiates evolutionary change (Slobodkin & Rapoport 1974).

Thelan & Smith's (1994) research suggests another important point. The linguistic/perceptual categories we used to describe behavior, for example, walking, mating, or parenting, are not likely to be at the level of analysis or granularity that results in natural selection. As in the case of walking, observational research indicates that human courtship initiation consists of a surprisingly consistent sequence of behavior that also suggests modular components (Perper 1985). Such findings are to be expected because evolution is a mosaic, jury-rigging process. Different features of an organism may evolve independently of others (within constraints) as products of "adaptively relevant environments" (Irons 1998). These are features of the organism-environment system with which the components making up the trait interact and contribute to reproduction and survival to reproductive age.

Caporael (1995, 1997) combines elements of multilevel selection theory and systems approaches (Caporael & Baron 1997). She suggests that the observation that psychologists attempt to explain by resorting to genes is recurrence. Rather than using genes in a metaphoric sense, she proposes a vocabulary based on the "repeated assembly" of reliably recurrent resources. Organisms, their settings, artifacts, and practices may be repeatedly assembled. The objective of evolutionary psychology would then be to understand the system dynamics that result in variation, retention, and selection of the component parts of repeated assemblies

(Caporael 1999). Taking a developmental-evolutionary approach, Caporael (1995, 1997) proposes a model of group structure with core subgroup configurations based on considerations of group size and modal tasks. For example, a dyad is a core configuration with a size of two and modal tasks that include interaction with an infant. A core configuration is an environment where certain capacities, such as finely tuned microcoordination (as used in interactional synchrony) can evolve. The other configurations are teams, demes, and macrodemes, analogous to the foraging parties, bands, and macrobands in anthropology. The basic hypothesis is that aspects of mental systems should correspond to features of modal tasks characteristic to configurations, which in turn are grounded in morphology and ecology.

Core configurations are repeatedly assembled from generation to generation, in an expanding circle of other actors during ontogeny, and in the day-to-day interaction of humans (cf Hendriks-Jansen 1996). The configurations both maintain and are maintained by cognitive specializations for small group living.

Limitations

Perhaps the greatest shortcoming of the evolutionary psychologies presented in this section is the difficulty of getting from theory to testable hypotheses. Coevolutionary theory (Boyd & Richerson 1985) and developmental systems theory (Oyama 1985) are both over 15 years old and have yet to generate a body of research results. Conversely, one could argue that they are only 15 years old—quite a deal younger than the nature-nurture dualism inspired by Francis Galton's work in the mid-nineteenth century—and more time is needed to see what they can produce. General evolutionary theories have a longer history than multilevel evolutionary or systems theories. However, they may be too diverse in their range of topics for a research community to form around them—an advantage amply illustrated by the success of inclusive fitness evolutionary psychology in creating an identifiable group of researchers, problem areas, and journals.

WORK TO BE DONE

Concepts and Methods

Evolutionary biologists use a number of methods and have several requirements for demonstrating adaptation, almost always including measures of fitness (Boake 1994, Endler 1986). They have demonstrated natural selection for human physiological traits (e.g. sickle cell anemia), but biologists' typical methods for studying evolution (Endler 1986) do not lend themselves to research on psychological constructs. The problem is not specific to the human sciences: Various disciplines such as ecology, paleontology, and developmental biology have begun reconstructing Darwinism to accommodate their research questions and subject matter (Boucher 1985, Eldredge & Grene 1992, Kauffman 1993). Signs of such reconstruction are showing in evolutionary psychology, for example, in the notion of repeated

assembly (Caporael 1999) or "virtual genes" (Dennett 1995) to indicate recurrence without making unwarranted causal assumptions.

Almost all evolutionary psychology relies on the same method Darwin used in his work, William Whewell's "consilience of inductions" (Forster & Wolfe 1999, Ruse 1989). (Whewell's consilience should not be confused with EO Wilson's 1998 use as a reduction to biology.) Darwin reasoned that whereas no single example could prove natural selection, it would be implausible to dismiss the fit among so many pieces of evidence. Experiments, archival data, animal observation, computer modeling, and narrative argument can provide a network of research findings for consilient arguments. The quality of a consilient argument depends on its plausibility given sets of constraints, which come from a variety of sources. The most familiar constraints come from existing research.

For example, hypotheses about the environment of evolutionary adaptedness are constrained by evidence from several fields. Fossils provide evidence about changes in hard tissues over time and provide the basis for inferences about diet, sexual dimorphism, and phylogenetic relationships (Johanson & Edgar 1996, Lewin 1998, Tattersall 1995). Comparative studies of primates (Boesch & Tomasello 1998, Cheney et al 1986, Cheney & Seyfarth 1990) are useful for understanding continuities and discontinuities among primate characteristics distinct from human characteristics. Ethnoarcheologists examine the material residue of modern hunter-gatherers so as to better interpret findings of ancient origins (Binford 1983), and behavioral archeologists attempt to recreate the performance characteristics of particular objects such as the wear pattern on stone tools (Schick & Toth 1994). Hunter-gatherers (Gowdy 1998) suggest a range of variation for theorizing about human evolution. Constraints are also introduced by conceptual analyses about the environment of evolutionary adaptedness (Foley 1996, Irons 1998).

Psychology, Society and Science

The evolutionary study of mind and behavior goes back to Charles Darwin and his contemporary Herbert Spencer (Richards 1987). In the twentieth century, the subject went through cycles of rejection and reprise that were influenced by the controversial politics of eugenics, the rise of behaviorism, and most recently, Nazism (Deichmann 1996). Although references to evolution continued in animal and infant research, a "tacit consensus" (Kaye 1986) against biological explanation of the adult human mind led to a hiatus in human evolutionary studies, which was broken only in the past 25 years. Nevertheless, the application of evolutionary theory to human behavior continues to be criticized on conceptual grounds for foreclosing or "sewing up" research on the human mind (Smith 2000) or for ideological implications not justified by the science (Lewontin et al 1984). These criticisms are significant for scientific practice.

In the human sciences, scientists are both subjects who study and objects being studied, which can complicate evolutionary psychological research. These complications could also be considered constraints against which scenarios and

hypotheses require testing. For example, evolutionary theorizing should be tempered by current psychological research on heuristics and biases, including resemblance, confirmatory biases, theory-driven data perception, overconfidence in judgment, and the relationship between the amount of detail in scenarios and their believability (cf Caporael et al 1989, Kahneman et al 1982). Conceptual history is another source of constraints because new ideas do not pre-exist; they emerge from their predecessors. Anthropologists have been more circumspect in their constructions of the evolutionary past since Landau (1984, 1991) demonstrated that many of their reconstructions had the narrative structure of hero-myths. Similarly, certain aspects of selfish gene theory share a conceptual deep structure with religion: Like the soul, the immortal genes are the essence of the individual, whereas the body, vessel of the soul or vehicle of the genes, is transitory and ephemeral (Caporael 1994; cf Dawkins 1976). Certain conventions used in reconstructions (Kuper 1988, Landau 1991), such as projection from the present to the past and narrative conventions, should also be considered as constraints contributing to the evaluation of scenarios.

Evolutionary psychology is vulnerable to a number of meta-scientific influences from the political, social, and psychological contexts of science (Brewer & Caporael 1990, Caporael & Brewer 1991). Increasingly, researchers are studying the exchange between science and its context. For example, Weingart et al (1997) concluded that evolutionary psychologists influence and are influenced by the ideological contexts of their work, although the direction of influences vary. More study is needed to understand how these mutual influences operate for three reasons. First, they need to be understood and treated as any confounding variable in the design and interpretation of research. Second, such "confounds" are scientifically interesting as data in the study of mind and associated ecologies of knowledge (Star 1995) and evolutionary epistemology (Campbell 1988). Third, such work may play an important role in understanding and improving theory construction. For example, deconstructing metaphors of "transmission" and "construction" imply two theoretically different notions of heritability in evolutionary psychology.

TOWARD A UNIFYING THEORY AND A HYBRID SCIENCE

Why Do We Want a Unifying Theory and What Would It Look Like?

The appeal of evolutionary theory is its potential to serve as a unifying theory in the human sciences (Alexander 1975, Buss 1999a), although there are numerous reasons to be pessimistic about this goal (Dupré 1993, Rosenberg 1994). Human cognition may impose a limit on understanding the complexity of the natural world; the natural world may be far more random and disordered than scientists expect it to be, and/or the linguistic conventions for describing the world at any particular level

of analysis cannot be mapped onto other levels. Nevertheless, there are many ways to have a unifying theory, aside from the usual convention of reduction to lower and lower levels, passing through culture, to psychology, to genes (Wilson 1998).

Thirty years ago, Campbell (1969) proposed replacing the disciplinary tribal model of science with a fish-scale model of omniscience. Instead of disciplines aggregating as clusters of specialties, they would be distributed in overlapping areas, much as the scales of a fish overlap. (The chapter by Weingart et al 1997 is the product of one such effort.) There are several forces that erode such attempts, including institutional and disciplinary structures that operate against an interdisciplinary field and promote ingroup-outgroup competition. However, other forces do promote a fish-scale-type of unification. Consilience as a research method imposes interdependence among scholars because constraints on theorizing come from other disciplines. For example, hypotheses about male jealousy as a universal adaptation (Buss 1999a) or reconstructions assuming that prehistoric women engaging in extramarital affairs suffered murder, physical abuse, or abandonment (Bjorklund & Kipp 1996) are constrained by anthropological research such as that in cultures where children are believed to made from the accumulation of semen and several men can share in their paternity (Beckerman et al 1998, Conklin & Morgan 1996). Unifying overlap would be produced by a problem-centered rather than disciplinary-centered overlap. Excellent examples include work on the study of language and artifacts (Gibson & Ingold 1993) and comparative female life histories (Morbeck et al 1997).

New Methodologies Such as Complex Adaptive Systems Research, Artificial Life, Simulations, and Situated Robotics

Most research concerned with human evolution concerns phenomena described at the perceptual/linguistic level. This level of analysis is easily communicable and makes possible cross-species and cross-cultural comparisons. However, it does not stand up well to close observation. As in the example of walking, early ethologists found that a purportedly evolved behavior like "parenting" in ducks breaks down into a number of distinct activities. The only common element is that they are centered on the duckling through the changing interactions between it and the mother duck. Information technology may represent new avenues for understanding the dynamic interactions between the micro- and macro-processes in development and evolution. Computer simulations have a relatively long history in understanding topics such as cooperation and are becoming increasingly sophisticated (Harms 1999). Advances in computation technologies have opened new possibilities by creating artificial models of living systems (Flake 1998). One of the most ambitious attempts to make these methods relevant for understanding human evolution is by Hendriks-Jansen (1996), who develops his arguments from ethology, developmental psychology, and artificial life research. Hendriks-Jansen observes that species-typical activity patterns arise through interactive emergence in three different senses: They emerge through an evolutionary history of selection, through

developmental processes, and through the execution of low-level activities in interaction with a species-typical environment. Hendriks-Jansen claims that robotic models can be used as existence proofs to confirm hypotheses about emergent interaction. For example, Maja Mataric (1992, cited in Hendriks-Jansen 1996) has created a robot that follows walls as if it had representations of landmarks and maps. However, there are no programs for wall-following; it is an emergent activity of some simple "reflexes" (e.g. STROLL, AVOID) and sensors in interaction with a stable environment. If the robot were an evolved creature, the evidence that wall-following was a stable component of its evolutionary history would come from the landmark detectors and maps. These are crucially dependent on the lower-level structured organism-in-setting that enables the situated activity of wall-following; if the structured activity was disrupted, the detectors and maps would fail.

Computational approaches and artificial models have a long way to go in proving themselves for understanding the evolution of mind and behavior. The most immediate problem is oversimplification. Nevertheless, they can suggest new concepts, and among the most important of these are notions of iteration, replication, recursion, and repeated assembly.

CONCLUSION: Interdisciplinarity and Reflexivity

It has been almost 150 years since Darwin published his theory of natural selection. It has been hotly debated in public life as few scientific theories have ever been. It has influenced the lives of millions of people, yet with little scientific understanding of how that influence occurs. The future of evolutionary psychology requires problem-centered, interdisciplinary research, both to solve problems within the discipline and to negotiate the boundaries of practice where subject and object and science and society are unavoidably intertwined.

This article suggests a continuum between what evolutionary psychology is and what it could become. At one extreme is inclusive fitness evolutionary psychology, which attempts to show how patterns of everyday life can be explained by adaptations to life in the past. Closer to the center are general selection and coevolutionary theories that rely on consilient methodology and interdisciplinary research. At the other extreme are systems theories that involve humans and robots and are struggling to find the levels of analysis and the language to ground a theory of mind and action in natural selection. It would be fair to say that the current state of evolutionary psychology is a working out of possible theories, languages, concepts, and methods. The evolutionary study of mind and behavior has more of the appearance of an adaptive radiation of species after the appearance of a major evolutionary novelty than it does the unifying look of a theory after all its competitors have become extinct. For those who hoped for a quick unification of the social sciences, some consolation can be taken from the Copernican Revolution; it took 150 years for people to believe that the sun, and not the earth, was the center of the universe. It should be no surprise if it takes that long for the Darwinian Revolution.

LITERATURE CITED

Alexander RD. 1989. Evolution of the human psyche. In *The Human Revolution*, ed. P Mellars, C Stringer, pp. 455–513. Princeton: Princeton University Press

Alexander RD. 1975. The search for a general theory of behavior. *Behav. Sci.* 20:77–100

Baker RR, Bellis MA. 1995. *Human Sperm Competition*. London: Chapman & Hall

Barkow JH, Cosmides L, Tooby J, eds. 1992. *The Adapted Mind*. New York: Oxford Univ. Press

Bechtel W. 1998. Representations and cognitive explanations: assessing the dynamicist challenge in cognitive science. *Cogn. Sci.* 22:295–318

Beckerman S, Lizzarralde R, Ballew C, Schroeder S, Fingelton C, et al. 1998. The Bari partible paternity project: preliminary results. *Curr. Anthropol.* 39:164–67

Bickerton D. 1990. *Language and Species*. Chicago: Univ. Chicago Press

Binford LR. 1983. *In Pursuit of the Past*. New York: Thames & Hudson

Bjorklund DF, Kipp K. 1996. Parental investment theory and gender differences in the evolution of inhibition mechanisms. *Psychol. Bull.* 120:163–88

Boake CRB, ed. 1994. *Quantitative Genetic Studies of Behavioral Evolution*. Chicago: Univ. Chicago Press

Boehm C. 2000. *Hierarchy in the Forest: The Evolution of Egalitarian Behavior*. Cambridge, MA: Harvard University Press

Boesch C, Tomasello M. 1998. Chimpanzees and human culture. *Curr. Anthropol.* 39: 591–614

Boucher DH. 1985. The idea of mutualism, past and future. In *The Biology of Mutualism*, ed. DH Boucher, pp. 1–28. New York: Oxford Univ. Press

Bowlby J. 1969. *Attachment and Loss*, Vols. 1–2. New York: Basic Books

Boyd R, Richerson PJ. 1985. *Culture and the Evolutionary Process*. Chicago: Univ. Chicago Press

Brandon R, Antonovics J. 1996. The coevolution of organism and environment. In *Concepts and Methods in Evolutionary Biology*, ed. R Brandon. New York: Cambridge Univ. Press

Brewer MB. 1997. On the social origins of human nature. In *The Message of Social Psychology*, ed. C McGarty, A Haslam, pp. 54–62. Oxford: Blackwell

Brewer MB, Caporael LR. 1990. Selfish genes versus selfish people: sociobiology as origin myth. *Motiv. Emot.* 14:237–42

Buss DM, Abbott M, Angleitner A, Biaggio A, Blanco-Villasenor A, et al. 1990. International preferences in selecting mates: a study of 37 cultures. *J. Cross-Cult. Psychol.* 21:5–47

Buss DM. 1994. The strategies of human mating. *Am. Sci.* 82:238–49

Buss DM. 1995. Evolutionary psychology: A new paradigm for psychological science. *Psychol. Inq.* 6:1–30

Buss DM. 1999a. *Evolutionary Psychology*. Boston: Allyn & Bacon

Buss DM. 1999b. Interactionism, flexibility, and inferences about the past. *Am. Psychol.* 54:443–45

Buss DM, Schmitt DP. 1993. Sexual strategies theory: a contextual evolutionary analysis of human mating. *Psychol. Rev.* 100:204–32

Buss LW. 1987. *The Evolution of Individuality*. Princeton, NJ: Princeton Univ. Press

Byrne RW, Whiten A, eds. 1988. *Machiavellian Intelligence*. Oxford: Clarendon Press

Callebaut W. 1993. *Taking the Naturalistic Turn, or, How Real Philosophy of Science is Done*. Chicago: Chicago Univ. Press

Calvin WH, Bickerton D. 2000. *Lingua ex Machina: Reconciling Darwin and Chomsky with the Human Brain*. Cambridge, MA: MIT Press

Campbell DT. 1969. Ethnocentrism of disciplines and the fish-scale model of omniscience. In *Interdisciplinary Relationships in the Social Sciences*, ed. M Sherif, CW Sherif, pp. 328–48. Chicago: Aldine

Campbell DT. 1988. *Methodology and Epistemology for Social Sciences*. Chicago: Univ. Chicago Press

Campbell DT. 1997. From evolutionary epistemology via selection theory to a sociology of scientific validity. *Evol. Cogn.* 3:5–38

Caporael LR. 1986. Anthropomorphism and mechanomorphism: Two faces of the human machine. *Comput. Hum. Behav.* 2:215–34

Caporael LR. 1994. Of myth and science: origin stories and evolutionary scenarios. *Soc. Sci. Inf.* 33:9–23

Caporael LR. 1995. Sociality: coordinating bodies, minds and groups. *Psycoloquy* 6:http://www.cogsci.soton.ac.uk/cgi/psyc/newpsy?6.01

Caporael LR. 1997. The evolution of truly social cognition: the core configurations model. *Pers. Soc. Psychol. Rev.* 1:276–98

Caporael LR. 1999. *From Selfish Genes to Repeated Assembly*. Presented at Annu. Meet. Am. Psychol. Assoc., Boston

Caporael LR, Baron RM. 1997. Groups as the mind's natural environment. See Simpson & Kenrick 1997, pp. 317–43

Caporael LR, Brewer MB. 1991. The quest for human nature. *J. Soc. Issues* 47:1–9

Caporael LR, Dawes RM, Orbell JM, van de Kragt AJC. 1989. Selfishness examined: cooperation in the absence of egoistic incentives. *Behav. Brain Sci.* 12:683–739

Cheney D, Seyfarth R, Smuts B. 1986. Social relationships and social cognition in nonhuman primates. *Science* 234:1361–66

Cheney DL, Seyfarth RM. 1990. *How Monkeys See the World*. Chicago: Univ. Chicago Press

Conklin BA, Morgan LM. 1996. Babies, bodies and the production of personhood in North America and a Native Amazonian society. *Ethos* 24:657–94

Corballis MC. 1997. The genetics and evolution of handedness. *Psychol. Rev.* 104:714–27

Cosmides L. 1989. The logic of social exchange: Has selection shaped how humans reason? Studies with the Wason selection task. *Cognition* 31:187–276

Cosmides L, Tooby J. 1987. From evolution to behavior: evolutionary psychology as the missing link. In *The Latest on the Best: Essays on Evolution and Optimality*, ed. J Dupré, pp. 277–306. Cambridge, MA: MIT Press

Crawford C, Krebs DL, eds. 1998. *Handbook of Evolutionary Psychology*. Mawah, NJ: Erlbaum

Crawford C, Smith M, Krebs D, eds. 1987. *Sociobiology and Psychology*. Hillsdale, NJ: Erlbaum

Crawford CB, Anderson JL. 1989. Sociobiology: an environmentalist discipline? *Am. Psychol.* 44:1449–59

Cziko G. 1995. *Without Miracles: Universal Selection Theory and the Second Darwinian Revolution.* Cambridge, MA: MIT Press

Darwin C. 1965 (1872). *The Expression of the Emotions in Man and Animals*. Chicago: Chicago Univ. Press

Dawkins R. 1976. *The Selfish Gene*. New York: Oxford Univ. Press

Deacon TW. 1997. *The Symbolic Species: The Co-evolution of Language and the Brain.* New York: Norton

Deichmann U. 1996. *Biologists Under Hitler*. Cambridge, MA: Harvard Univ. Press

Dennett DC. 1995. *Darwin's Dangerous Idea.* New York: Simon & Schuster

Depew DJ, Weber BH. 1996. *Darwinism Evolving*. Cambridge, MA: MIT Press

Donald M. 1991. *Origins of the Modern Mind.* Cambridge, MA: Harvard Univ. Press

Dunbar RIM. 1993. Coevolution of neocortical size, group size and language in humans. *Behav. Brain Sci.* 16:681–735

Dupré J. 1993. *The Disorder of Things.* Cambridge, MA: Harvard Univ. Press

Durham WH. 1991. *Coevolution: Genes, Culture and Human Diversity*. Stanford, CA: Stanford Univ. Press

Eagly AH, Wood W. 1999. The origins of

sex differences in human behavior: evolved dispositions versus social roles. *Am. Psychol.* 54:408–23

Edelman GM. 1992. *Bright Air, Brilliant Fire*. New York: Basic Books

Eibl-Eibesfeldt I. 1971. *Love and Hate*. London: Methuen

Eibl-Eibesfeldt I. 1989. *Human Ethology*. New York: Aldine

Ekman P, Rosenberg EL, eds. 1997. *What the Face Reveals: Basic and Applied Studies of Spontaneous Expression Using the Facial Action Coding System (FACS)*. New York: Oxford Univ. Press

Eldredge N, Grene M. 1992. *Interactions: The Biological Context of Social Systems*. New York: Columbia Univ. Press

Ellis BJ, McFadyen-Ketchum S, Dodge KA, Pettit GS, Bates JE. 1999. Quality of early family relationships and individual differences in the timing of pubertal maturation in girls: a longitudinal test of an evolutionary model. *J. Pers. Soc. Psychol.* 77:387–401

Endler J. 1986. *Natural Selection in the Wild*. Princeton, NJ: Princeton Univ. Press

Fiske AP. 1991. *Structures of Social Life: The Four Elementary Forms of Human Relations*. New York: Free Press

Fiske AP. 2000. Complementarity theory: why human social capacities evolved to require cultural complements. *Pers. Soc. Psychol. Rev.* 4:76–94

Flake GW. 1998. *The Computational Beauty of Nature: Computer Explorations of Fractals, Chaos, Complex Systems and Adaptation*. Cambridge, MA: MIT Press

Fodor JA. 1983. *The Modularity of Mind*. Cambridge, MA: MIT Press

Foley R. 1996. The adaptive legacy of human evolution: a search for the environment of evolutionary adaptedness. *Evol. Anthropol.* 4:194–203

Forster MR, Wolfe A. 1999. *Conceptual Innovation and the Relational Nature of Evidence: The Whewell-Mill Debate*. http://philosophy.wisc.edu/forster/papers/Whewell1.pdf

Gangestad SW, Simpson JA. 1990. Toward an evolutionary history of female sociosexual variation. *J. Pers.* 58:69–96

Gibson KR, Ingold T, eds. 1993. *Tools, Language and Cognition in Human Evolution*. New York: Cambridge Univ. Press

Gottlieb G. 1992. *Individual Development and Evolution*. New York: Oxford Univ. Press

Gottlieb G. 1998. Normally occurring environmental and behavioral influences on gene activity: from central dogma to probabilistic epigenesis. *Psychol. Rev.* 105:792–802

Gould SJ, Lewontin RC. 1979. The spandrels of San Marco and the Panglossian paradigm. *Proc. R. Soc. London Ser. B* 205:581–98

Gowdy J, ed. 1998. *Limited Wants, Unlimited Means: A Reader on Hunter-Gather Economics and the Environment*. Washington, DC: Island

Greenfield PM. 1991. Language, tools and brain: the ontogeny and phylogeny of hierarchically organized sequential behavior. *Behav. Brain Sci.* 14:531–95

Griffiths PE. 1997. *What Emotions Really Are: The Problem of Psychological Categories*. Chicago: Chicago Univ. Press

Griffiths PE, Gray RD. 1994. Developmental systems and evolutionary explanation. *J. Philos.* 91:277–304

Hamilton WD. 1964. The genetical evolution of social behavior, I & II. *J. Theor. Biol.* 7:1–52

Harms W. 1999. *The Evolution of Cooperation on Hostility Gradients*. http://eame.ethics.ubc.ca/Hostility/index.html

Hejl PM, Falk R, Hendrichs H, Jablonka E. 1997. Complex systems: multilevel and multiprocess approaches. In *Human by Nature: Between Biology and the Social Sciences*, ed. P Weingart, SD Mitchell, PJ Richerson, S Maasen, pp. 387–425. Mahwah, NJ: Erlbaum

Hendriks-Jansen H. 1996. *Catching Ourselves in the Act*. Cambridge, MA: MIT Press

Heyes CM. 1998. Theory of mind in nonhuman primates. *Behav. Brain Sci.* 21:101–48

Ho M-W. 1991. The role of action in evolution: evolution by process and the ecological approach to perception. *Cult. Dyn.* 4:336–54

Humphrey NK. 1976. The social function of intellect. In *Growing Points in Ethology*, ed. PPG Bateson, RA Hinde, pp. 303–21. Cambridge: Cambridge Univ. Press

Hutchins E. 1996. *Cognition in the Wild*. Cambridge, MA: MIT Press

Irons W. 1998. Adaptively relevant environments versus the environment of evolutionary adaptedness. *Evol. Anthropol.* 6:194–204

Jablonka E. 1994. Inheritance systems and the evolution of new levels of individuality. *J. Theor. Biol.* 170:301–9

Janicki MG. 1998. Evolutionary approaches to culture. See Crawford & Krebs 1998, pp. 163–207

Johanson D, Edgar B. 1996. *From Lucy to Language*. New York: Simon & Schuster

Jolly A. 1966. Lemur social behavior and primate intelligence. *Science* 153:501–6

Jones D. 1999. Evolutionary psychology. *Annu. Rev. Anthropol.* 28:553–75

Kahneman D, Slovic P, Tversky A, eds. 1982. *Judgment Under Uncertainty: Heuristics and Biases*. New York: Cambridge Univ. Press

Kalick SM, Zebrowitz LA, Langlois JH, Johnson RM. 1998. Does human facial attractiveness honestly advertise health? Longitudinal data on an evolutionary question. *Psychol. Sci.* 9:8–13

Kauffman SA. 1993. *The Origins of Order*. New York: Oxford Univ. Press

Kaye HL. 1986. *The Social Meaning of Modern Biology: From Social Darwinism to Sociobiology*. New Haven, CT: Yale Univ. Press

Kenrick DT. 1995. Evolutionary theory versus the confederacy of dunces. *Psychol. Inq.* 6:56–62

Kipnis D. 1997. Ghosts, taxonomies, and social psychology. *Am. Psychol.* 52:205–11

Kitcher P. 1985. *Vaulting Ambition: Sociobiology and the Quest for Human Nature*. Cambridge, MA: MIT Press

Kuper A. 1988. *The Invention of Primitive Society: Transformations of an Illusion*. New York: Routledge

Laland KN, Odling-Smee J, Feldman MW. 2000. Niche construction, biological evolution, and cultural change. *Behav. Brain Sci.* 23:131–75

Landau M. 1984. Human evolution as narrative. *Am. Sci.* 72:262–68

Landau M. 1991. *Narratives of Human Evolution*. New Haven, CT: Yale Univ. Press

Levins R, Lewontin R. 1985. *The Dialectical Biologist*. Cambridge, MA: Harvard Univ. Press

Lewin R. 1998. *Principles of Human Evolution*. Malden, MA: Blackwell Sci.

Lewontin RC. 1982. Organism and environment. In *Learning, Development and Culture*, ed. HC Plotkin, pp. 17–38. New York: Wiley & Sons

Lewontin RC, Rose S, Kamin LJ. 1984. *Not in Our Genes*. New York: Pantheon

Lloyd EA. 1999. Evolutionary psychology: the burdens of proof. *Biol. Philos.* 14:211–33

MacDonald K. 1994. *A People that Shall Dwell Alone: Judaism as a Group Evolutionary Strategy*. Westport, CT: Praeger

Maynard Smith J. 1987. Science and myth. In *The Natural History Reader in Evolution*, ed. N Eldredge, pp. 222–29. New York: Columbia Univ. Press

Maynard Smith J, Szathmáry E. 1995. *The Major Transitions in Evolution*. New York: Freeman

Mellars P, Gibson K, eds. 1996. *Modelling the Early Human Mind*. Oxford: McDonald Inst. Archaeol. Res.

Miller LC, Fishkin SA. 1997. On the dynamics of human bonding and reproductive success: seeking windows on the adapted-for-human-environmental interface. See Simpson & Kenrick 1997, pp. 197–235

Moore HDM, Martin M, Birkhead TR. 1999. No evidence for killer sperm or other selective interactions between human spermatozoa in ejaculates of different males in vitro. *Proc. R. Soc. London* 266:2343–50

Morbeck ME, Galloway A, Zihlman AL, eds. 1997. *The Evolving Female*. Princeton, NJ: Univ. Princeton Press

Orians GH, Heerwagen JH. 1992. Evolved responses to landscapes. See Barkow et al 1992, pp. 555–79

Oyama S. 1985. *The Ontogeny of Information*. New York: Cambridge Univ. Press

Oyama S. 1989. Ontogeny and the central dogma: Do we need the concept of genetic programming in order to have an evolutionary perspective? In *Systems and Development. The Minnesota Symposia on Child Psychology*, ed. MR Gunnar, E Thelen, 22:1–34. Hillsdale, NJ: Erlbaum

Oyama S, Griffiths PE, Gray RD, eds. 2000. *Cycles of Contingency: Developmental Systems and Evolution*. Cambridge, MA: MIT Press

Perper T. 1985. *Sex Signals: The Biology of Love*. Philadelphia: ISI Press

Pinker S. 1997. *How the Mind Works*. New York: Norton

Richards RJ. 1987. *Darwin and the Emergence of Evolutionary Theories of Mind and Behavior*. Chicago: Univ. Chicago Press

Rose H, Rose S. 2000. *Alas, Poor Darwin: Arguments Against Evolutionary Psychology*. New York: Harmony Books

Rosenberg A. 1994. *Instrumental Biology or the Disunity of Science*. Chicago: Univ. Chicago Press

Rozin P, Lowery L, Ebert R. 1994. Varieties of disgust faces and the structure of disgust. *J. Pers. Soc. Psychol.* 66:870–81

Ruse M. 1989. *The Darwinian Paradigm*. New York: Routledge

Schick KD, Toth N. 1994. *Making Silent Stones Speak: Human Evolution and the Dawn of Technology*. New York: Simon & Schuster

Simpson JA, Kenrick DT, eds. 1997. *Evolutionary Social Psychology*. Mahwah, NJ: Erlbaum

Singh D. 1993. Adaptive significance of waist-to-hip ratio on judgments of women's attractiveness. *J. Pers. Soc. Psychol.* 65:293–307

Slobodkin L, Rapoport A. 1974. An optimal strategy of evolution. *Q. Rev. Biol.* 49:181–200

Smith BH. 2000. Sewing up the mind: the claims of evolutionary psychology. See Rose & Rose 2000, pp. 129–43

Smith EA, Winterhalder B, eds. 1992. *Evolutionary Ecology and Human Behavior*. New York: Aldine

Sober E, ed. 1994. *Conceptual Issues in Evolutionary Biology*. Cambridge, MA: MIT Press

Sober E, Wilson DS. 1998. *Unto Others: The Evolution and Psychology of Unselfish Behavior*. Cambridge, MA: Harvard Univ. Press

Star SL, ed. 1995. *Ecologies of Knowledge: Work and Politics in Science and Technology*. Albany, NY: SUNY Press

Symons D. 1979. *The Evolution of Human Sexuality*. New York: Oxford Univ. Press

Symons D. 1992. On the use and misuse of Darwinism in the study of human behavior. See Barkow et al. 1992, pp. 137–59

Tassinary LG, Hansen KA. 1998. A critical test of the waist-to-hip-ratio hypothesis of female physical attractiveness. *Psychol. Sci.* 9:150–55

Tattersall I. 1995. *The Fossil Trail*. New York: Oxford Univ. Press

Thelen E. 1992. Development as a dynamic system. *Curr. Dir. Psychol. Sci.* 1:189–93

Thelen E, Smith LB. 1994. *A Dynamic Systems Approach to the Development of Cognition and Action*. Cambridge, MA: MIT Press

Thiessen D. 1996. *Bittersweet Destiny: The Stormy Evolution of Human Behavior*. New Brunswick, NJ: Transaction

Thornhill R, Palmer CT. 2000. *A Natural History of Rape*. Cambridge, MA: MIT Press

Tooby J, Cosmides L. 1992. The psychological foundations of culture. See Barkow et al 1992, pp. 19–136

Trivers RL. 1971. The evolution of reciprocal altruism. *Q. Rev. Biol.* 46:35–57

Trivers RL. 1972. Parental investment and sexual selection. In *Sexual Selection and the Descent of Man*, ed. B Campbell, pp. 136–79. Chicago: Aldine

Trivers RL. 1974. Parent-offspring conflict. *Am. Zool.* 14:249–64

Waal FBM de, Lanting F. 1997. *Bonobo: The Forgotten Ape*. Berkeley: Univ. Calif. Press

Wahlsten D. 1999. Single-gene influences on brain and behavior. *Annu. Rev. Psychol.* 50:599–624

Weingart P, Maasen S, Segerstråle U. 1997. Shifting boundaries between the biological and the social: the social and political contexts. In *Human by Nature: Between Biology and the Social Sciences*, ed. P Weingart, SD Mitchell, PJ Richerson, S Maasen, pp. 65–102. Mahwah, NJ: Erlbaum

Wilson DS. 1975. A theory of group selection. *Proc. Natl. Acad. Sci. USA* 72:143–46

Wilson DS. 1983. The group selection controversy: history and current status. *Annu. Rev. Ecol. Syst.* 14:157–87

Wilson DS. 1997. Altruism and organism: disentangling the themes of multilevel selection theory. *Am. Nat.* 150:S122–34

Wilson EO. 1975. *Sociobiology*. Cambridge, MA: Harvard Univ. Press

Wilson EO. 1998. *Consilience: The Unity of Knowledge*. New York: Knopf

Wimsatt WC. 1999. Generativity, entrenchment, evolution and innateness. In *Biology Meets Psychology: Constraints, Connections and Conjectures*, ed. V Hardcastle. Cambridge, MA: MIT Press

Wimsatt WC. 1980. Reductionistic research strategies and their biases in the units of selection controvery. In *Scientific Discovery: Case Studies*, ed. T Nickles, pp. 213–59. Dordrecht, The Netherlands: Reidel