



## Evolutionary Psychology: Adaptationist, Selectionist, and Comparative

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## Evolutionary Psychology: Adaptationist, Selectionist, and Comparative

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We share Buss's enthusiasm about the potential of evolutionary ideas as "a new paradigm for psychological science." Psychology's basic hypothetical constructs—from afterimages to attribution processes, from sex-role socialization to synaptic plasticity—are already almost invariably formulated at a level of abstraction chosen to escape the locally and historically particular and thus to describe human (or other species') "nature." In other words, the entities and processes of central interest to psychologists are hypothesized biological adaptations. As Buss aptly stresses, evolution by selection is the only known process capable of producing such adaptations. It follows that keeping abreast of conceptual developments in evolutionary biology can be an aid to psychologists, as it is to other life scientists.

In this commentary, we expand on the implications of evolutionary thinking for psychology, emphasizing three points that are not explicit in Buss's treatment. The first is that assumptions and hypotheses about adaptive function are inescapable in the life sciences, including psychology, and are nothing to be ashamed of; the popular notion that "hard sciences" eschew such "teleological" ideas is both wrong and an impediment to the generation of sophisticated hypotheses about complex systems. Our second point is that sound adaptationist thinking is facilitated by explicit consideration of the process of evolution by selection. Our third point is that evolutionary thinking is often especially illuminating in the context of cross-species comparative analyses, particularly with respect to convergent rather than homologous attributes.

### Adaptationism Is Essential in the Life Sciences

The past three decades have witnessed an explosion of adaptationist, selectionist theorizing and research in

evolutionary (especially behavioral) biology. The word *adaptationist* refers to explicit consideration of how attributes, including such psychological attributes as decision-making and information-processing algorithms, are suited to their functions. *Selectionist* implies explicit consideration of how natural selection and sexual selection operate to shape adaptations over generations. These developments in evolutionary behavioral biology have been called the *sociobiological revolution*, although most contemporary participants prefer to call their field *behavioral ecology*.

Adaptationist thinking is a ubiquitous and inescapable element of investigation in the life sciences. As the eminent evolutionary biologist Ernst Mayr (1983) noted, for example, in response to a misguided complaint about adaptationism within biology:

The adaptationist question, "What is the function of a given structure or organ?" has been for centuries the basis for every advance in physiology. If it had not been for the adaptationist program, we probably would still not yet know the functions of thymus, spleen, pituitary, and pineal. Harvey's question "Why are there valves in the veins?" was a major stepping stone in his discovery of the circulation of blood. If one answer turned out to be wrong, the adaptationist program demanded another answer until the true meaning of the structure was established or until it could be shown that this feature was merely an incidental byproduct of the total genotype. (Mayr, 1983, p. 328)

Assumptions and hypotheses about adaptive function pervade psychology for the same reason that they pervade physiology—because the mechanisms under study are so obviously organized in such a way as to "achieve something." Investigation is guided by conceptions of what that "something" might be—whether signal detection, or perceptual constancy, or self-actualization, or relief from cognitive dissonance. Unfortu-

nately, adaptationist thinking in psychology has often been naive due to failures to make use of contemporary understandings of selection—the process that creates adaptations.

Oddly, despite the transparently adaptationist nature of psychological constructs and theories, many psychologists remain skeptical of explanations that invoke ends. According to Sober (1983), “psychology has regularly looked to the other sciences for some indication of how to progress” (pp. 115–116), and the message it derived from the history of physics is “that a science progresses by replacing teleological concepts with ones that are untainted by goals, plans, and purposes” (p. 115). Moreover, argued Sober, the fore-swearing of functional explanation “received further impetus from the Darwinian revolution in biology” (p. 115), because Darwin replaced a purposeful creator with a blind process. The irony is that Darwin’s discovery of natural selection did not obviate seemingly “teleological” concepts; it legitimized them, by showing how and why the consequences of biological phenomena constitute an essential part of the explanation for their existence. Darwin’s discovery should have rendered the simplistic “physics envy” described by Sober obsolete, because it provided a materialistic explanation for the manifest but previously incomprehensible fact that living things have complex purposiveness instantiated in their structures.

### Selectionism Guides Sophisticated Adaptationism

If psychological research is already guided by assumptions and hypotheses about the adaptive organization of psychological entities and processes, why should psychologists trouble to learn some evolutionary biology? One answer is that, although they correctly apprehend that they are studying complex systems organized to achieve something, psychologists’ notions of what that “something” might be are often incomplete. There are clearly hierarchies of function; lateral inhibition in the retina, for example, is a means to the end of edge detection, which is a means to the end of object recognition, which is a means to the ends of foraging and predator avoidance, which are means to the ends of energy accrual and survival. Psychologists have wandered down innumerable garden paths by imagining that the summit to this hierarchy of functions—the end to which all the organism’s immediate objectives are subsidiary—is homeostatic quietude, or personal growth, or longevity, or “the reproduction of the species,” or even death, when the “something” that organisms are organized to achieve is none of these. According to contemporary evolu-

tionary understanding, the “something” that organisms are organized to achieve is Darwinian fitness—the replicative success of an organism’s genes, relative to its alleles, in a statistical aggregate of the environments encountered by the organism’s ancestors.

In selectionist light, many expectations generated by everyday adaptationist thinking are suspect. Can we expect, for example, that the evolved mechanisms of “hunger” will motivate action to avert starvation? No, we cannot, if feeding behavior’s predictable side-effects on fitness are sufficiently negative; this insight has led to the discovery of a variety of “adaptive anorexias” (Mrosofsky & Sherry, 1980), unsuspected by hunger researchers unaccustomed to selection theory. And, implications of contemporary evolutionary models extend even further than the insight that adaptations are functionally reproductive rather than merely survival promoting. Can we expect, for example, that evolved mechanisms of maternal–fetal interaction will promote fetal well-being with minimal energetic and material wastage? No, we cannot, if reproduction is sexual, so that maternal and fetal fitnesses are disjunct (Trivers, 1974); this insight has illuminated a host of otherwise puzzling phenomena in human pregnancy (Haig, 1993). Thus, evolutionarily sophisticated adaptationism facilitates insights and discoveries that the naive adaptationism of most psychologists overlooks.

Unfortunately, scientists ill-versed in evolutionary theory often imagine that its concept of functionality is isomorphic with an account of goals and drives. In other words, adaptationist theorizing is commonly misconstrued as a claim that fitness itself is what people and other animals strive for. As Buss notes (in explaining why he is “not a sociobiologist”), the same misunderstanding occasionally afflicts evolutionists, too. However, we do not think it is apt to call this the *sociobiological fallacy*, for behavioral ecologists and sociobiologists usually invoke fitness consequences appropriately—not as direct objectives or motivators, but as explanations of why certain more proximal objectives and motivators have evolved to play their particular roles in the causal control of behavior. In our experience, the so-called sociobiological fallacy is more frequently committed by evolutionarily unsophisticated critics of “sociobiology,” who invoke phenomena like voluntary childlessness and exclusive homosexuality as evidence against “the theory.” These challenges are empty because, as Buss rightly emphasizes, adaptation is not prospective. No version of the theory of evolution by selection predicts that organisms will magically zero in on whatever it takes to maximize their fitness in novel environments with important differences from those in which their adaptations evolved.

### Cross-Species Comparative Analyses Elucidate Adaptation

In addition to constraining adaptationist speculation with selectionist rigor, evolutionary biology offers psychologists an explicitly comparative agenda quite different from the classical concerns of rat-pigeon-monkey psychology. Recent advances in cross-species comparative analysis (e.g., Harvey & Pagel, 1991) are not primarily concerned with the elucidation of phylogenetic continuities (what cognitive precursors of language can we find in apes, etc.) and still less with the use of arbitrary “animal models” to study “basic” processes of great taxonomic sweep, like conditioning. Instead, what recent evolutionary thinking offers psychology is a disciplined way to understand both similarities and differences in the attributes of closely and distantly related species in relation to species-characteristic ecologies and the adaptive problems they entail (e.g., Beecher, 1990).

Consider Trivers's (1972) theory of parental investment and sexual selection, which Buss uses as his principal example (Figure 1) of “middle-level evolutionary theories.” The illustrative “hypotheses” that Buss derives from this theory are implicitly comparative, but it is perhaps unfortunate that his illustrative lower level “predictions” are then concerned solely with the preferences of women and men and thus fail to fully convey the predictive power of the theory. Trivers's analysis has been influential primarily because it organized and made sense of a great deal of information about cross-species variations in morphology, social behavior, and life-history parameters and about the magnitude and direction of sex differences therein. His claim that sex differences in parental investment entail selection pressures for sex differences in courtship, for example, was made convincing by its success in predicting cross-species diversity in courting behavior (e.g., Gwynne, 1983).

Particular adaptive problems are characteristic of particular ways of living, so requisite psychological mechanisms, described at the level of their adaptive functions, can often be predicted from ecology. Closely related animal species, for example, incur variable risk of misdirecting their parental investment to unrelated young, so we may predict variability in the psychological mechanisms of “discriminative parental solicitude” (Daly & Wilson, 1994). Bank and cliff swallows nest colonially, whereas rough-winged and barn swallows nest more dispersedly; newly flying young sometimes return to the wrong nest in the two colonial species but seldom or never in the dispersed species (Beecher, 1990). Beecher and colleagues have predicted and demonstrated superior offspring recognition in the colonial species and have shown that selection for offspring recognition has affected attributes of both

the chicks and their parents. The calls of colonial-species chicks are intrinsically more discriminable than those of dispersed-species chicks, as shown both by informational analyses of the physical properties of the calls (Beecher, 1988) and by superior discrimination of the calls of colonial-species chicks by adults of either nesting type, as well as by other animal species (Loesche, Beecher, & Stoddard, 1992; Loesche, Stoddard, Higgins, & Beecher, 1991). Adaptation on the parental side is indicated by the fact that adult cliff swallows (colonial) outperform adult barn swallows (dispersed) on these tasks, even when the calls to be distinguished are those of barn swallows (Loesche et al., 1991). This work illustrates how species differences in a complex cognitive capability can be elucidated, not as characteristics of some “level” on an evolutionary “scale,” but as adaptations to species differences in social ecology.

This comparative perspective on adaptations entails a serious challenge to psychologists' uncritical uses of “lower” mammals as “models” in which to seek simpler versions of our own mental adaptations. Consider mammalian mothering. Its physiology has been studied primarily in rats and other burrow-dwelling rodents, who, like the dispersed-nesting swallows, have not experienced a history of selection for rapid discriminative attachment to their own young. There is one intensively studied mammalian species, however, that has experienced precisely such selection—sheep. An individualized bond between ewe and lamb is typically established within 3 hr of parturition (Poindron & Le Neindre, 1980), as indeed it must be, because young are precociously mobile and are born close together in both time and space. Although many elements of the neuroanatomy and chemistry of maternal motivation are similar in sheep and rats and may even be universal in Mammalia (e.g., Kendrick, Keverne, Hinton, & Goody, 1992), sheep also possess a complex set of neurophysiological and neurochemical adaptations to the specific problem of individualized maternal responsiveness (Kendrick, Lévy, & Keverne, 1992). These mechanisms, apparently absent in rats and other burrow-dwelling rodents who do not encounter the same adaptive problem, were discovered in sheep only because Kendrick and his collaborators recognized that precocious, gregarious animals need psychological mechanisms for rapid, selective maternal bonding. Physiological mechanisms of parental motivation are adapted to species-specific social ecologies, and a physiological psychology that lacks this insight will never make sense of species differences.

Related to this problem of discriminative parental bonding is a subject treated at length in Buss's target article—the evolutionary consequences of the sex difference in “certainty of parenthood.” In animals with internal fertilization, males are vulnerable to “cuck-

oldry”—that is, to investing their efforts in caring for young produced by their mates but sired by rivals. Recent field studies using “DNA fingerprinting” have shown cuckoldry to be a surprisingly prevalent selective force in “monogamous,” biparental bird species (Birkhead & Møller, 1992), favoring the evolution of countermeasures. For example, male birds often guard their mates during their fertile periods and have been shown experimentally to modulate this guarding in response to a variety of cues indicative of cuckoldry risk, including behavioral correlates of impending ovulation and the appearance of an egg in the nest (indicative of daily fertilization opportunities until the clutch is complete), as well as the number, proximity, rate of intrusion, and relative attractiveness of male neighbors who might cuckold the guarding male (Birkhead & Møller, 1992). Many of the same cues also influence the male’s rate of copulating with his mate—a “sperm competition” tactic by which he increases his expected paternity of his brood if his mate has in fact engaged in an extra-pair copulation (Birkhead & Møller, 1992). Moreover, after the eggs hatch, male birds have been shown to adjust their paternal care in relation to events such as neighbor intrusions and lapses in mate guarding during the earlier mating period, which constitute circumstantial evidence of cuckoldry (e.g., Davies, 1992; Møller, 1988b).

In light of these bird studies, it is striking how little we know about anti-cuckoldry tactics in our own species. The substantial body of social psychological literature on sexual jealousy has yet to address how (or even whether) jealous feelings and actions might track the fertility and mate value of their objects (Wilson & Daly, 1992). Human sperm competition *has* begun to be considered by evolutionists, and morphological, physiological, and psychological evidence is converging to imply that polygamous inclinations on the part of women as well as men have been significant selective forces (see Baker & Bellis, 1995; Møller, 1988a). Nevertheless, the natural history of human mate-guarding remains virtually unexplored, with the exception of studies by the evolution-minded anthropologist Flinn (1988), who showed that potentially fertile women in a Caribbean village were more consistently accompanied by their spouses than were those who were pregnant or postmenopausal. The bird research cited earlier also suggests many hypotheses about possible psychological links between sexually proprietary motives and other motivational systems such as libido and parental affection, but such hypotheses have yet to be tested or even articulated by psychologists lacking a comparative, selectionist perspective.

Comparative evidence can also aid us in better characterizing the adaptive functions of particular attributes in a focal species, such as *Homo sapiens*. We might blithely interpret mate-guarding, jealousy, and sperm-competition

tactics as anti-cuckoldry adaptations, for example, until it is drawn to our attention that similar adaptations are ubiquitous in species in which males play no parental role and therefore cannot be cuckolded. The copulatory plugs of male rats and the postcopulatory guarding of cows by male bison illustrate the fact that adaptations for male sexual rivalry are endemic regardless of whether males play a parental role. Mate guarding *per se* therefore cannot be interpreted as an anti-cuckoldry adaptation. However, one might hypothesize that guarding’s priority within the male’s time budget is affected by cuckoldry risk, and an appropriate test of such a hypothesis would involve comparing species in which males make significant paternal investments with related species in which they do not.

Whether human male psychology incorporates specific anti-cuckoldry adaptations—over and above the adaptations to intrasexual rivalry that we might expect in a species with solely maternal care—has scarcely yet been addressed. Such adaptation might be manifested more clearly in parental psychology and behavior than in mate guarding. Davies’s (1992) and Møller’s (1988b) demonstrations of modulated paternal investment in response to probabilistic cues of paternity, for example, provide clear evidence that males of some species possess anti-cuckoldry adaptations over and above their adaptations for intrasexual competition for fertilizations. Do men? One hypothesis suggested by this line of thinking is that the psychology of human parental affection should be sexually differentiated, with men’s but not women’s feelings influenced by cues such as the child’s resemblance to self. Perhaps surprisingly, no nonhuman species has been shown to use such phenotype matching as a paternity cue, but human males may (see Daly & Wilson, 1982; Regalski & Gaulin, 1993).

Psychologists are increasingly aware that the human psyche encompasses an indeterminately large number of adaptations to ancestral social and material environments and that sophisticated selectionism can help elucidate them (see, e.g., Barkow, Cosmides, & Tooby, 1992; Tooby & Cosmides, 1992). Still relatively rare is an appreciation of the potential value of considering human attributes within the rigorous comparative framework expounded by Harvey and Pagel (1991).

#### Note

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## The New Evolutionary Psychology: Prospects and Challenges

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Evolutionary thinking is, of course, no stranger to psychology. The historical footings of psychological science stand in the soils of two other disciplines: (a) German physiological science wedded with British empiricism and (b) 19th-century Darwinian biology. The former are emphasized in historical texts that draw on the writings of Boring (1950). Many developments during the formative years of psychological science, however, cannot be appreciated in absence of a recognition of Darwinian influences. Naturally, behavioral geneticists explicitly acknowledge the influences of quantitative geneticists such as Fisher (1918) and Wright (1921). Many developmentalists and comparative psychologists too recognize the historical importance of Darwinism to their fields (e.g., Cairns, 1983).

Even many schools of thought that largely concern environmental factors, however, are deeply rooted in Darwinian thought. Clark Hull paid homage to two intellectual ancestors of other disciplines—Maxwell and Darwin. Freud’s reliance on evolutionary notions, albeit highly Lamarckian ones, have been well-documented (Sulloway, 1979). Even radical behaviorists have noted an alliance with evolutionary “selectionist” thinking (e.g., Catania, 1978).

### The New Evolutionary Psychology

If Darwinism has pollinated virtually every sub-discipline and perspective within psychology, does evolutionary psychology offer our science a “new