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# The Past Explains the Present

## Emotional Adaptations and the Structure of Ancestral Environments

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Present conditions and selection pressures are irrelevant to the present design of organisms and do not explain how or why organisms behave adaptively, when they do. To whatever non-chance extent organisms are behaving adaptively, it is 1) because of the operation of underlying adaptations whose present design is the product of selection in the past, and 2) because present conditions resemble past conditions in those specific ways made developmentally and functionally important by the design of those adaptations. All adaptations evolved in response to the repeating elements of past environments, and their structure reflects in detail the recurrent structure of ancestral environments. Even planning mechanisms (such as "consciousness"), which supposedly deal with novel situations, depend on ancestrally shaped categorization processes and are therefore not free of the past. In fact, the categorization of each new situation into evolutionarily repeating classes involves another kind of adaptation, the emotions, which match specialized modes of organismic operation to evolutionarily recurrent situations. The detailed statistical structure of these iterated systems of events is reflected in the detailed structure of the algorithms that govern emotional state. For this reason, the system of psychological adaptations that comprises each individual meets the present only as a version of the past.

**KEY WORDS:** Emotion; Adaptation; Adaptationist program; Evolutionary psychology; Environment of evolutionary adaptedness.

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[I]t is very weak methodologically for sociobiology to appeal to past advantages as an explanation of present behavior . . . Widespread current behaviors have consequences in terms of inclusive fitness at the present time. If they are to be explained on biological grounds at all, they are to be explained in terms of their contribution to inclusive fitness at the present time.

Austin Hughes (1987, p. 417)

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The variety of social systems and social strategies that we see even within a given species is simply the consequence of the same deep structure rule (say "Maximize the number of offspring you rear to maturity") finding expression in a variety of different forms depending on the particular demographic and environmental context. . . .

[T]hose that concentrate on a search for species-wide universals in behaviour or morphological traits are likely to be disappointed. The number of genuinely universal traits are, I suspect, likely to run to single figures at most and probably correspond to the handful of biological "needs" like warmth, food, and procreation.

Robin Dunbar (1988, pp. 166–168)

My main criticism of Medawar's statement is that it focuses attention on the rather trivial problem of the degree to which an organism actually achieves reproductive survival. The central biological problem is not survival as such, but design for survival.

George Williams (1966, p. 159)

## THE ADAPTATIONIST PROGRAM VERSUS THE CORRESPONDENCE PROGRAM

**T**here is a deep though largely unexplored schism in modern evolutionary thought over the nature of evolutionary functionalism. Differences reflecting this schism revolve around the question of what role present conditions as opposed to past conditions play in the functional explanation of a species' set of adaptations. Those who emphasize the role of ancestral conditions tend to focus on such concepts as design; adaptation; mechanism; fitness, as a property of a design or the genes underlying a design; histories of selection; complexity of functional design; standards of evidence for adaptations (such as efficiency, economy, and precision); the prevalence of species-typicality in complex functional design; the characterization of ancestral conditions or environments of evolutionary adaptedness; and, most of all, the cause and effect relationship between ancestral conditions and present adaptations (see, e.g., Barkow 1984, 1989; Cosmides and Tooby 1987; Daly and Wilson 1988; Dawkins 1976, 1982, 1986; Tooby and Cosmides 1989a, 1989c; Williams 1966, 1985; see especially Symons 1987, 1989, 1990). Those who emphasize the role of the present tend to focus on adaptiveness; behavior; fitness, as the property of individuals; the assessment of fitness differentials between individuals; ongoing selection; individuals construed as inclusive fitness-maximizers or fitness-strivers; claims that contextually appropriate behavioral variation is driven by fitness-maximization; an antagonism to characterizing species-typicality (or even stable design) presented as a principled opposition to typological thinking; the present as the environment to which individuals are adapted; the fitness consequences of present behavior; and, most of all, the *correspondence* between present conditions and present fitness-maximizing behaviors (see, e.g., Alexander 1979a, 1979b, 1981; Betzig 1989; most of the articles

in Betzig, Borgerhoff Mulder and Turke 1988; Borgia 1989; Caro and Borgerhoff Mulder 1987; Dunbar 1988; Hughes 1987; Smuts 1989). Although the literature cited deals largely with humans, where the debate is particularly active, it accurately reflects a division that extends throughout the community of behavioral ecologists, and, in fact, throughout biology as a whole. To identify these ideas as a single integrated viewpoint associated with specific individuals as if they were consistent exponents of one side of a binary debate would be a mistake, because nearly everyone in the evolutionary community employs, at one time or another, most of these common concepts for varied purposes. For example, Turke (1990) attempts to produce a hybrid of the two approaches, which starts out arguing for something resembling an adaptationist program, but ends up endorsing and practicing something closer to the second view. Leaving aside the question of within individual consistency, the ways in which these concepts are systematically used in evolutionary discourse add up to profoundly different visions of the role of the concept of function in evolutionary biology. It is the validity of these alternative approaches to the concept of function, not the views of specific individuals, which is at issue. We will refer to the first approach as the *adaptationist program* and to the second approach as the *correspondence or adaptiveness program* (Symons 1990).

As we and others have argued previously (Cosmides and Tooby 1987; Tooby and Cosmides 1989a, 1989c; Symons 1989, 1990, in press), an evolutionary functionalism that leapfrogs the characterization of adaptations and in its place simply catalogues correspondences between present behavior and present fitness is incomplete and is often guided by serious misinterpretations of Darwinism. We summarize the correspondence (or adaptiveness) view as follows:

Evolutionary theory states that organisms evolved to be inclusive fitness-maximizers and therefore predicts that organisms ought to be behaving adaptively in their present circumstances. This means that functional analysis involves viewing present behavior (or morphology) as the attempt to solve the adaptive problems posed by present circumstances. Darwinism or functional analysis is therefore the investigation of how an individual's present behavior corresponds to or leads to fitness-maximization in its present circumstances.

Taken literally, these widely used concepts are incorrect, and they ought to be abandoned as veridical characterizations of Darwinism, functional analysis, and phenotypes. As thought experiments or heuristic devices, however, they can sometimes be useful in guiding thinking, model building, and experimentation, as long as their fundamentally metaphorical nature is not forgotten. Unfortunately, these constructs are now being treated not as heuristic devices, but as uncontroversial factual claims about the character of modern evolutionary and behavioral ecological theory. This process has gone so far that the adaptationist-based evolutionary functionalism that logically derives from the theory of evolution by natural selection has been

obscured and in many literatures nearly supplanted by the correspondence program. The difference in views is most striking in how each treats the role of the past.

In *Adaptation and Natural Selection*, Williams criticized (among many other things) the attribution of foresight and anticipation to the evolutionary process, which some claimed created “adaptations designed to meet the demands of geologically future events” (1966, p. 21). This criticism also applies to positing adaptations that evolved to meet the demands of present conditions. An organism’s genetic endowment is fixed at conception, and the conditions the developing phenotype faces constitute an unknown future with respect to the evolutionary processes that determined that genetic endowment. Present adaptations were constructed by natural selection in the past, over evolutionary time, without foreknowledge of the conditions they would encounter in the present. Moreover, the effect of present environments on present genetic variability in adaptive designs is the process of ongoing selection, which produces future but not present adaptations. Consequently, the study of ongoing selection is not closely connected to the study of adaptations either, although each may cast some light on the other.

The causal link between past conditions and present biological design is the necessary, logical core of Darwinian explanation. In contrast, the adaptive correspondence between present conditions and present behavior, to the extent that it exists, is contingent, derived, and incidental to Darwinian explanation. It depends solely on how much the present ontogenetic environment of an individual happens to reflect the summed features of the environment during recent evolutionary history, that is, on how different the present environment is from ancestral conditions. In no sense is the correspondence between present conditions and present adaptations a cause of those adaptations, and the current consequences of those adaptations on inclusive fitness is not a cause or an explanation for those adaptations. Present selection pressures or environmentally imposed tasks are causally irrelevant to the present design of organisms and have no role in explaining them. For a Darwinian, the explanation for our present system of adaptations lies completely in the past, starting one generation ago, and extending back across phylogenetic time to include the history of selection that constructed those designs.

## TELEOLOGY

The human mind seems to love teleology. As human beings, one of the most important things we do is try to understand, explain, and predict the behavior of others, and we have powerful folk theories for doing so. Desires, purposes, strategies, goal-seeking, and intentions are teleological concepts that play a powerful role in these folk theories. The appeal of teleological concepts is so strong that even physicists, who have systematically expunged teleology

from any formal role, informally discuss concepts and experiments in teleological terms, saying, for example, “the muon wants to decay, but is blocked from doing so because . . .” (Daston, personal communication; Galison, personal communication; Malament, personal communication). Teleological metaphors can make reasoning about certain problems far easier, and there is nothing wrong with this, unless and until one forgets the limitations on their applicability and takes them to be facts.

We suggest that the search for adaptiveness has displaced the search for adaptations because the theoretical logic of adaptationism is expressed in nonteleological causal terms, whereas the correspondence program is expressed primarily in appealing teleological terms such as goal-seeking (“the goal of evolution”), purpose (“adaptive purpose”), striving (“fitness striving”), attempts (“the organism’s attempt to solve the adaptive problem”), pursuit (“the pursuit of fitness”), strategies (“the organism pursues a fitness-promoting strategy”), interests (“fitness interests”), motivational characterizations (“selfishness”), and so on. Teleology seems to be far more congenial to spontaneous human thinking, creating the danger that teleological analogy may drive out nonteleological causal reasoning. We suspect this preference for teleology stems from the fact that humans have conscious access to evolved cognitive processes involved with planning, choosing goals, assessing others’ motivations, and improvising methods for seeking goals (see Alexander 1989), but not to many of our innately derived models of physical causality (Proffitt and Gilden 1989). For this reason, we tend to impose teleological models on the world, sometimes very inappropriately (e.g., the goal of evolution was to produce humans), and sometimes because feedback-driven causal processes somewhat resemble teleological processes (e.g., the “goal” of evolution is fitness-maximization or gene propagation).

Problems caused by the noncorrespondence between the causal processes in evolution and our teleologically expressed intuitive models become especially acute when behavior is at issue. Few are tempted to attribute goal-seeking to morphological structures, but some psychological structures do contain goal-seeking subsystems—feedback mechanisms that regulate behavior such that an internally represented state of the world is achieved. The fact that feedback processes in evolution superficially resemble goal-seeking mechanisms in organisms leads to the seductive error of believing that the two levels—evolutionary processes and psychological mechanisms—are really one level or refer to the same elements (Tooby and Cosmides 1989c). This error is the source of claims that evolution’s “goal” is the goal of organisms; that because evolution fitness-maximizes, organisms are goal-seeking fitness-maximizers; that evolution’s “purposes” are the organism’s purposes, and so on. Once this conflation of evolutionary process with psychological mechanism is made—once organisms are construed as the agents of the evolutionary process, effortfully striving to accomplish the goal of fitness-maximization—then the evolutionary study of behavior becomes transformed into the search for the correspondence between observed

behavior and fitness-maximization in present conditions. Ancestral conditions seem to be logically irrelevant, or at most a “weak” (Hughes 1987) explanation perhaps to be dragged in *ad hoc* or as a last resort to explain some residue of behavior that is not presently fitness-maximizing.

## THE MODERN SYNTHESIS AND THE STUDY OF VARIATION

A second reason why the study of fitness variation has mostly eclipsed the study of adaptation in modern evolutionary biology has to do with the central ideas of the Modern Synthesis. Synthesizing Darwinism with Mendelism was a signal achievement and produced an elegant formal algebra with which to describe the ongoing process of natural selection. Nearly all of population genetics consists of the elaboration of a mathematics to describe the varieties of genetic change and ongoing selection (Fisher 1958; Wright 1968, 1969, 1977, 1978). Evolution went from being described as the modification of designs along lineages (Darwin’s approach), to being described as change in gene frequencies (Fisher 1958). There is no corresponding formalism with which to describe the complex functional designs that are the accumulating product of ongoing selection. What’s more, there is no formalism for describing the process of natural selection as transitions between designs. In population genetics, designs show up purely as some allele or combination of alleles, that is, as part of some system of genetic variation. As alleles become fixed they tend to disappear from the analysis, leaving the accumulated uniformity of the evolving organisms’ complex design invisible to these tools of mathematical analysis.

Because this elegant formalism only spoke to issues of genetic variation, such as the dynamics of drift and ongoing selection, empirical studies tended to focus on related phenomena that were observable: the distribution of genetic variation; the relationship between genetic variation and phenotypic variation; the patterns of variability within and between populations; fitness differentials between individuals (Dobzhansky 1937, 1970; Mayr 1963). In this research, the study of design was usually limited to the study of ongoing selection, with fitness differentials being related to heritable differences. With some exceptions, analysis with these kinds of tools depends upon the ability to observe variation between individuals. For this reason, there are many studies of such phenomena as environmental gradients associated with genetic or phenotypic gradients. But when a gene reaches fixation it no longer creates heritable differences between individuals; at that point it disappears from the analytic scope of the study of variation. Consequently, present variation in design and ongoing selection was visible to these methods, whereas the uniform design reflecting already completed selection was invisible. Unfortunately, the vast preponderance of organic design representing the accumulated effects of four billion years of selection reflects

completed rather than ongoing selection. To study variation is to bypass most of the structure of complex functional design.

Of course, such formal models of gene propagation (e.g., Hamilton 1964; Fisher 1957) are essential to understanding the process of natural selection. These families of analysis have the effect of concentrating attention on what might be called the dynamical present of the model, that is, the time at which gene substitution takes place. But this dynamical present is always changing in the real world: each historical moment was the dynamical present for some evolutionary event. Unfortunately, this contributes to the unwarranted tendency for some evolutionary biologists to associate the dynamical present of their models with the observed present of the real world and thus to emphasize the present over the series of present moments that constitute the past history of life.

## FROM CORRESPONDENCES TO CAUSAL EXPLANATIONS

There is nothing wrong *per se* with documenting correspondences, and in fact, such investigations can be very worthwhile. Sciences often begin as the discovery of some pattern of correspondence in the world and are extended by the discovery of others. The east coast of the Americas appears to correspond to the west coast of Europe and Africa. The chemical properties of the elements show recurrent patterns that allow them to be organized into a periodic table. Economists attempt to explain behavioral observations by trying to show how such behavior corresponds to rational utility maximization, a simple axiomatized idealization. In evolutionary biology, the correspondence view frames behavioral investigations as a kind of evolutionary economics, in which one shows how behavior corresponds to “rational fitness-maximization” in present conditions (Hughes 1987). For those who use such correspondence theories, the primary task is taken to be explaining how a set of observations corresponds to the operation of such a principle.

But genuine understanding is found when one not only has rules of correspondence (e.g., continental boundary parallels), but when one also has a causal model of why those correspondences are there (e.g., plate tectonics). As a field matures, one set of correspondences is shown to be the causal expression of another more basic set (although, of course, some final level of principles such as quantum mechanics is simply a given). The discovery of such correspondences is one possible starting point in the evolutionary analysis of behavior or morphology (Turke 1990). But the adaptationist and correspondence programs diverge in how they treat these correspondences and why they are considered important. For the correspondence researcher, the analysis of how behavior corresponds to fitness maximization *is* the evolutionary explanation, whereas for the adaptationist

the discovery of such a correspondence is not an explanation at all, but rather a phenomenon—however much expected—that itself requires explanation.

For an adaptationist, the causal explanation runs as follows. Either the correspondence between some specified present behavior and what it takes to fitness-maximize (really, fitness-promote) in present conditions is either a coincidence or brought about through systematic causal processes. If an organism is behaving in a certain way in response to a given environmental variable, it is because some set of properties in the organism cause it to do so. To make the claim that behavior is adaptive and that this adaptiveness is not a coincidence is to make the claim that the organism has an adaptation that is solving the adaptive problem. To make the claim that such adaptations exist is to make the claim that they were shaped by a history of selection in ancestral conditions, because natural selection is the only known process (aside from intelligent manufacture) that can create complex functional design over time (Dawkins 1986). To whatever extent, great or small, a particular present behavior is still adaptive, it is because present conditions still happen to resemble ancestral conditions. Therefore, adaptations are the causal explanation for whatever adaptiveness manifests itself and characterizing adaptations constitutes a necessary part of the explanation of any principle of correspondence, such as why foragers approximately follow the marginal value theorem (Charnov 1976). The theory that describes the logic of the entire causal process responsible for adaptations is Darwinism.

## DARWINISM AND ADAPTATIONS

From a Darwinian perspective, the defining property of life is the reproduction by systems of new and similarly reproducing systems. From this defining property, reproduction, the deductive structure of Darwinism can be built (Dawkins 1976; Williams 1985). The logical core of Darwinism is the theory of natural selection, involving reproduction of design, inheritance of design, variation in design, and differential rates of reproduction caused by differences in design.<sup>1</sup> The fact that the properties of designs have an

<sup>1</sup> Complications are introduced by the transition from asexual to sexual reproduction because the identity or replicative concordance between genome and gene (or organism's design and transmitted design) was broken, creating the potential for intragenomic conflict (Cosmides and Tooby 1981; Tooby 1982). Sexual reproduction breaks the genome into subsets of genes whose reproduction can be, and often is, accomplished under different circumstances, or with different probabilities. Each set (coreplicon) is selected to modify the phenotype of the organism in a way that maximally propagates the genes comprising that set, and hence in ways inconsistent with the other sets that comprise the total genome. Because fitness cannot be maximized for all genes in an individual in the same way, fitness cannot be a property of individuals, but instead can only be assigned to coreplicons, genes, or to inherited designs with a certain specified or assumed kind of genetic basis (cytoplasmic, autosomal, X-chromosomal, generalized Mendelian, etc.). Fitnesses should not be assigned to individuals in any case, because fitnesses are the expected outcomes of certain designs, and not the actual specific reproduction of an individual phenotype. Nevertheless, although the evolution of sex modifies certain elements in Darwinism, the central logic of Darwinism remains essentially intact.



impact on their rate of reproduction creates a system of positive and negative feedback, called natural selection, that forges an organized relationship between the properties of historically encountered environments, the properties of designs, and their frequency in the world. Usually this leads to fixation of the favored design, although frequency-dependent equilibria sometimes set an upper limit on design frequency in the population. Natural selection is the only known process capable of accounting for complex functional design in living things (Williams 1985; Dawkins 1986), and all non-random functionality in living systems must be attributed to the action of adaptations. Adaptations are mechanisms or systems of properties “designed” by natural selection to solve the specific problems posed by the regularities of the physical, chemical, ecological, informational, and social environments encountered by the ancestors of a species during the course of its evolution. As a result of the operation of natural selection, organisms (properly described) consist largely of complexly articulated designs. The detailed specification of adaptations is the most appropriate way of describing and organizing our observations about these designs.

The outcomes of the evolutionary process break down into three basic categories: 1) adaptations (often, though not always complex); 2) concomitants or by-products of adaptations; and 3) random effects. Because concomitants and random flux are usually only identifiable as what is left over after adaptations have been discovered and described, the characterization of a species’ adaptations should generally be procedurally prior to investigating claims about random processes or concomitants (“spandrels”). Adaptations are the result of coordination brought about by selection as a feedback process; they are recognizable by “evidence of special design” (Williams 1966)—that is, by a highly nonrandom coordination between recurring properties of the phenotype and the ancestral environment, which mesh to promote fitness (genetic propagation). Standards for recognizing special design include such factors as economy, efficiency, complexity, precision, specialization, and reliability (Williams 1966). The demonstration that an aspect of the phenotype is an adaptation is always, at core, a probability argument concerning how nonrandom this coordination is. Concomitants of adaptation are those properties of the phenotype that do not contribute to adaptation *per se*, but are tied to properties that do, and are therefore incorporated into the organism’s design; they are incidental by-products of adaptations. Any number of concomitants can be “manufactured” at will by the process of describing an organism without reference to its adaptations. There are an infinite number of traits and phenomena one can define and measure, but evolutionarily analyzable order will tend to be found only in those that are causally related to adaptive function.

The study of adaptations can be broken (somewhat arbitrarily) into two halves: evolutionary psychology—the study of the adaptations that regulate behavior—and physiology—the study of morphological structures and processes, whether or not they regulate behavior. To understand the design of

human (or any living species') psychology or physiology is usually a problem in reverse engineering: we have working exemplars of the design in front of us, but we need to organize our observations of these exemplars into a systematic functional description of the design. The central tool for organizing these observations is the concept of adaptation. Approximately, an adaptation is:

- 1) A cross-generationally recurring set of characteristics of the phenotype developmentally manufactured according to instructions contained in its genetic specification or basis, in interaction with stable and recurring features of the environment (i.e., a design);
- 2) whose genetic basis became established and organized in the species (or population) over evolutionary time, because
- 3) the set of characteristics systematically interacted with stable and recurring features of the environment (the "adaptive problem"),
- 4) in a way that systematically promoted the propagation of the genetic basis of the set of characteristics better than the alternative designs existing in the population during the period of selection. This promotion takes place through enhancing either the reproduction of the individual bearing the set of characteristics or the reproduction of the relatives of that individual, or both.

## ADAPTATIONIST ANALYSIS

In approaching a given species' behavior from an adaptationist perspective, evolutionary analysis requires several nested but distinct levels (Tooby and Cosmides 1989c). These are:

1. Models of the evolutionary process, involving definitions of fitness, selection, adaptation, genes, the role of stochastic factors, and general models of such topics as kin-directed altruism, cooperation, sexual recombination, and sexual selection.

2. An analysis of how these principles were manifested as a species-specific array of selection pressures, refracted through the specific ecological, social, genetic, phylogenetic, and informational circumstances experienced along a given species' evolutionary history (Tooby and DeVore 1987). This is the characterization of ancestral conditions, sometimes referred to as "the environment of evolutionary adaptedness." This involves construction of computational theories (Marr 1982; Cosmides and Tooby 1987, 1989), that is, task analyses of what information-processing problems an adaptation must solve.

3. A description of the species' inherited adaptations that evolved to solve the problems posed by the species-specific array of ancestral selection pressures. Steps 1 and 2 are significant because they allow the discovery, investigation, description, and functional analysis of the adaptations. They constitute the ultimate explanation for the design of the adaptations, by specifying the selection pressures and the enduring ancestral conditions in which these selection pressures operated. (It is useful, and often essential,

to have a good description of these adaptations as conditional developmental programs that map environmental input into phenotypic output.)

4. A description of the present environment, the environment of ontogeny, in terms of a) the state of those features that must be stably present for the organism's adaptations to reliably develop, and b) the state of those features that the organism's adaptive procedures take as input and process into structured phenotypic output, such as environmental cues that regulate facultative adaptations, information processed by cognitive mechanisms, or anything else to which the developmental programs contingently respond.

5. To understand and explain all current behavior, whether adaptive or maladaptive, one needs to integrate the information present in steps 3 and 4 into the particular developmental trajectory of an individual (with other individuals modeled as developmental inputs). The developmental programs that conditionally describe adaptations (and by-products and noise, if they are of interest) plus the environment of ontogeny together provide a proximate explanation for current behavior ("vertically integrated" explanations [Barkow 1989]).

Consider, for example, the Westermarck mechanism for promoting incest avoidance (Shepher 1983; Wolf and Huang 1980; Tooby and Cosmides, in press). Analyzing the selection pressures against inbreeding, such as making deleterious recessives homozygous or increasing disease load (Tooby 1982), constitutes the first stage in the analysis. Analyzing the operation of these forces during our evolutionary history constitutes the second step: what were the statistical properties of the genetic loads and pathogen pressures that our foraging ancestors encountered? What were the demographic risks of inbreeding for various categories of kin, given the range and distribution of experienced social structures? What cues were available for mechanisms to use to assess various kinship relations, and how reliable were they? For humans, like most other long-lived mammals, the genetic loads and pathogen pressures were high enough to create a substantial selection pressure; moreover, given the nature of hunter-gatherer life, social structures were commonly such as to make incest a real possibility, and infant and childhood association provided reliable cues of kinship about potential incest partners. The third step is the discovery, investigation, and characterization of the resulting adaptation or adaptations. In this case, it appears to involve a mechanism that "judges relatedness" for the purpose of incest avoidance (at least) by the duration of mutual intimate exposure in the first several years of life. It uses this cue to dampen sexual interest: familiarity breeds sexual disinterest, a process that lowered the probability of incest between relatives raised together ancestrally. Establishing that something is an adaptation involves showing how it manifests evidence of special design for solving a problem that existed ancestrally and that endured long enough to constitute a selection pressure that could have built a specialized structure as complex as the one observed.

To analyze particular cases of modern behavior, such as within-creche

cohort sexual avoidance in Israeli kibbutzim, one needs to describe the relevant ontogenetic environment (step 4): unrelated children of both sexes were raised in small, intimate groups from the earliest ages. The outcome (step 5) was a lack of sexual interest between nonrelatives raised in this fashion. The present behavior—sexual avoidance of reproductively appropriate and accessible nonrelatives—is understood as the operation of underlying adaptations, within a particular ontogenetic environment. There is nothing particularly adaptive about this outcome. But whether avoiding creche-mates happens to be currently adaptive or maladaptive is completely irrelevant to its explanation. Regardless of its present fitness consequences, it remains patterned by underlying adaptations forged in the past.

The research approach is very different for those who see evolutionary functional analysis as the investigation of how an individual's present behavior corresponds to or leads to fitness-maximization in his or her present circumstances. The observation that creche-mates avoided each other as sexual partners would prompt the search for how this "strategy" leads to enhanced fitness in the kibbutzim. An endless series of hypotheses could be advanced and even tested (e.g., if one can deceive relative strangers better than those who have known one from infancy, then perhaps strangers should be preferred as more manipulable mates). The fitness of creche-mate avoiders could be compared to the fitness of those (if any) who married creche-mates. "Feasible" alternative strategies (creche-mate avoidance versus creche-mate preferring) could be scrutinized for why each was explained by its fitness consequences, given the particular resources and constraints available to the two sets of strategists. Constructing accounts of why present behaviors lead to positive fitness consequences is always possible, if necessary by invoking additional situational variables and constraints until adaptiveness is demonstrated.

The error in the correspondence program is to finesse steps 2 and 3 and to instead leap directly from general models of evolution (step 1) to current conditions (step 4), in an attempt to "explain" present behavior (step 5) as fitness maximization in present environments. What creates a nonrandom adaptive correspondence between present conditions and present behavior, whenever there is one, is solely the causal structure of steps 2 and 3, plus the contingent fact that the environment of ontogeny resembles the EEA with respect to that adaptation.

### **The Definition of the Environment of Evolutionary Adaptedness**

Characterizing an adaptation involves characterizing the ancestral conditions and selection pressures—the adaptive problem—that the adaptation solves. The "environment of evolutionary adaptedness" (EEA) is not a place or a habitat, or even a time period. Rather, it is a statistical composite of the adaptation-relevant properties of the ancestral environments encountered by members of ancestral populations, weighted by their frequency and

fitness-consequences. These properties are selected out of all possible environmental properties as those that actually interacted with the existing design of the organism during the period of evolution. These ancestral conditions must be characterized when functionally analyzing an adaptation. To establish that something is an adaptation one must establish an improbably close coordination between the adaptive problem constituted by the statistical composite of ancestral conditions and the design features of the adaptation. This description of ancestral conditions is one indispensable aspect of characterizing an adaptation and constitutes part of what we have called the task analysis or computational theory phase of the functional analysis of an adaptation (see Cosmides and Tooby 1987; Tooby and Cosmides 1989; Marr 1982). Ignoring this logical step does not eliminate it as a necessary part of any evolutionary functional argument—it simply renders functional analysis weak or meaningless.

The concept of the EEA has been criticized under the misapprehension that it refers to a place, or to a typologically characterized habitat, and hence fails to reflect the variability of conditions organisms may have encountered (see Turke 1990). Humans, for example, undoubtedly encountered a variety of specific habitats during many periods of their evolution and should not be typologically characterized as adapted to living in, for example, the Kalahari desert. Turke and others have complained that to invoke the EEA is to depict the past as a “featureless monolith,” or in the human case as a simple constant that only began to change after the rise of agriculture (Turke 1990). (We found, much to our surprise, that we were described as believing that the Pleistocene was relatively simple and constant and were somewhat justified in thinking so.) There is no basis in the concept of the EEA for any claims of stasis, simplification, or uniform ancestral conditions in the usual sense. As a complex statistical composite of structurally described contingencies of selection, the idea of an EEA involves no oversimplification. Rather the error is to think that a literal place or a habitat, defined by ostension, is a description of the ancestral condition component of the definition of an adaptation. The concept of ancestral conditions or the EEA, as a statistical composite, is necessarily invoked whenever one is making an adaptationist claim, which means whenever one is making an adaptiveness claim, whether researchers are aware of it or not. As a composite, it is necessarily “uniform” in the abstract sense, although that uniform description may involve the detailed characterization of any degree of environmental variability.

To the extent that there is an ambiguity in the concept of the environment of evolutionary adaptedness, it is because of the time-dimension of the problem. Because the history of any evolving lineage extends back several billion years to the origins of life, the characterization of ancestral conditions requires a time-structured approach matching specific statistical environmental regularities against specific instances of evolutionary modification in design. To the extent that the adaptation has assumed an equilibrium design under stabilizing selection, the period of stabilizing selection itself becomes

a primary part of the EEA, although for some purposes one may want to distinguish the EEA of stabilizing selection from the EEA during the period of sequential fixations. For this reason, the EEA is adaptation-specific and evolutionary change-specific, with the EEA for the human eye being somewhat distinct from the EEA for the human language faculty. The EEA refers to the statistical composite of environments that were encountered during the period when a design feature changed from one state into another (and was subsequently maintained, if it was). The EEA for the human language faculty consists of the statistical composite of relevant environmental features starting from the incipient appearance of the language faculty until it reached its present structure (although to do a real analysis, this period may need to be partitioned according to particular intermediate steps). Nevertheless, for most ordinary analytic purposes, the EEA for a species (i.e., for its collection of adaptations) can be taken to refer to the statistically weighted composite of environmental properties of the most recent segment of a species' evolution that encompasses the period during which its modern collection of adaptations assumed their present form. We have used the word "Pleistocene" in this sense to refer to the human EEA, because its time depth was appropriate for virtually all adaptations of anatomically modern humans, with a few minor exceptions such as the postweaning persistence of lactase among pastoralist peoples (Tooby 1985; Tooby and DeVore 1987; Cosmides and Tooby 1987; Tooby and Cosmides 1989; on lactase, see McCracken 1971).

### **The Ontogenetic Environment**

The role that present conditions play in the logical structure of Darwinism is highly circumscribed: present conditions participate in the system of causation as the ontogenetic environment (and trivially, as a single increment in the EEA of future adaptations). The individual organism, fixed at conception with a given genetic endowment regulating its developmental programs, encounters its specific ontogenetic environment, which it processes as a set of inputs to these developmental programs. In other words, the organism blindly executes the programs it inherits, and the ontogenetic conditions it encounters serve as parametric inputs to these programs. The putatively species-typical Westermarck incest avoidance mechanism, presented with the particular set of inputs provided by the ontogenetic environment of the kibbutz, led to the sexual avoidance of otherwise appropriate partners. For the evolved relationship between an animal's genes and its ontogenetic environment to remain coordinated across generations (and hence adaptive), the twin inheritances, genes and environmental invariances (the constellation of environmental features used by development or interacted with by adaptations) must be passed on, intact and relatively unchanged. A single environmental "mutation" (change in an invariance) can be sufficient to make the environment "novel" with respect to many adaptations—that is,

can make behavior in many domains maladaptive and “off-track.” For example, raising nonrelatives in the same creche is an environmental mutation with respect to the Westermarck mechanisms, which depend for their adaptive expression on an environment in which relatives are creche-mates. This environmental mutation creates potentially maladaptive behavior in mate choice.

### Statistical Regularities Define the EEA

The conditions that characterize the EEA are usefully decomposed into a constellation of specific environmental regularities that had impact on fitness and that endured long enough to work evolutionary change on the design of an adaptation. We will call these statistical regularities *invariances*. Invariances need not be conditions that were absolutely unwavering, although many, such as the properties of light or chemical reactions, were. Rather, an invariance is a single descriptive construct, calculated from the point of view of a selected adaptation or design of a given genotype at a given point of time. No matter how variable conditions were, they left a systematically structured average impact on the design, and that systematic impact needs to be coherently characterized in terms of the statistical and structural regularities that constituted the selection pressure responsible. These invariances can be described as sets of conditionals of any degree of complexity, from the very simple (e.g., the temperature was always greater than freezing) to a two-valued statistical construct (e.g., the temperature had a mean of 31.2 C. and standard deviation of 8.1), to any degree of conditional and structural complexity that is reflected in the adaptation (e.g., predation on kangaroo rats by shrikes is 17.6% more likely during a cloudless full moon than during a new moon during the first 60 days after the winter solstice if one exhibits adult male ranging patterns). Such descriptions are essential parts of the construction of a task analysis or computational analysis of the adaptive problem a hypothesized adaptation evolved to solve (Cosmides and Tooby 1987; Tooby and Cosmides 1989).

### Adaptations as a Record of the Past

Turke (1990) repeats the common complaint that characterizing the past is impractical because it is not available for direct observation and our present knowledge of it is inadequate. Yet the degree of difficulty in observation is no excuse for logical errors, and substituting present conditions for ancestral conditions in evolutionary functionalism is simply an error. In any case, the task of characterizing the past is not irremediably difficult, but will be easy or difficult depending on the specific issue, on the sophistication of the research community, and on the power of the methods developed. The essence of Darwin’s principled historical framework is that the present world is full of information about the past, as the present consists entirely of outcomes

of past causal processes. We do not need a time machine to observe the past. The present, studied with specialized theoretical, inferential, and observational tools allows observation of the past. Paleontological methods, of course, form one important set of tools, but reliance on them alone, in isolation from other techniques, has contributed unfairly to the idea that our knowledge of the past is “inadequate” for adaptationist analyses. For many purposes the study of present environments as models of past environments are our best window on the past, because an enormous number of factors, from the properties of light to chemical laws to the existence of parasites, have stably endured. Evolutionary theory itself provides a series of powerful inferential tools for characterizing the past which should be integrated with existing paleontological methods of more direct observation (Tooby and DeVore 1987). For example, validated evolutionary principles also constitute descriptions of constraints operating in the past, from the minimal (finding a mate of the opposite sex is necessary to reproduction in bisexual species) to the more sophisticated (the possibility of cheating limits the evolution of cooperation).

The discovery and characterization of adaptations is the single most reliable way of discovering the characteristics of the past, because each species’ design functions as an instrument that has registered, weighted, and summed enormous numbers of encounters with the properties of past environments. Species are data recording instruments that have directly “observed” the conditions of the past through direct participation in ancestral environments. A specific complex adaptation constitutes, in the improbability of its specialization of design, a probability test about ancestral conditions based on an enormous and representative sample of the past. Eyes tell one that light was a part of the EEA. Immune systems tell one that disease was both present and an important selective agent. The presence of psychological mechanisms producing male sexual jealousy tells one that female infidelity was part of the human and ring dove EEAs (Daly and Wilson 1988; Erickson and Zenone 1977). Observation of the structure of present adaptations and logical deductions from these observations constitutes a system for reading back what these ancient but still operational data recorders have to tell us about the past. The study of human cognitive specializations, including human emotional adaptations, may prove to be a surprisingly detailed record of the structure of the past.

### **Adaptations Are the Best Test of Evolutionary Theory**

The study of adaptations is also the most reliable way of testing hypotheses about—or the validity of—alternative evolutionary principles such as inclusive fitness theory, optimal foraging theory, parental investment theory, and reciprocation theory. Adaptations are condensed records of enduring conditions, and because selection pressures are one kind of enduring condition, adaptations are the best test of theories about the nature of selection



pressures. If reciprocity theory or parental investment theory are correct, then their accuracy can be gauged by the nature of the adaptations that have been constructed. Although this approach is the essence of comparative tests (Clutton-Brock and Harvey 1984), it applies with equal force to the study of functional design in single species (e.g., Kaplan and Hill 1985). This method can also test more particular hypotheses about the role of specific selection pressures on species: If information-processing specializations to hunting but not scavenging were found in humans, this would also test the relative role of the two in recent human evolution.

The most favored method currently employed in evolutionary biology is the measurement of the operation of ongoing selection in present environments. Such studies can certainly test assumptions (e.g., the heritability of fitness; Partridge 1980) or give plausibility to one hypothesis or another. But any study of ongoing selection in the present is only one brief sample—of unknown representativeness—out of four billion years of selection. In trying to understand the forces that laid down the sediments at the Grand Canyon over millions of years, studies of which way the wind is presently blowing can only contribute so much. They document the explanation of the last 0.02 millimeters of the upper layer, but may lead to entirely incorrect conclusions about the events that created the other 3000 meters of sediment deposition. A better use of such studies is to increase general understanding of the mechanism of particle dispersion and atmospheric transport. Similarly, the clearest test about evolutionary hypotheses is to be found in the study of the adaptations of present organisms, not in the interaction of the remaining variability in design with the vagaries of the present environment. The study of adaptation is what establishes the validity of the major principles of evolutionary theory. The ultimate arbiters of what the structure of the evolutionary process has been over the last four billion years are the phenotypic designs that have been produced over that four billion years, not any snapshots of fitness differentials at one moment in time. Studying the distribution of present fitnesses against the present distribution of phenotypes, while ignoring the design of adaptations, will cause one to miss the major source of information about the process of evolution itself.

These considerations provide the answer to Turke's question (1990) about why the last 500 human generations are less important than the preceding 500 generations. They are not, of course: rather, the appropriate comparison is the last 500 generations as against the last 50,000, and the answer to this version of Turke's question is: the last 50,000 are 100 times more important than the last 500. The contribution of recent generations is rather trivial in comparison to stretches of time that potentially incorporate enough generations and selection events to have significantly shaped complex adaptations. The relevant length of time is proportionate to the genetic complexity of the adaptation under question: single gene adaptations are limited solely by how long it takes them to spread through the gene pool,

complex adaptations are limited by the number of generations required for multiple fixations.

This approach, when stated globally, sounds circular (use the study of adaptations to discover the past; use the study of adaptations to discover evolutionary principles; use the past plus evolutionary principles to discover adaptations), but when practiced on individual adaptations as part of a larger network of inferences (Tooby and DeVore 1987) it gains power and loses its circularity. Each adaptation can inform one about a whole host of properties in the past, and the comparative study of many species can validate evolutionary principles that can be safely (if carefully) applied to new cases. The study of human psychological adaptations to potential infidelity, sexual jealousy, informs one about mating patterns in the past (Daly and Wilson 1988; Wilson and Daly, in press), as do physiological adaptations to sperm competition (Harcourt et al, 1981) and the finding that female decision rules about mate selection weight male resources highly (Buss 1989). To the extent that adaptations can be precisely characterized (that is, how improbably specialized to the hypothesized functional problem is it), characterization of ancestral conditions and selection pressures becomes reliable. The problem of circularity is solved when the number of reliable inferences exceeds the number of unknowns in the problem (like Gaussian elimination in algebra). Each species consists of hundreds or thousands of adaptations, each containing information about different overlapping subsets of past conditions. By putting them all together, one can rule out hypothesis after hypothesis. Evolutionary biology, evolutionary psychology, and paleoanthropology can be integrated into a single inferential system for unpacking human evolution, and its product, modern human design (Tooby and DeVore 1987).

### **Adaptations Are Usually Population or Species-Typical**

The differences between the correspondence and adaptationist programs become clear through considering how each treats the topic of universals versus variability. For someone following the correspondence program, the search for universals is typological and misguided (see Dunbar 1988; and Borgia's 1989 and Smuts' 1989 criticisms of Buss 1989). Because the organizing explanatory principle is held to be that organisms do whatever it takes in a situation to maximize fitness, then because circumstances vary, behaviors should and will vary also, and in any way that is appropriate to the goal of fitness maximization in those circumstances. Behavioral (and morphological! [Dunbar 1988, p. 168]) traits will rarely be universal, and such universals will only be elicited when the same *current* environmental challenge is presented to all members of a species. The universal does not reside in phenotypes or in phenotypic designs, but in principles such as the "deep structure rule" "maximize the number of offspring you rear to maturity" (Dunbar 1988).

According to evolutionary theory, however, nonaccidental adaptiveness occurs solely because of the operation of adaptations, which in turn entail

both a history of selection in ancestral conditions and a genetic basis. Therefore, the distribution of this genetic basis should also be characterized, and in fact commonly falls into only a few alternative patterns (species-typicality, frequency-dependence, population-universality, etc.). Because many or most adaptive problems are complex, they require complex adaptations to solve them. To the extent that the adaptations under discussion are complex adaptations (defined as adaptations that require the coordinated gene action of more than a very small number of genes), then it follows that they will nearly always be universal in the population, and given the population structure of most long-lived species, they will probably be species-typical as well. Their expression may be limited by sex, life history stage, or circumstance, but at the genetic or design level the adaptation will almost always be species-universal (Tooby and Cosmides 1990). Complex adaptations necessarily require many genes to regulate their development, and sexual recombination makes it combinatorially improbable that all the necessary genes for a complex adaptation would be together at once in the same individual, if genes coding for complex adaptations varied substantially between individuals.<sup>2</sup> Selection, interacting with sexual recombination, enforces a powerful tendency toward uniformity in the genetic architecture underlying complex functional design at the population level, and usually at the species level as well.<sup>3</sup> Aside from neutral mutations, the bulk of genetic variation is present in populations because it is pathogen-driven frequency dependent selection for biochemical diversity, rather than because it specifies different functional adaptations between individuals (see Tooby 1982 for discussion). For these reasons, adaptive design should most often be species-typical design, and may include hundreds to tens of thousands of adaptations (depending on whether one is a lumpner or splitter in categorizing them), rather than number

<sup>2</sup> The genetic basis for frequency-dependent alternative strategies will tend to be universal also, except for genetic switches (if any) that regulate which strategy an individual will instantiate. Thus, the sexually differentiated adaptations of males and females—two frequency-dependent alternative strategies—will be coded for by genes that are simultaneously present in both sexes, with the exception of the H-Y antigen, which is a genetic switch. Moreover, selection will tend to restrict the total number of alternative complex strategies through a kind of quasi-senescence process. If there are fifty equally likely alternative ESS's, selection will only have a chance to improve any one of them in one out of fifty generations, while it will be acting on the ESS-general aspects of the phenotype every generation. Senescence-like trade-offs between general and expression-limited traits should limit how numerous and how complexly differentiated alternative ESS's can become.

<sup>3</sup> Exceptions to the rule of combinatorially enforced design uniformity include single gene adaptations, overdominants, single locus frequency-dependent systems, favorable mutations prior to reaching fixation, genetic switches, and quantitative genetic variation. The argument about the prevalence of species-typicality depends on sufficient gene flow between populations over evolutionary time, a condition that appears to be met by humans. But if populations become isolated enough for long enough periods of time and develop different complex adaptations specified by different sets of alleles, then population-typicality will substitute for species-typicality for many adaptations, creating a situation of incipient speciation. Given length limitations, the slight qualifications in certain arguments about adaptation that may need to be made in the light of certain categories of genetic diversity (e.g., quantitative genetic diversity, single gene adaptations to local conditions) would be too cumbersome to introduce at every appropriate juncture, and so have been left out. They introduce no essential difference into the argument.

in the “single figures” (Dunbar 1988). Human nature is a rich, incredibly intricate articulated structure, and one can expect the evolved information-processing mechanisms that regulate social behavior to be no less intricate and complex than the vertebrate eye.

### **Variability in Expression, Uniformity in Design**

Even where the genetic basis of a phenotypic trait is not species- or population-universal, for a structure to qualify as an adaptation it must be recurrent. An adaptation is more than a mere collection of phenotypic properties which, in a particular individual, happen to have the effect of enhancing reproduction—winning the lottery, burning coal, and irrigating fields are not adaptations. An adaptation is a recurrent design that reappears across generations and across individuals. For selection (as opposed to chance) to have manufactured a structure, the evolved design must have had repeated encounters with recurrent properties of the world. Those encounters constitute the history of selection for that design. If characteristics emerge uniquely every generation, or haphazardly from individual to individual, then selection cannot organize them.

This means that the phenotype of an individual organism must be carefully distinguished from the design of the phenotype—fitnesses should be assigned to designs, not to individuals. Natural selection involves design, defined as those properties that are stable across all individuals of the same genotype. As Williams says, “[t]he central biological problem is not survival as such, but design for survival” (Williams 1966, p. 159). The individual phenotype manifests innumerable transient properties, which disappear with the death of the phenotype or change idiosyncratically over the lifespan. Although some of these transient properties may promote reproduction, they are chance produced beneficial effects, not adaptations (Williams 1966). Because adaptations are responsible for all non-chance adaptiveness, any claim of adaptiveness must be traced back to underlying adaptations.

The principle confusion of the correspondence program is that most researchers documenting adaptiveness do not distinguish between transient properties, which cannot be adaptations, and design properties, which can. Their reluctance to make this distinction, we suspect, stems from the sense they have that there is far too much transitory adaptiveness to be accident, and in this they are correct. If they were to exclude from evolutionary analysis everything that apparently varied, there would be scarcely anything left. They point out that organisms frequently vary their behavior adaptively in synchrony with contextual variables (Borgia 1989; Smuts 1989). This has led some to define behavioral ecology itself as the study of variation, with such variation held to be explained by the principle of fitness-maximization, combined with how contextual variables elicit appropriate variations in behavior. The search for universals is rejected as the typological activity of those who do not really understand evolution (Dunbar 1988). This approach to behav-

ioral ecology is caught in the paradox that transient phenomena have no position in the logic of Darwinism, and yet such phenomena seem adaptive, rule-governed, and apparently explained by the principle of fitness-maximization.

### The Role of Phenotypic Description

The solution to this apparent contradiction is found in the task of describing phenotypic design. The logically necessary process of relating adaptiveness to underlying adaptations involves the process of redescribing the variable and the transitory in terms of that which is recurrent and stable. This process of description is key: by choosing the wrong categories, everything about the organism can seem variable and transitory, so that humans appear to have less than ten universal morphological and behavioral traits (Dunbar 1988, p. 168). By choosing the right categories—adaptationist categories—an immensely intricate species-typical architecture appears, with some limited additional layers of frequency-dependent or population-specific design as well. Discovering the underlying recurrent characteristics that generate the surface phenotypic variability is essential to the discovery of adaptations. Adaptations may be variable in expression, but must be uniform in design (Tooby and Cosmides 1990).

Because behavior and physiology does vary, underlying design will often be described in terms of conditional rules such as developmental programs or decision rules. This process of description will be obstructed without the recognition that adaptations are the conditional rules of expression of phenotypes, and not phenotypes themselves. One cannot discern adaptations in the variable features of phenotypes, but only in their uniform underlying architecture. Thus, individual phenotypes are instances of designs, but not designs themselves. For example, the cleaner fish, *Labroides dimidiata*, is a protogynous sequential hermaphrodite, which means that an individual typically begins as a female and turns into a male only when it becomes the largest fish in the group (Robertson 1972). The adaptation is not being male or being female, different for different phenotypes with the same genotype. Rather, the adaptation is the conditional rule “change to male if you are the largest conspecific in the group, remain female if you are not” that regulates which phenotype is expressed, together with the design specification of those organs and properties that make a phenotype a male or female of that species.

Unless genes are different, adaptations are the same. Therefore, to recover adaptive design out of behavioral or morphological observations, one needs to determine what is variable and what is invariant across individuals: only the recurrent is a candidate adaptation. One reason why the avunculate, the English language, cross-cousin marriages, and Tibetan polyandry cannot be adaptations is because they vary from human to human in a way that is

not (plausibly) caused by genetic differences between them. These are expressions of adaptations, but not adaptations themselves.

### Additional Rules for Functional Analysis

These considerations suggest that several new principles for discussing function and for recognizing or ruling out adaptations can be applied to organize observations about phenotypes.

1) A set of phenotypic properties is not an adaptation if it is transient, varying from individual to individual, and is not part of the recurrent design of individuals of that genotype (in an EEA-standard environment).

2) Therefore, adaptations (as uniform designs) should be distinguished from their expression (which may vary from context to context). Observations about variable behavior need to be sifted for relational invariances to detect underlying adaptations. Any contingent behavioral or physiological phenomenon needs to be related to an underlying recurrent structure.

3) A set of phenotypic properties is not an adaptation if it was absent in the EEA.<sup>4</sup>

4) A set of phenotypic properties is not an adaptation if it did not solve an adaptive problem in the EEA, however fitness-promoting it may be during the present generation.

5) A description of a set of phenotypic properties does not properly characterize an adaptation if that description involves terms and elements for things that did not exist in the EEA.

6) Although population differentiation and frequency-dependent selection may lead to some restricted exceptions, of limited genetic complexity, the designs of most adaptations will be species-typical for species with an open population structure, however condition-limited the expression of those designs may be (Tooby and Cosmides 1990). Consequently, high heritabilities usually indicate that the heritable component of the phenotypic variation is not an adaptation.

7) Functional analysis should be expressed in adaptationist terms, specifying the selection pressures, recurring environmental elements representing ancestral conditions, and so on. Adaptive or functional outcomes must be linked to underlying uniform adaptations to qualify as a Darwinian account. In contrast, a description of how a culture-specific behavior contrib-

<sup>4</sup> A drill press is highly nonrandomly organized to perform a function, it is efficient, precise, and specialized, and it may even increase the reproduction of those that use them. Nevertheless, a drill press is not an adaptation because it was not present in the EEA. A second, equally sufficient reason to rule it out as an adaptation is that it is not a recurrent product from individual to individual of the same genotype, in an EEA-resembling environment. Its failure to qualify as an adaptation (or, really, as a part of the description of an adaptation) has nothing to do with the fact that it is an artifact. As part of an extended phenotype, a widely recurring artifact that reappeared across generations and whose developmental rules of expression had been the target of selection would qualify as part of the characterization of an adaptation (for *Homo erectus*, bifaces—so called handaxes—might qualify as such an adaptation).

utes more to fitness than alternative behaviors does not constitute a functional account of the behavior.

8) Characterizing adaptations requires that one speak in the language of causation rather than teleology. Adaptations are systems of properties that, against a given environmental background, cause the solution to an adaptive problem. Specifying the “goal” of the process, that is, the recurrent fitness-promoting outcome, is only one part of characterizing adaptations. It is further incumbent on the researcher to specify the causal process, method, or procedure that accomplishes the goal. Characterizing the method or procedure that reaches the goal is not an onerous burden, but instead frequently leads to new insights about the nature of the adaptive problem itself. For example, the marginal value theorem (Charnov 1976) specifies an adaptive problem: how to regulate the behavior of the forager such that it follows the marginal value theorem (e.g., leave patch when gain rate drops to the average in the environment). Attempting to characterize how this goal is achieved raises the question of how the organism could obtain the information necessary to achieve it (what is the average gain rate for the environment; what is the average travel time; how are patch types recognized; and so on). This led to the consideration of additional adaptations that solve these problems (Stephens and Krebs 1986). Noting a correspondence (e.g., between behavior and the marginal value theorem) does not constitute the characterization of an adaptation; instead it prompts the search for the adaptations responsible for that correspondence.

## BEHAVIOR VERSUS MECHANISM

We have argued elsewhere for the importance of distinguishing adaptive design from its phenotypic expression, but we phrased the argument in terms of the utility of studying the mechanisms regulating behavior rather than simply behavior itself (Cosmides and Tooby 1987; Tooby and Cosmides 1989). Turke argues that behavior can be an adaptation just as much as any other phenotypic property can be (Turke 1990), and, depending on exactly what is meant by the word “behavior,” we agree with him. Dawkins’ (1982) discussion of the extended phenotype was perfectly correct in pointing out that any kind of phenotypic consequence is comparable to any other kind in the logic of Darwinism, in its potential for constituting an adaptation. But the issue here turns on what one means by “behavior”: behavior as manifest phenotype expression, or behavior as recurrent underlying design. We favor discussing mechanism over behavior because of the usual meaning given to those words: behavior usually refers to any kind of transitory individual phenomenon (she ate spinach; when he became sick he went to the physician and was bled, etc.). When one redescribes behavior in terms of underlying, recurrent design—a requirement for characterizing an adaptation—the resulting description is almost never sufficient unless it uses mechanistic as

opposed to behavioral language. Spinach-eating, polygyny, monogamy, agriculture, and the avunculate are no doubt often adaptive behaviors, but are not adaptations. The hypothetical decision rule "eat if blood sugar is below a threshold level and search and handling costs are not too high" is a candidate for an adaptation involved in spinach eating (albeit minimally described), because it could potentially be a universal design feature. To find a human adaptation describable purely in behavioral terms, one would have to fall back on the simple, manifestly universal movements (such as thrusting during copulation) that behavioral ecologists would rather leave to physiologists (see Symons 1989, 1990, *in press*). Behavior is not a useful level for describing adaptations because the language of behavior cannot easily describe design-universals, *i.e.*, the whole structure of environment-procedure-behavioral outcome relationships. Researchers who employ purely behavioral descriptions rarely manage to describe design in a sufficiently precise way to capture what the target of selection was. Moreover, when Turke (1990) invokes neural plasticity to say that mechanisms can vary just as much as behavior can, it is clear that he is using the word "mechanism" in a different sense than we are. By "mechanism" we do not mean "wet" tissues or any aspect of the expressed phenotype. Instead we mean a description of some part of the underlying design of the phenotype. For a given genotype, the description of the underlying design should not vary—if it does, then it has not been described properly. Phenotypes of the same genotype, whether behavioral or physiological, vary. By definition, designs of the same genotype do not.

## TURKE'S PROPOSED PROGRAM

Turke (1990) attempts to synthesize the adaptationist and adaptiveness programs, largely by trying to justify research into modern adaptiveness as a tool for discovering adaptations. This leads to large areas of agreement: many modern behaviors are no doubt adaptive; some categories of modern behavior are probably maladaptive; for many categories of behavior, the modern world may not be so different from the human EEA; one cannot claim, without reference to the nature of specific human psychological adaptations, that modern life is or is not different from the human EEA; and so on. In one area in particular, we wish to stress our agreement: modern ethnographic studies, conducted with an eye to behaviors and environmental variables that are important to reproduction are intensely interesting. Studies of marriage and male attempts to control female reproduction (Dickemann 1979), Yanamamo conflict (Chagnon 1988), or Yomut (Irons 1980), Ifaluk (Turke and Betzig 1985), or Kipsigis reproductive behavior (Borgerhoff Mulder 1987) provide important data which are very useful in trying to construct models of human adaptations. Different cultures constitute natural



psychological experiments: what do the same set of species-typical adaptations do given different inputs?

Areas of disagreement emerge on other issues. Turke advocates testing hypotheses “that can potentially account for how the traits are (or were) adaptive,” but he does not distinguish between transient behavioral phenomena as traits (the avunculate, bleeding, the special male Yanomamo status of having killed) and cross-generationally recurring traits. Only recurrent design features could potentially be adaptations. More critically, Turke appears to regard the demonstration that a behavior is adaptive as an explanation for it, when in fact the appropriate explanation involves relating it to the operation of an underlying adaptation and showing how that underlying adaptation was adaptive under ancestral conditions. Although Turke pays lip service to the importance of exploring and describing adaptations, only the most general of conclusions about adaptations are presented as being probed by studies of adaptiveness (e.g., human psychology is more general purpose than might be supposed, or that “humans generate and use culture adaptively”). These links to supposedly adaptationist questions lack nearly any specification of phenotypic design, and appear instead to be pretexts to reanimate the correspondence program by trying to argue that present behavior is generally adaptive (an irrelevant point in any case).

Turke compares holding the belief that many modern behaviors are maladaptive to the antiadaptationism of a century ago, accusing adaptationists of being “too ready to believe that it would be impossible to account for many of the unique and unusual features of organisms in terms of individual reproductive advantage.” But the adaptationist question is not how much behavior is explained by present reproductive advantage. The point of the adaptationist critique is that no present behavior can be explained, even in principle, by present reproductive advantage. Consequently, the debate is not primarily about the prevalence of adaptive versus maladaptive behavior in the modern world, or about how similar or different the present is from the EEA. Rather, it concerns the irrelevance of behavior’s present adaptiveness to its explanation. As a purely secondary matter, the adaptationist emphasis on designs as produced by selection in ancestral environments makes the possibility of environmental mutation salient and the many cases of modern maladaptiveness obvious.

## **AGGREGATED AND DISAGGREGATED ADAPTIVENESS**

We have sometimes been interpreted as arguing that modern behavior is necessarily maladaptive because of cultural change, but this is not our argument: such issues demand a case by case treatment. Instead, we have argued that present adaptiveness and maladaptiveness are usually imprecise and uninformative categories, and refer to concepts that have only an incidental role in Darwinian analyses of behavior and morphology. Indeed, as

we pointed out previously (Tooby and Cosmides 1989), we know from the observation that the total human population has grown from five million to five billion over the last ten thousand years that post-Neolithic humans have, on average, been behaving overwhelmingly “adaptively” in the sense of achieved reproductive outcomes. Yet even given this fact, there is no *a priori* reason to expect that any particular modern behavior is adaptive. The problem with using this observation to validate the theory that specific human behaviors are best modeled as rational fitness maximization responses to present environmental contingencies lies in two separate meanings for the word “adaptive.” Adaptiveness in one sense means that total lifetime inclusive fitness is high (relative to some standard), and in another sense means high specific functionality in some particular behavior or phenotypic expression (e.g., that the eye achieves the special purpose of seeing well, whether or not that contributes to reproduction in any specific instance). Advocates of the correspondence view take high aggregated net reproduction (the first meaning of adaptive) to imply the second meaning of adaptive (high disaggregated functionality in all or most mechanisms), even though the second proposition depends on the distribution of performances among the hundreds or thousands of adaptations humans have. If a few mechanisms are, under conditions of rapid post-Neolithic cultural innovation, operating extremely well, the majority of others could be misfiring to one degree or another.

Specifically, improvements in the technologies of food production and in public health and medicine are two areas of “behavior” that have vastly decreased prereproductive mortality and increased lifetime reproductive success. They are largely—perhaps entirely—responsible for the population increase. By aggregating the consequences of all behaviors together, one loses the ability to detect whether specific categories of behavior (categorized by which specific mechanisms they are the expressions of) continue to be adaptive, that is, continue to be functionally coordinated with the ontogenetic environment. That is why measuring fitness outcomes is so rarely illuminating: to evaluate the performance of a particular mechanism one needs to separate its effects from that of all other mechanisms, yet achieved reproduction necessarily sums effects from the operation of many mechanisms. Fitness variation will usually be a particularly poor variable to examine, because lifetime reproductive success (the measure of adaptiveness) will involve innumerable acts and choices throughout the individual’s lifespan, making it particularly cumbersome and distal as a measure of the regulatory outcome of some particular adaptive design. More appropriate measures tend to be those that detect some specially targeted aspect of proximate performance, the “special purpose” of the adaptation. Does hand-eye motor coordination skill acquisition allow humans to hit targets?; does jealousy-regulated deterrent violence occur after cues of potential infidelity?; do social exchange algorithms promote cheater detection?; and so on.

By increasing the population by three orders of magnitude, improve-

ments in food production and public health have swamped and hence masked the effects of most mechanisms on reproduction. In short, post-Neolithic population growth is entirely consistent with the possibility that most post-Neolithic acts and behaviors have not contributed at all to enhanced fitness and that many or even most mechanisms, due to changed circumstances, are no longer producing adaptive outcomes. This net population growth says nothing about whether kin-directed behavior, fertility regulation by income, inter-ethnic violence, political behavior, or any other behavior is presently adaptive. In particular, this observation is irrelevant to Alexander's (1971, 1979a, 1979b, 1987) and others' arguments about the role of social competition in human evolution. Social competition is inherently zero-sum or negative sum, therefore it cannot directly explain enhancements in the average reproduction of the species.

### **Maladaptive Behavior Is Equally Informative**

The relevance of Darwinism stems from the fact that every behavior, adaptive or maladaptive, is the product of adaptations (or other linked aspects of underlying design) and hence is patterned by the structure of those adaptations. Its relevance does not depend in the slightest on whether all, most, or no modern behavior is presently adaptive. When framed by adaptationist questions, maladaptive behavior (in the sense of a mechanism's specific disaggregated performance) can be every bit as informative as adaptive behavior. An enormous wealth of modern behavioral phenomena such as recreational drugs, pornography, films, television, sports, recreational as opposed to procreative sex, gambling, New Age nostrums, horoscopes, anonymous charitable work, blood donation, political dissidence, voting, seeking advice through trance channeling, alcohol use, romance novels, the adoption of nonrelatives, doing evolutionary biology, music, hiking, the sexual abuse of children, and on and on, do not contribute to fitness over known, "feasible" alternatives practiced by others in similar circumstances.<sup>5</sup> Proximate fitness-maximization is not the principle that explains these behaviors and trying to show (for example) that the purchase of pornography or cocaine enhances the average reproduction of purchasers over nonpurchasers practicing the best "feasible" alternative is sterile, since their present adaptiveness has nothing to do with their existence (see Turke 1990, on "fea-

<sup>5</sup> Turke questions our example of the modern initiation of war as obviously maladaptive behavior, given that competition for resources always has winners and losers. We consider such decisions usually maladaptive for another reason: unlike in conditions of primitive warfare, virtually no decision-making elite has been reproductive-resource limited in modern nation states. Modern economies offer expansive opportunities for the rational discovery of benefit-benefit relations which provide far more resources than conquest can. We argue that zero-sum games were far more prevalent in the relatively unproductive foraging economies that persisted throughout much of human evolution. This leads to a tendency for decision-making elites to frame situations as resource-limited and zero-sum when they are not, leading to dramatic examples of major and unnecessary wastes of resources, labor, and reproduction in costly and often unsuccessful modern warfare.

sibility’’).<sup>6</sup> Instead, the purchase of pornography by males must reflect some underlying adaptation, such as the hypothetical and obviously oversimple decision rule: “move towards situations that produce retinal images of naked nubile females and become sexually aroused.” Because the EEA lacked artificially created images of females, such a rule would plausibly have been fitness-promoting. Maladaptive behaviors similarly give information about the functional structure of our adaptations and are therefore worth studying.

Demographic research (discussed in Vining 1986; and Turke 1990) and everyday observation confirm that prosperous individuals in modern industrial nations are having far fewer children than they could and fewer than many poorer families in those same societies. Each of us is familiar with poor and middle class families with large numbers of healthy children. North American Hutterites *average* more than ten children per family and have sustained this performance stably for years without exciting much interest from others or prompting any notable tendency for others to imitate the few simple steps that have led to such high reproductive rates. Unusually low cleavage in a famous actress excites more attention than reports that some cultural group has found methods to successfully increase their reproductive rate, and this tells us a great deal about the nature of our adaptations. The fact that large numbers of individuals take drugs, buy pornography, and practice contraception as a means of forgoing reproduction rather than optimally allocating it, rules out large classes of hypotheses about the evolved decision rules in the human psyche. We regard as promising Turke’s (1989, 1990) and Draper’s (1989) hypothesis that prosperous but socially isolated women in industrial societies may feel poor compared to “poor” women living in extended families, and consequently unnecessarily restrict their reproduction. On this hypothesis, women’s resource assessment mechanisms use cues inappropriate to modern circumstances, but appropriate to the Pleistocene—they monitor how large local kin support networks are, rather than the availability of (more abstract) financial resources.

### Hyperadaptiveness as Instantaneous Lamarckianism

The more purely the adaptiveness program is pursued, the more closely it approaches a mutant variant of Lamarckianism. Darwinism is about how

<sup>6</sup> The concept of “adaptation” has a clear-cut definition and a set of standards of evidence for recognizing it. But when closely scrutinized, “adaptiveness” is a far vaguer concept, because adaptiveness is relative to alternative expressions of real or supposed alternative adaptations. “Adaptive” means “relatively more fitness-promoting”; to be meaningful, it requires some preexisting specification of the alternative designs and design-expressions being compared, something rarely provided. The question of whether behavior is adaptive or not, without referring to the relative output of alternative designs is meaningless. Turke attempts to remedy this by defining adaptiveness as relative to “feasible alternatives,” but in so doing invokes a nonexistent theoretical superstructure which would outline in advance all of the forces that would impact on the long-run fitness of a specified strategy as compared to the total set of alternative “feasible” strategies (financial costs of nurses; hypothetical status costs to keeping female children alive in India, etc.). One can only agree with Turke that “it is difficult to know if an imagined behavioral strategy is really more adaptive than actual strategies because it is difficult to also imagine all of the constraints that would apply” (Turke, 1990).

the causal action of past conditions causes present designs. Lamarckianism's first principle is about how present conditions cause adaptive changes in structure to be acquired within the lifespan through the animal's effortful striving to solve the problems the present environment creates. If, as a thought experiment, one imagines as perfect and instantaneous the hypothetical Lamarckian power of the environment to sculpt an organism immediately into the optimal design required by each newly encountered circumstance, one would have a system that resembles what many advocates of an adaptiveness approach describe: "the basic message of evolution for behavioral studies is that behavior always depends on context; individuals tend to behave appropriately in the various and changing circumstances they encounter—with 'appropriately' defined as whatever it takes to survive and reproduce" (Smuts 1989, p. 32). The structure of present behavior "reflect[s] moment by moment solutions to problems that are particularly pressing in biological terms" (Dunbar 1988, p. 166). If organisms change instantaneously to incarnate the solutions required by each successive circumstance they enter, the second Lamarckian principle, the inheritance of these acquired characteristics, becomes superfluous, as does Mendelism, because there is no inheritance of traits in such a theory, acquired or not. Offspring are like parents if they face the same conditions, and differ if and when conditions change. What is inherited is solely the trait: "be an all-purpose inclusive fitness maximizer." The principle of fitness maximization, as a kind of all-prevailing magnetic force, in interaction with specific circumstances, rapidly or instantly impresses itself on the plastic form of organisms to create their present design. Cultures and societies should reflect present selection pressures, unmediated by past-reflecting mechanisms.

Characterized in this way, of course, no one would endorse such a view, but as an implicit set of principles it explains a large number of curious predictions, criticisms, and hypotheses in the literature. Borgia (1989), for example, commenting on Buss's cross-cultural study of human mate preference, criticized Buss's "typological" predictions derived from considerations of hunter-gatherer life—not on the grounds that the human EEA varied, and therefore mechanisms should assess such variation, but on the grounds that selection pressures vary in *modern* cultures. He states "Buss has failed to do what is necessary in this type of comparison: offer convincing evidence that the observed similarity in cross-cultural patterns of mate preference is due to convergent evolution" (Borgia 1989, p. 16). If we assume that Borgia is not positing that genetic differences between human cultures explain their differences, these remarks imply a failure to distinguish the logic of cross-specific comparisons (e.g., Clutton-Brock and Harvey 1984; Tooby 1982) from the logic of cross-cultural comparisons. Of course there *is* no distinction for those who explain current traits through present fitness-maximization. Cross-specific comparisons show how patterns of convergent and divergent adaptations are created by parallel and divergent *selection pressures* acting on different species over evolutionary time. They test the-

ories about the long-term effects of selection pressures on species design. Barring investigations of genetic differences between cultures—a relatively minor possibility (Tooby and Cosmides 1990)—cross-cultural comparisons involve tracking how the same species-typical set of mechanisms performs differently given different environmental inputs over historical time. They test theories about the design of human species-typical adaptations that were created in the human EEA: for example, these adaptations should track ancestral environmental cues that signaled situational variation in the EEA. Finding uniformity of complex adaptive design between different cultures does not require convergent evolution because different cultures are not different species.

### **All-Purpose Fitness Maximization: The Ultimate ESS**

The hyperadaptive Lamarckianism inherent in the claim that current behaviors are “to be explained in terms of their contribution to inclusive fitness at the present time” (Hughes 1987) is generally given a superficially Darwinian gloss, something like this: Because the one constant of evolutionary history has been that success consisted of inclusive fitness promotion, it follows that the best possible adaptation would be a general purpose inclusive fitness-maximizing device, therefore organisms are equipped with such devices. Such an adaptation would monitor the present action of every selection pressure, calculate what it took to maximize fitness under this particular configuration of forces, and implement that strategy. Thus, “human beings, the product of millions of years of evolution within social groups, have the capacity to read the social environment in which they find themselves in a particular instance, to determine with reasonable certainty the behavioral strategy that will maximize inclusive fitness, and to adopt it. Our biological heritage endows us with the ability to make the best of diverse situations in terms of inclusive fitness” (Hughes 1987, p. 421). In fact, adaptivist behavioral ecologists attribute this property to organisms generally, by describing organisms as inclusive fitness maximizers, or by saying that they can be expected to behave “as if” they were inclusive fitness maximizers.

A phenotypic design that under all possible circumstances always fitness-maximized would be the ultimate ESS, displacing all other designs in the population (indeed, all other life in the universe), because every other “strategy” would on some occasions be inferior. If organisms were equipped with such a device, then of course adaptivist behavioral ecologists would be correct: present circumstances, analyzed according to presently acting selection pressures, would constitute an ontogenetic explanation for behavior. For an adaptationist, present behavior differs between individuals of the same species in the absence of genetic differences because underlying adaptations are monitoring some variable part of the environment as a cue to regulate behavior, as in the decision rule, “attack only if you are larger than your rival.” But for an adaptivist, behavior varies in response to whatever

**Table 1. The Changing Causal Structure of Environments Over Time**

Time 1: cue <sub>1</sub> → outcome <sub>1</sub> cue <sub>2</sub> → outcome <sub>2</sub>	Example: Incest avoidance and the Kibbutz (raised with child <sub>i</sub> → no sex with sibling) (not raised with child <sub>i</sub> → sex with a nonsibling)
Time 2: cue <sub>1</sub> → outcome <sub>3</sub> cue <sub>2</sub> → outcome <sub>4</sub>	(raised with child <sub>i</sub> → no sex with a nonsibling) (not raised with child <sub>i</sub> → sex with sibling)

Over time, the relationship between cues, behavioral outcomes, and their fitness consequences changes, making an all-purpose inclusive fitness maximizing device impossible in principle.

selection favors under present circumstances (see Hughes' 1989 analysis of human kinship systems). If organisms are equipped with adaptations that inclusive fitness maximize under all circumstances, then the distinction between selection pressures and cues monitored by adaptations would evaporate, and the current properties of ancestral conditions would become irrelevant. Hyperadaptive Lamarckianism and the theory of modern behavioral ecology would merge in a Neo-evolutionary synthesis. The discovery and characterization of how such a miraculous adaptation would operate would be of no small biological interest.

Elsewhere we have discussed at length why we think such a mechanism could not, in principle, exist (Cosmides and Tooby 1987), but we will summarize one argument briefly here. Acts are regulated by decisions, and decisions are made by procedures or decision rules. For a decision rule to produce adaptive decisions, it depends on the environment having a specific structure that corresponds to the decision rule. For a decision rule to operate, a cue must lead, with some probability, to some outcome. A decision rule that operates in all possible environments—an all-purpose inclusive fitness maximizer—would have to correspond to the structure of all possible environments. That means that no cue could be used by the general decision rule, because a cue that is associated with one outcome in one environment will be associated with another outcome in another environment. (see Table 1). By varying the structure of the environment, any cue could become associated with any outcome with equal probability, so no cue would ever be informative. A decision rule that gains no information from the environment can produce only random decisions—which would not maximize fitness in any environment, let alone in every environment. To gain information from the environment, the procedure must already reflect some of the causal structure of the environment. Learning depends equally on cues, for discriminating success from failure and for many other subtasks as well. The idea of an adaptation that is an all-purpose inclusive fitness maximizer is simply not coherent. In fact, natural selection shapes decision rules and the cues they monitor.

### **Consciousness: The Human Inclusive Fitness Maximizer?**

Turke (1990), following Alexander (1989), proposes “consciousness” (or consciousness plus other psychological mechanisms) as an inclusive fitness-

maximizing system that, although not perfectly general-purpose, is general enough to make modern human behavior inclusive fitness maximizing. As a minor note, most psychologists prefer to use terms other than "consciousness," because of this term's multiplicity of meanings and vagueness concerning what specific design is being hypothesized. We prefer procedural language, involving information-processing steps, decision rules, and conditional relations, because its precision allows one to evaluate the claims involved. In any case, we will interpret the suggestion that humans employ consciousness to "scenario build" as the hypothesis that human beings have cognitive mechanisms whose function is planning, and that these mechanisms are adaptations to the problem of decision-making. By planning, we mean creating cognitive representations of past, present, and future states of the world, evaluating alternative courses of action by representing consequences and matching these against goals, and so on.

We certainly agree with the hypothesis that the capacity to plan is an evolved adaptation, and suspect that most psychologists since Miller, Galanter, and Pribram (1960) would also (see also Symons 1979, on consciousness and planning in rare or novel circumstances). Moreover, the human entry into the "cognitive niche" appears to have involved the evolution of cognitive adaptations for improvising novel sequences of behavior to reach targeted goals of certain kinds, and the breadth of applicability of these mechanisms has obviously allowed humans to penetrate new habitats and subsist in new ways (Tooby and DeVore 1987). For this reason, we also agree with Alexander (1989) and Turke (1990) that human planning widens the range of environments humans can survive and reproduce in. But to say that the human psyche does incorporate some goal-oriented decision rules and planning mechanisms does not mean that humans are generalized inclusive fitness maximizers. As Irons puts it, evolution "has produced a conscious striving for intermediate goals—such as a good diet or sexual satisfaction" (Irons 1983, p. 200) (Daly and Wilson (1988) call these intermediate goals or cues "fitness tokens"). Fitness, being a long-term future consequence of present acts, is intrinsically unobservable at the time actions are taken, so that the goal-specifications of planning mechanisms must always use cues that were probabilistically associated with fitness during ancestral conditions.

### **The Central Role of Ancestral Cues**

Cues provide irreplaceable information, and much of psychological architecture is organized around the ancestral cue structure of the world. For example, displays of naked nubile females are a cue in the hypothetical decision rule "move toward situations that produce retinal displays of naked nubile females and become sexually aroused." Pursuing goals such as proximity to nubile females only leads to fitness as long as the cues that define these goals continue to have positive fitness consequences. A change in the



cue-decision rule-outcome relationship may break the linkage between the decision rules and adaptive outcomes, and may do so to any degree.

One process among many that has disturbed these relationships is the accumulation across historical time of technological expertise. As modern culturally generated technical expertise grows, the ability to contrive situations that have the cues that in the past signaled fitness—but that are now dis severed from their prior long-term fitness consequences—has grown in magnitude. People can now easily fabricate situations that concentrate cues that are completely stripped of their ancestrally coupled fitness payoffs: saccharine displays perceptual cues that once reliably signaled nutritional value, without the ancestrally associated nutritional value; magazine erotica displays perceptual cues of opportunities for fertile copulation, without the reality; narcotics can artificially produce highs that once were only stimulated during actual fitness-promoting activities; films, novels, and television provide cues of fitness-relevant information about people who our mechanisms spuriously judge to be part of our social world, and so on. Because these cues define the goals that figure in human planning, the adaptiveness of planning mechanisms are at the mercy of the structure of the environment. Therefore they do not constitute a system for seeing past the cue-structure of the world into the present structure of selection pressures.

Although it is appealing to think that consciousness or rationality could be free of these constraints, a consideration of what all decision rules need to function indicates that this is not so. Planning requires goals, cues for recognizing goal states, cues for recognizing intermediate states, decision rules, inference procedures and so on, all of which must ultimately derive from relationships found in the EEA. Although planning mechanisms may function as a high-level executive in the psychological architecture, the detailed conformations of the past are even more obviously reflected in the overarching procedures that make planning possible: emotional adaptations. These tie together the structure of past environments, the cues used to construct interpretations of present conditions, and the psychological mechanisms regulated by such interpretations, including planning mechanisms. As we will discuss, although the emotions do make planning possible, they do so through imposing on the present world an interpretative landscape derived from the covariant structure of the past, and so not even planning offers an escape from the past.

### **The Emotions as Adaptations to Recurring Situations**

If the mind is viewed as an integrated architecture of different special purpose mechanisms, “designed” to solve various adaptive problems, a functional description of emotion immediately suggests itself. Each mechanism can operate in a number of alternative ways, interacting with other mechanisms. Thus, the system architecture has been shaped by natural selection to structure interactions among different mechanisms so that they function particularly harmoniously when confronting commonly recurrent (across

generations) adaptive situations. Fighting, falling in love, escaping predators, confronting sexual infidelity, and so on, each recurred innumerable times in evolutionary history, and each requires that a certain subset of the psyche's behavior-regulating algorithms function together in a particular way to guide behavior adaptively through that type of situation. This structured functioning together of mechanisms is a mode of operation for the psyche, and can be meaningful interpreted as an emotional state. The characteristic feeling that accompanies each such mode is the signal which activates the specific constellation of mechanisms appropriate to solving that type of adaptive problem. (Tooby 1985, p. 118).

Animals subsist on information. The single most limiting resource to reproduction is not food or safety or access to mates, but what makes them each possible: the information required for making adaptive behavioral choices. The selection pressure that brings into existence all psychological adaptations (and many nonpsychological ones as well) is the problem of turning encounters with the world into information and using this information to regulate biological processes. Perhaps the greatest adaptive problem facing animals is the decisional opacity of the environment. There are an infinite number of behaviors that an organism could, in principle, engage in; the subset of behaviors that is adaptive in any given situation is, therefore, astronomically small. For this reason, it is not transparent from inspecting the environment which decisions to make—the environment is decisionally “opaque.” If there exists no reliable procedure for making a given kind of decision, then performance will be random, and random performance is usually reproductive death—the random firing of each muscle fiber in your body, for example, will lead in short order to death. The present environment poses, but does not solve, the decision making problem for the organism: it does not compel one decision over another, absent decision rules in the animal.

Moreover, the world is always in flux. It is logically possible to experience it, Zen-like, as an endless series of unique and unprecedented events. Whether events are considered novel or repeated is not just a property of events, but of the system used to categorize them. Every event and circumstance in the world can be considered as unique or as a repetition of an earlier event, depending on the system of categorization used. A system of categorization that experiences each event in the world as unique is useless for making decisions. Natural selection, therefore, will act on the organisms's systems of categorization, so that each encounter with the world is perceived and processed in terms of instances of recurring categories. What makes a particular partitioning of events into classes useful to the organism is whether a decision rule based on that categorization leads to adaptive outcomes. For example, deciding between fleeing or not fleeing requires categorizing situations by the cue “predator present”/“predator absent.”

Cognitive adaptations must use perceived and categorized events as cues for nonperceivable but recurrent sets of conditions. Alternative fitness-promoting courses of action define which cues a decision rule will be selected

to use: cues are useful to the extent that they can be reliably detected and reliably predict the hidden structure of conditions that determines the success of alternative courses of action. For example, the cue “night” predicts the nonperceivable but recurrent condition “situation in which my ability to detect predatory or enemy ambush far enough in advance to take protective measures is very low,” and should therefore regulate decisions about whether to travel, whether to travel alone, how much attention to give to ambiguous stimuli, and so on. The selection pressure that creates adaptations that categorize night as different from day is the need to make these kinds of behavioral decisions. Without cues, animals could not regulate their behavior in adaptive ways. Animals depend on the cue structure of the world.

Cues need not be of uniform sensory characteristics, but can be defined in relation to any recurrently identifiable properties of the world or the animal. For example, rats will eat a novel food if they smell it on the mouth of another rat, but not if they smell it on some other part of another rat’s body (Galef 1990). For the purposes of this decision rule, the category “acceptable to eat” is not defined by any uniform sensory properties in the food itself, but rather by whether its sensory properties match the templates created when the rat encountered and smelled other rats. Similarly, the bundle of stimuli that uniquely identify a greylag goose become recognizable to the decision rules in the hatched offspring through a relational cue that is something like “form a template of the first large mobile entity encountered after hatching that remains close by for greater than a threshold period” (Lorenz 1970). Many cues that humans use are of this relational kind. Invariances in emotional expression, for example, provide relational cues that allow the assignment of biological meaning to events and stimuli (e.g., the meaning “predator” may be assigned to any large animal that conspecifics express fear towards) (Darwin 1872; Cosmides 1983). There is enormous variety in the way objects, situations, and other entities can appear to the senses under different circumstances, but to be reacted to by decision-making algorithms, they must be assigned a meaning in terms that these algorithms use. Representational processes that attach or link the contingent appearance of entities and situations to an evolved algorithm are essential to the operation of any decision rule. If the rule is “flee predators when observed,” then there must be an associated algorithm that determines what counts as having observed a predator. Although the cues used may be constant sensory invariances (“is large and has fangs and claws”), relational cues can often improve accuracy (“anything that causes conspecifics to shriek and flee”). Some biological categories have no uniform appearance from generation to generation—for example, one cannot distinguish one’s mother from other human females by appearance alone. In such cases, relational cues are essential (e.g., “mother” = “the human female who nursed and took care of me during infancy”). Superficial variability in cultural phenomena masks an underlying uniformity in cues and algorithms.

The requirement that stimuli be sorted into recurrent categories is why “novelty” cannot, in principle, be a discrete selection pressure like temperature. If something is genuinely unprecedented, mechanisms will not assign it to the categories that trigger the correct decision rules, except by chance. Mechanisms that appear able to handle novelty do so only because the apparent novelty resides in one aspect of the phenomenon, while algorithms are operating on other aspects that display subtle or relational cues based on some underlying recurrent uniformity. The ability to handle a certain kind of variation depends on selectively significant encounters with cues probabilistically linked to that type of variation in the evolutionary past.

### **Situation Cues Elicit Emotions**

The human environment of evolutionary adaptedness had a statistically defined structure, which included the association of cues with recurrent conditions. Repeated relationships among conditions constitute evolutionarily recurrent situations. For example, the condition of having a mate plus the condition of one’s mate copulating with someone else adds up to a situation of sexual infidelity. To the extent that situations are structured and recurrent over evolutionary time, their statistical properties can be used as the basis for a special kind of psychological adaptation: an emotion. An emotion corresponds to a distinctive system of coordination among the mechanisms that regulate each controllable biological process. That is, “[e]ach emotional state manifests design features ‘designed’ to solve particular families of adaptive problems, whereby the psychological mechanisms assume a unique configuration. Using this approach, each emotional state can be mapped in terms of its characteristic configuration, and of the particular mode each identifiable mechanism adopts” (Tooby 1985, p. 120). Thus, each emotion state—fear of predators, guilt, sexual jealousy, rage, grief, and so on—will correspond to an integrated mode of operation that functions as a solution designed to take advantage of the particular structure of the recurrent situation these emotions correspond to. Discovering one’s mate in a sexual liaison signals a situation that threatens future reproduction and present investment allocation; this cue should therefore activate sexual jealousy (Daly, Wilson, and Weghorst 1982). The emotion of sexual jealousy constitutes an organized mode of operation specifically designed to deploy the programs governing each psychological mechanism so that each is poised to deal with the exposed infidelity: physiological processes are prepared for violence; the goal of deterring, injuring, or murdering the rival emerges; the goal of punishing or deserting the mate appears; the desire to make oneself more competitively attractive emerges; memory is activated to reanalyze the past; and so on.

### **How to Characterize an Emotion**

To characterize an emotion adaptation, one must identify the following properties of environments and of mechanisms.

1) *A situation.* A recurrent structure of environmental and organismic properties, characterized as a complex statistical composite of how such properties covaried in the environment of evolutionary adaptedness. Examples of situations are being in a depleted nutritional state, competing for maternal attention, being chased by a predator, being about to ambush an enemy, having few friends.

2) *The adaptive problem.* The identification of which organismic states and behavioral sequences will lead to the best average functional outcome, given the situation. For example, what to do given you are being chased by a predator; what to do given you are in a depleted nutritional state.

3) *Cues that signal the presence of the situation.* For example, low blood sugar signals a depleted nutritional state, the looming approach of a large fanged animal signals the presence of a predator, seeing your mate having sex with another signals sexual infidelity; finding yourself alone or avoided by others signals that you have few friends.<sup>7</sup>

4) *Algorithms that monitor for situation-defining cues.* Including perceptual mechanisms, proprioceptive mechanisms, and situation-modeling memory.

5) *Algorithms that detect situations.* These mechanisms take the output of the monitoring algorithms in (4) as input, and through integration, probabilistic weighting, and other decision criteria, identify situations as either present or absent (or present with some probability).

6) *Algorithms that assign priorities.* A given world-state may correspond to more than one situation at a time, for example, you may be nutritionally depleted *and* in the presence of a predator. The prioritizing algorithms define which emotion modes are compatible (e.g., hunger and boredom), which are mutually exclusive (e.g., feeding and predator escape). Depending on the relative importance of the situations and the reliability of the cues, the prioritizing algorithms decide which emotion modes to activate and deactivate, and to what degree.

7) *An internal communication system.* Given that a situation has been detected, the internal communication system sends a situation-specific signal to all relevant mechanisms; the signal switches them into the appropriate adaptive emotion mode.

8) *A set of algorithms specific to each mechanism that regulates how*

<sup>7</sup> The assignment of a situation interpretation to present circumstances is a problem in signal detection theory (Swets, Tanner and Birdsall 1964; see also Gigerenzer and Murray 1987)—the animal needs to “detect” what situation it is on the basis of cues, and specialized interpretation algorithms. Selection will not shape decision rules so that they act solely on the basis of what is most likely to be true, but rather on the basis of the weighted consequences of acts given that something is held to be true. Should you walk under a tree that might conceal a predator? Even if the algorithms assign a 51% (or even 95%) probability to the tree being predator-free, under most circumstances the decision rule should cause you to avoid the tree—to act as if the predator were in it. The benefits of calories saved via a shortcut, scaled by the probability that there is no predator in the tree, must be weighed against the benefits of avoiding becoming catfood, scaled by the probability that there is a predator in the tree. Because the costs and benefits of false alarms, misses, hits, and correct rejections are often unequal, the decision rules may still treat as true situations that are unlikely to be true.

*it responds to each specialized emotion state.* These algorithms determine whether the mechanism should switch on or switch off, and if on, what emotion-specialized performance they will implement.

Any controllable biological process that, by shifting its performance in a specifiable way, would lead to enhanced average fitness outcomes should come to be partially governed by emotional state [see (8)]. Such processes include:

*Goals.* The cognitive mechanisms that define goal-states and choose among goals in a planning process should be influenced by emotions. For example, vindictiveness—a specialized subcategory of anger—may define “injuring the offending party” as a goal state to be achieved. (Although the functional logic of this process is deterrence, this function need not be represented, either consciously or unconsciously, by the mechanisms that generate the vindictive behavior.)

*Motivational priorities.* Mechanisms involved in hierarchically ranking goals, or, for nonplanning systems, other kinds of motivational and reward systems, should be emotion-dependent. What may be extremely unpleasant in one state, such as harming another, may seem satisfying in another state (e.g., aggressive competition may facilitate counter-empathy).

*Information-gathering motivations.* Because establishing which situation you are in has enormous consequences for the appropriateness of behavior, the process of detection should in fact involve specialized inference procedures and specialized motivations to discover whether certain suspected facts are true or false. What one is curious about, what one finds interesting, what one is obsessed with discovering should all be emotion-specific.

*Imposed conceptual frameworks.* Emotions should prompt construals of the world in terms of concepts that are appropriate to the decisions that must be made. If in an angry mood, domain-specific concepts such as social agency, fault, responsibility, and punishment will be assigned to elements in the situation. If hungry, the food-nonfood distinction will seem salient. If endangered, safety-categorization frames will appear. The world will be carved up into categories based partly on what emotional state an individual is in.

*Perceptual mechanisms.* Perceptual systems may enter emotion-specific modes of operation. When fearful, acuity of hearing may increase. Specialized perceptual inference systems may be mobilized as well; if you’ve heard rustling in the bushes at night, human and predator figure-detection may be particularly boosted, and not simply visual acuity in general. In fact, non-threat interpretations may be depressed, and the same set of shadows will “look threatening”—that is, given a specific threatening interpretation such as “a man with a knife”—or not, depending on emotion-state.

*Memory.* The ability to call up particularly appropriate kinds of information out of long-term memory will be influenced. A woman who has just found strong evidence that her husband has been unfaithful may find a torrent

of memories about small details that seemed meaningless at the time but that now fit into an interpretation of covert activity. We also expect that what is stored about present experience will also be differentially regulated, with important or shocking events, for example, stored in great detail.

*Attention.* The entire structure of attention, from perceptual systems to the contents of high-level reasoning processes, should be regulated by emotional state. If you are worried that your spouse is late and might have been injured, it is hard to concentrate on other ongoing tasks.

*Physiology.* Each organ system, tissue, or process is a potential candidate for emotion specific regulation, and “arousal” is doubtless insufficiently specific to capture the detailed coordination involved. Changes in circulatory, respiratory, and gastrointestinal functioning are well-known and documented, as are changes in levels of circulating sex hormones. We expect thresholds regulating the contraction of various muscle groups to change with certain emotional states, reflecting the probability that they will need to be employed. Similarly, immune allocation and targeting may vary with disgust, or with the potential for injury, or with the demands of extreme physical exertion.

*Communication processes.* What individuals communicate, whether “voluntarily” or “involuntarily,” will be influenced by emotion state. The role of emotional expression as a form of functional communication of situation (including intentions) goes back to Darwin, and is widely appreciated (Darwin 1872; Ekman 1982). The value of providing information to others, or of obscuring it, will depend on the situation one is in, which is also defined by who one is with. Expressiveness and the content of expression will be different depending on whether one is alone, with people one trusts, or with social antagonists (where leakage of damaging information will be suppressed). An emotion state of pride should be activated when an individual is in situations in which it will benefit her that certain kinds of information become easily available to others. Body posture, willingness to participate in social activities, and other factors will ease the release of this information through its association with her appearance. The converse is true when someone is ashamed; concealment of information should occur through reticence to speak or be noticed and through avoidance of social situations that would lead others to associate the shameful act with that individual.

*Behavior.* All psychological mechanisms are involved in the generation and regulation of behavior, so obviously behavior will be regulated by emotion state. More specifically, however, mechanisms proximately involved in the generation of actions (as opposed to processes like face recognition that are only distally regulatory) should be very sensitive to emotion state. Not only may highly stereotyped behaviors of certain kinds be released (as during sexual arousal or rage, or as with species-typical facial expressions and body language), but more complex action-generation mechanisms should be regulated as well. Specific acts and courses of action will be more available as responses in some states than in others, and more likely to be im-

plemented. Emotion mode should govern the construction of organized behavioral sequences that solve adaptive problems.

*Specialized inference.* Emotion mode should be one factor that governs the activation of specialized inferential systems, such as cheater detection (Cosmides 1985, 1989; Cosmides and Tooby 1989), bluff detection, and so on.

*Reflexes.* Muscular coordination, tendency to blink, threshold for vomiting, shaking, and many other reflexes should be regulated by emotion mode.

*Learning.* Emotion mode will also regulate learning mechanisms. What someone learns from stimuli will be greatly altered by emotion mode, because of attentional allocation, motivation, situation-specific inferential algorithms, and a host of other factors. Emotion mode will cause the present context to be divided up into situation-specific functionally appropriate categories so that the same stimuli and the same environment may be interpreted in radically different ways, depending on emotional state. For example, which stimuli are considered similar should be different in different emotional states, distorting the shape of the individual's psychological "similarity space" (Shepard 1987).

*Affective coloration of events and stimuli.* A behavioral sequence is composed of many acts. Each of these acts can be thought of as an intermediate "factor" in the production of a behavioral sequence. Determining which courses of action are worthwhile and which are not is a major informational problem. The payoff of each "factor of production"—of each act in the sequence—must be computed before one can determine whether the whole sequence is worthwhile. Every time there is a change in the world that affects the probable payoff of an act or new information that allows a better evaluation of payoffs, this value needs to be recomputed. Evaluating entire chains as units is not sufficient, because each item in a chain (staying behind from the hunt, making a tool, borrowing materials from a friend, etc.) may be used in another unique sequence at a later time. Therefore, effort, fitness token payoffs (rewards), risks, and many other components of evaluation need to be assigned continually to classes of acts. For this reason, there should be mechanisms that assign hedonic values to acts, tallied as intermediate weights in decision processes. Our stream of actions and daily experiences will be affectively "colored" by the assignment of these hedonic values. If our psychological mechanisms were not using present outcomes to assign hedonic weights to classes of acts, there would be no function to suffering, joy, and so on. Emotion mode obviously impacts the assignment of hedonic values to acts.

*Energy level and effort allocation.* Overall metabolic budget will, of course, be regulated by emotion, as will specific allocations to various processes and facilitation or inhibition of specific activities. The effort that it takes to perform given tasks will shift accordingly, with things being easier or more effortful depending on how appropriate they are to the situation



reflected by the emotion. Thus, fear will make it more difficult to attack an antagonist, while anger will make it easier. The confidence with which a situation has been identified should itself regulate the effortfulness of situation-appropriate activities. Confusion should inhibit the expenditure of energy on costly behavioral responses and should motivate more information gathering and information analysis. Nesse (in press) has suggested that the function of mood is to reflect the propitiousness of the present environment for action, a hypothesis with many merits. We would take his general approach in a somewhat different direction, since the action-reward ratio of the environment is not a function of the environment alone, but an interaction between the structure of the environment and the individual's present understanding of it. (By understanding, we mean the correspondence between the structure of the environment, the structure of the algorithms, and the weightings and other information they use as input parameters.) The phenomenon that should regulate this aspect of mood is a perceived discrepancy between expected and actual payoff. The suspension of activity accompanied by very intense cognitive activity in depressed people looks like an effort to reconstruct models of the world so that future action can lead to payoffs. Depression should be precipitated by a heavy investment in a behavioral enterprise that was expected to lead to a large payoff, but that either failed to materialize, or was not large enough to justify the investment.

*Recalibration and imagined experience.* Information about outcomes is not equally spread throughout all points in time and all situations. Some situations are information-dense, full of ancestrally stable cues that reliably predicted the fitness consequences of certain decisions and could therefore be used to alter weightings in decision rules. For example, Hamilton's (1964) rule gives the logic for allocating benefits between self and kin, but not the procedures by which a mechanism could estimate the value of, say, a particular piece of food to oneself and one's kin. The payoffs of such acts of assistance vary with circumstances, consequently, each decision about where to allocate assistance depends on inferences about the relative weights of these variables. These inferences are subject to error. Imagine an individual is allocating meat according to Hamilton's rule, using the best information available to her to weigh the relative values of the meat to herself and her sister. The sudden discovery that her sister has become very sick and emaciated may function as an information-dense situation allowing the recalibration of the algorithms that weighted the relative values of the meat. The sister's sickness functions as a cue that the previous allocation weighting was in error and that the variables need to be reweighted—including all of the weightings embedded in habitual action sequences. Guilt, for example, may function as an emotion mode specialized for recalibration, as may a number of other emotions. Previous courses of action are brought to mind (I could have helped then, why didn't I think to?) to reset choice points in decision rules. The negative valence of depression may be explained similarly; former actions that seemed pleasurable in the past, but which ulti-

mately turned out to lead to bad outcomes, are reexperienced in imagination with a new affective coloration, so that in the future entirely different weightings are called up during choices.

*The role of imagery and emotion in planning.* Imagery is the representation of perceptual information in a format that resembles actual perceptual input. Being in an environment displaying specific perceptually detectable cues (sweetness, predators, running sores, emotion expressions) triggers certain decision and evaluation rules. Recreating those cues through imagery may trigger the same algorithms (minus their behavioral manifestations), allowing the planning function to evaluate imagined situations by using the same circuits that evaluate real situations. This would allow alternative courses of action to be evaluated in a way similar to the way in which experienced situations are evaluated. In other words, image-based representations may serve to unlock, for the purposes of planning, the same evolved mechanisms that are triggered by an actual encounter with a situation displaying the imagined perceptual and situational cues. For example, imagining the death of your child can call up the emotional state you would experience had this actually happened, activating previously dormant algorithms and making new information available to many different mechanisms. As many have recognized, this simulation process can help in making decisions about future plans. Even though you have never actually experienced the death of a child, for example, an imagined death may activate an image-based representation of extremely negative proprioceptive cues that “tell” the planning function that this is a situation to be avoided. Paradoxically, grief provoked by death may be a byproduct of mechanisms designed to take imagined situations as input: it may be intense so that, if triggered by imagination in advance, it is properly deterrent. Alternatively (or additionally) grief may be intense in order to recalibrate weightings in the decision rules that governed choices prior to the death. If your child died because you make an incorrect choice, then experiencing grief may recalibrate you for subsequent choices. Death may involve guilt, grief, and depression because of the problem of recalibration of weights on courses of action. One may be haunted by guilt, meaning that courses of action retrospectively judged to be erroneous may be replayed in imagination over and over again, until the reweighting is accomplished. Similarly, joyful experiences may be savored, that is, replayed with attention to all of the details of the experience, so that every step of the course of action can be colored with positive weightings as it is rehearsed, again, until the simulated experience of these pseudo “learning trials” has sufficiently reweighted the decision rules.

People can be expected to respond to ancestral cues whether or not they are still predictively valid, and the imagery and emotion systems induce them to plan the pursuit of proprioceptive goal cues such as pain relief, endorphin-highs, sexual arousal, and sweetness, whether or not these are still valid predictors of inclusive fitness. People plan to steal to get money

to take artificial opiates, plan to buy erotica rather than search for a mate, plan to eat injurious, but delicious sweets. In India, the poor sometimes sell their blood to buy movie tickets. Humans are not fitness-maximizers; to the extent they can be characterized as goal-seeking maximizers of any kind, they are ancestral-environment fitness-cue maximizers, a profoundly different thing.

Ever since Darwin (1871, 1872), emotions have been seen as the product of the evolutionary process, and usually, although not always, as functional adaptations (Arnold 1960, 1968; Chance 1980; Daly, Wilson, and Weghorst 1982; Darwin 1872; Eibl-Eibesfeldt 1971; Ekman 1982; Frijda 1986; Hamburg 1968; Izard 1977; Otte 1974; Plutchik 1980; Tomkins 1962, 1963; and many others) In fact, much of the best work in evolutionary psychology to date stems from an evolutionary-functional approach to emotions (e.g., Bowlby 1969; Daly, Wilson, and Weghorst 1982; Ekman 1982). The particular interpretive framework advanced here (Tooby 1985, see also Tooby and Cosmides 1990) is consistent with much of the vast literature on emotion, and is simply an attempt to integrate into a modern adaptationist framework the idea that the mind consists primarily of a collection of evolved function-specific information processing mechanisms (Cosmides and Tooby 1987; Cosmides 1985, 1989; Tooby and Cosmides 1989; Tooby 1985) with such views as that emotions are coordinated systems (Arnold 1960, 1968; Izard 1977; Frijda 1986; Lazarus, Kanner, and Folkman 1980; Plutchik 1980) that organize action (Frijda 1986; Lazarus 1968; Leeper 1948) appropriate to situations (Arnold 1960; Frijda 1986; Lazarus, Kanner, and Folkman 1980; Tolman 1923; see especially Neese's excellent discussion, in press).

### **Emotions and the Meaning of Situations**

The fitness consequences of an act are not a feature of the world that the individual can use to regulate its behavior. Fitness is the expected long-term consequences on genetic propagation of a particular phenotypic design relative to alternative designs. As such, it is inherently unobservable at the time the design alternative actually impacts the world, and therefore cannot function as a cue for a decision rule. The "decision" to allocate 12% rather than 14% of metabolic activity to immune function at six months of age may change every subsequent action in some way, and its impact on reproduction at age 42, for example, is not observable to the infant. Because fitness is relative, the infant would have to have an inventory of all alternative designs to be hypothetically chosen among, cross-tabulated against their expected completed reproduction and inclusive fitness effects. Each course of action (or any hypothetical aspect of phenotypic design) is, from the point of view of an individual, an uncontrolled experiment, providing few grounds for conclusions about alternatives at the time they are undertaken. (Actions repeated sufficiently often over an individual's life can be evaluated by their immediate and observable consequences, according to some decision rule—

that is, learning is possible—but the decision rule that evaluates trials and guides learning is itself an ontogenetically uncontrolled and unevaluated experiment.) Instead of the individual computing the course of action with the highest fitness—an impossibility—the world “evaluates” alternative designs cross-generationally and selects the one that propagates, on average and over the long term, most effectively.

The organism cannot directly perceive its present situation according to the actual fitness-contingencies related to alternative courses of action. It cannot follow the cinematic decision rule “do the right thing.” Instead, the organism “perceives” its present situation in terms of the recurrent structure of ancestral environments and assigns interpretations to the present environment based on the phylogenetically encountered categories of the past. The ancestrally recurrent structured situation that the organism categorizes itself as being in is the “meaning” of the situation for that organism. It “sees,” i.e., is organized to respond to, previous fitness contingencies, not present ones. Built into the physiological architecture is the “assumption” that the present parallels the statistical structure of past conditions and fitness contingencies. Thus, part of what emotions make “visible” are the fitness contingencies of actions, but only to the extent that the present recreates the past.

## THE WORLD AS A COMPUTER

According to this analysis of the emotions, the many mechanisms comprising our psychological architecture are deployed according to the “best bet” for how each mechanism should operate in subsequent choices and actions, given the cued situation. This best bet is based on the long-run average of how one specific setting versus alternative settings succeeded over hundreds of thousands of cue-defined ancestral encounters. If potentially lethal violence followed in 24% of the situations in which men discovered infidelity in their mates, then women’s mechanisms should be programmed based on that statistical average. No organism’s nervous system could possibly model all of the necessary features of the environment nor do all the calculations required to figure out what the best arrangement for each mechanism would be, given present stimuli. The “computation” conducted by the evolutionary process requires nothing less than the world itself as an enduring cross-generational laboratory that measures the frequency of environmental conditions, the reliability of cues, the heritable variations in mechanism-states, the actions taken, and their consequences. The results of this “experiment” or “computation” are stored in the form of evolved phenotypic design. This evolutionary process brings the ancestrally recurrent cue-discriminated and cue-defined situation into a specialized correspondence with the mode of operation of the psychological architecture, so that the algorithms regulating each mechanism are prepared to operate adaptively in those (interpreted as opposed to actual) circumstances. Detailed studies of the cognitive proce-

dures constituting the emotions, representing as they do complex decision rules and statistical weightings, may prove over the next several decades to be our most reliable window into the evolutionary past. Whether (and to what extent) war, paternal care, monogamy, infidelity, food-sharing, and scavenging were major features of our hunter-gatherer past should all be testable by investigating our emotional adaptations. Because emotions reflect the structure of the human past, they constitute a treasure-house of information about the nature of ancestral conditions and about the power of various evolutionary processes.

The cues that the present situation displays function as predictors of a larger encompassing structure of conditions and contingencies that the individual cannot directly observe. Emotions and other component mechanisms lead organisms to act as if certain things were true about their present circumstances, whether or not they are, because they were true of past circumstances. They allow the animal to “go beyond the information given” (Bruner 1973). In this lies their strength and their weakness. They allow organisms to infer on probabilistic grounds the presence of invisible structural features of the world and to navigate among these features. Because many crucial decisions must be made in the absence of sufficiently observationally available information, these mechanisms allow adaptive behavior that could not be “rationally” justified based on the information available to one individual accumulated in one lifetime. For the same reason, however, such mechanisms cannot detect when the invariances that held true ancestrally no longer obtain. That is their weakness.

## CONCLUSIONS

Acceptance of these conclusions means that some widely used concepts are invalid and must be abandoned. The question inevitably arises as to how such an abundance of misinterpretation has arisen. I believe the major factor is that biologists have no logically sound and generally accepted set of principles and procedures for answering the question: “What is its function?”

*George Williams (1966: 252)*

The last three decades in evolutionary biology have seen enormous advances in the sophistication and power of evolutionary thinking, but the goal of developing “a logically sound and generally accepted set of principles and procedures for answering the question: ‘What is its function?’” remains still unfinished. Although orthogenesis and inappropriate group selection models have departed, hyperadaptive near-Lamarckianism, the unwarranted neglect of the role of the past, the evasion of the characterization of adaptations, and many other confusions and poor practices have replaced them in various biological literatures.

In this article, we have emphasized how adaptations reflect the configuration of the past. To invert Hughes’ (1987) almost Lamarckian dicta on evolutionary explanation (with which we began this article), we have argued

that it is illogical for evolutionary biologists to appeal to present advantages as an explanation for present adaptations. Although widespread current behaviors have consequences in terms of inclusive fitness at the present time, these present consequences are entirely irrelevant to explaining the adaptations that produce those behaviors. If these adaptations are to be explained on biological grounds at all, they must be explained in terms of their contribution to inclusive fitness during their past encounters with ancestral conditions, without regard to whether they happen to be fitness-promoting at the present time. Nevertheless, observations about specific patterns of present adaptiveness can provide clues about the structure of specific adaptations. If a set of present behaviors is too fitness-promoting to be coincidence, this suggests the operation of some underlying adaptation, which should be characterized.

For an adaptationist, no large issue hangs on whether modern human behavior is globally described as "adaptive" or not, or on the degree to which the modern world resembles the human EEA. The relevance of Darwinism to human behavior is logically inescapable and would not be in the least diminished if no modern behavior were adaptive. Our inherited design is the same regardless of our circumstances, and it can only be understood with reference to our evolutionary history, whether we are Ache foragers or astronauts orbiting Pluto.

Although humans, as intelligent, cultural, conscious, planning animals, might appear to be fitness-strivers, prospective fitness is not a goal that can be directly observed in a way that can be used to regulate behavior. A general purpose inclusive fitness maximizer is impossible, and possessing consciousness (or a planning capacity) does not make people fitness-strivers or inclusive fitness maximizers. Describing humans as fitness-strivers is perhaps more appropriate than describing them as, say, ascribed role implementers, vehicles for arbitrary semiotic systems, profit-maximizers, group solidarity-promoters, or the other descriptions not inspired by Darwinism. Still, it is an erroneous characterization: humans are adaptation-executers, not fitness-strivers. For this reason, human behavior is not well explained by attempts to show how it corresponds to contextually appropriate fitness pursuit. Instead, it should be explained as the output of adaptations (using present circumstances as input), which are themselves the constructed product of selection under ancestral conditions. Far from being governed by "rational fitness-maximization" (Hughes 1987), the operation of human psychological mechanisms are orchestrated by emotions that frame present circumstances in terms of the evolutionary past. For a Darwinian, there is no escaping the past.

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## REFERENCES

- Alexander, R.D. The search for an evolutionary philosophy of man. *Proceedings of the Royal Society of Victoria*, 84: 99–120, 1971.
- Alexander, R.D. *Darwinism and human affairs*. Seattle: University of Washington Press, 1979a.
- Alexander, R.D. Evolution and culture. In: *Evolutionary Biology and Human Social Behavior*. Napoleon Chagnon and William Irons, eds. pp. 59–78. 1979b. North Scituate, Mass.: Duxbury Press.
- Alexander, R.D. Evolution, culture, and human behavior: some general considerations. In: R.D. Alexander and D.W. Tinkle (eds.) *Natural Selection and Social Behavior*, 1981. 509–520. New York: Chiron Press.
- Alexander, R.D. *The biology of moral systems*, 1987. New York: Aldine.
- Alexander, R.D. Evolution of the human psyche. In P. Mellars and C. Stringer, eds. *The human revolution*, 1989. University of Edinburgh Press.
- Alexander, R.D. and Tinkle, D.W. (eds). *Natural Selection and Social Behaviour: Recent Research and New Theory*, 1981. Chiron Press, New York.
- Arnold, M.B. *Emotion and Personality*, 1960. New York: Columbia University Press.
- Arnold, M.B. *The nature of emotion*, 1968. London: Penguin Books.
- Barkow, J.H. Culture and Sociobiology. *American Anthropologist*. 80: 5–20, 1978.
- Barkow, J.H. The distance between genes and culture. *Journal of Anthropological Research*, 37: 367–379, 1984.
- Barkow, J.H. *Darwin, sex, and status: Biological approaches to mind and culture*, 1989. Toronto: University of Toronto Press.
- Barkow, J., Cosmides, L. and Tooby, J. (eds.) *The Adapted Mind: Evolutionary psychology and the generation of culture*, Oxford University Press. In press.
- Betzig, L. Rethinking human ethology: A response to some recent critiques. *Ethology and Sociobiology*, 19: 315–324, 1989.
- Betzig, L., Borgerhoff Mulder, M., and Turke, P. *Human reproductive behavior*, 1988. Cambridge: Cambridge University Press.
- Borgia, G. Typology and human mating preferences. *Behavioral and Brain Sciences*. 12: 16–17, 1989.
- Bruner, J. *Beyond the information given*, 1973. (J. M. Anglin, ed.) New York: Norton & Co.
- Buss, D.M. Sex differences in human mate selection criteria: An evolutionary perspective. In Crawford, C.B., Smith, M.F., & Krebs, D.L. (Eds), *Sociobiology and psychology*, 1987. Hillsdale, NJ: Erlbaum.
- Buss, D.M. Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. *Behavioral and Brain Sciences*. 12(1): 1–49, 1989.
- Chagnon, Napoleon. "Mate competition, favoring close kin, and village fissioning among the Yanomamo Indians." In: *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective*, 1979. N. Chagnon and W. Irons, eds. Duxbury.
- Chance, M.R.A. An ethological assessment of emotion. In *Emotion: Theory, research, and experience*, R. Plutchik & H. Kellerman, (eds.). pp. 81–111, 1980.
- Clutton-Brock, T.H. and Harvey, P.H. Comparative approaches to investigating adaptation. In Krebs, J. and Davies, N. (eds.) *Behavioral ecology: an evolutionary approach. Second Edition*, 1984. Sunderland, Mass.: Sinauer.
- Cosmides, L. Invariances in the acoustic expression of emotion during speech. *Journal of Experimental Psychology: Human Perception and Performance*, 9: 864–881, 1983.
- Cosmides, L. *Deduction or Darwinian Algorithms? An explanation of the "elusive" content effect on the Wason selection task*, 1985. Doctoral dissertation, Harvard University. University Microfilms.

- Cosmides, L. The logic of social exchange: Has natural selection shaped how humans reason? Studies with the Wason selection task. *Cognition*, 31: 187–276, 1989.
- Cosmides, L. and Tooby, J. Cytoplasmic inheritance and intragenomic conflict. *Journal of Theoretical Biology*, 89: 83–129, 1981.
- Cosmides, L. and Tooby, J. Evolutionary psychology and the generation of culture. Part II. Case study: A computational theory of social exchange. *Ethology and Sociobiology*, 10: 51–97, 1989.
- Cosmides, L. and Tooby, J. From evolution to behavior: Evolutionary psychology as the missing link. In Dupre, J. (Ed.), *The latest on the best: Essays on evolution and optimality*, 1987. Cambridge, MA: MIT Press.
- Daly, M., Wilson, M., and Weghorst, S.J. Male sexual jealousy. *Ethology and Sociobiology*, 3: 11–27, 1982.
- Daly, M. and Wilson, M. *Homicide*, 1988. New York: Aldine.
- Darwin, C. *On the Origin of Species*, 1859. London: Murray. (New edition: Cambridge, MA: Harvard University Press.)
- Darwin, C. *The descent of man and selection in relation to sex*, 1876. Murray, London.
- Darwin, C. *The expression of emotions in man and animals*, 1872. London: John Murray.
- Dawkins, R. *The selfish gene*, 1976. Oxford: Oxford University Press.
- Dawkins, R. *The extended phenotype: The gene as the unit of selection*, 1982. Oxford: W.H. Freeman.
- Dawkins, R. *The blind watchmaker*, 1986. New York: W.W. Norton.
- Dickemann, M. "The reproductive structure of stratified societies: a preliminary model." In: *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective*, 1979. N. Chagnon and W. Irons, eds. Duxbury.
- Dobzhansky, T. *Genetics and the origin of species*, 1937. Columbia Univ. Press, New York.
- Dobzhansky, T. *Genetics of the evolutionary process*, 1970. Columbia Univ. Press, New York.
- Draper, P. African marriage systems: Perspectives from evolutionary ecology. *Ethology and Sociobiology*, 10: 145–169, 1989.
- Dunbar, R.I.M. Darwinizing Man: A commentary. In: Betzig, L., Borgerhoff Mulder, M., and Turke, P. (eds.) *Human reproductive behavior*, 1988. Cambridge: Cambridge University Press.
- Ekman, P. (ed.) *Emotion in the human face. Second Edition*, 1982. Cambridge: Cambridge University Press.
- Erickson, C.J. and Zenone, P.G. Courtship differences in male ring doves: avoidance of cuckoldry? *Science* 192: 1353–1354, 1977.
- Fisher, R.A. *The genetical theory of natural selection (Second revised edition)*, 1958. New York: Dover.
- Fox, R. *The red lamp of incest*, 1980. New York: E.P. Dutton.
- Frijda, N.H. *The emotions*, 1986. London: Cambridge University Press.
- Galef, B.G. An adaptationist perspective on social learning, social feeding, and social foraging in Norway rats, 1990. In: D. Dewsbury (Ed.), *Contemporary issues in comparative psychology*. Sunderland, Mass.: Sinauer.
- Gigerenzer, G. and Murray, D.J. *Cognition as intuitive statistics*, 1987. Hillsdale, N.J.: Lawrence Erlbaum Associates.
- Hamburg, D.A. Emotions in the perspective of human evolution. In *Perspectives on human evolution*. S.L. Washburn and P.C. Jay, eds. pp. 246–257, 1968. New York: Holt, Rinehard and Winston.
- Hamilton, W.D. The genetical evolution of social behaviour. *Journal of Theoretical Biology*, 7: 1–52, 1964.
- Harcourt, A.H., Harvey, P.H., Larson, S.G., and Short, R.V. Testis weight, body weight and breeding system in primates. *Nature*, 293: 55–57, 1981.
- Hughes, A.L. Social and antisocial behavior. *Quarterly Review of Biology*. 62(4): 415–421, 1987.
- Izard, C.E. *Human Emotions*, 1977. New York: Plenum.
- Irons, W. Is Yomut behavior adaptive? In G. Barlow and J. Silverberg, (eds.) *Sociobiology: beyond nature/nurture?* 1980. Boulder, CO.: Westview Press .
- Irons, W. Human female reproductive strategies. In S.K. Wasser, (ed.) *Social behavior of female vertebrates*, 1983. New York: Academic Press.



- Kaplan, H. and Hill, K. Food-sharing among Ache foragers: Tests of explanatory hypotheses. *Current anthropology*, 26: 223–246, 1985.
- Lorenz, K. Companions as factors in the bird's environment. In *Studies on animal and human behavior*. Vol. 1. K.Z. Lorenz (ed.). 1970. Harvard University Press, Cambridge, Mass.
- Marr, D. *Vision: A computational investigation into the human representation and processing of visual information*, 1982. San Francisco: Freeman.
- Mayr, E. *Animal species and evolution*, 1963. Belknap Press, Harvard Univ. Press, Cambridge, Mass.
- McCracken, R. Lactase deficiency: An example of dietary evolution. *Current Anthropology*, 12: 479–517, 1971.
- Miller, G.A., Galanter, E., and Pribram, K.H. *Plans and the structure of behavior*, 1960. NY: Holt.
- Otte, D. Effects and functions in the evolution of signaling systems. *Annual Review of Ecology and Systematics*, 5: 385–417, 1974.
- Partridge, L. Mate choice increases a component of offspring fitness in fruit flies. *Nature*, 283: 290–291, 1980.
- Plutchik, R. *Emotion: A psychoevolutionary synthesis*, 1980. New York: Harper & Row, 1980.
- Proffitt, D.R. and Gilden, D.L. Understanding natural dynamics. *Journal of experimental psychology: Human perception and performance*, 15:384–393, 1989.
- Robertson, D.R. Social control of sex reversal in a coral-reef fish. *Science*, 177: 1007–1009, 1972.
- Shepher, J. *Incest: a biosocial view*, 1983. New York: Academic Press.
- Shepard, R.N. Evolution of a mesh between principles of the mind and regularities of the world. In J. Dupre (Ed.), *The latest on the best*, 1987. Cambridge, MA: The MIT Press.
- Smuts, R.W. Behavior depends on context. *Behavioral and Brain Sciences*, 12: 16–17, 1989.
- Swets, J.A., Tanner, W.D., and Birdsall, T.G. Decision processes in perception. In J.A. Swets (Ed.) *Signal detection and recognition by human observers*, 1964. New York: Wiley.
- Symons, D. *The evolution of human sexuality*, 1979. Oxford: Oxford University Press.
- Symons, D. If we're all Darwinians, what's the fuss about? In Crawford, C.B., Smith, M.F., and Krebs, D.L. (Eds), *Sociobiology and psychology*, 1987. Hillsdale, NJ: Erlbaum.
- Symons, D. A critique of Darwinian anthropology. *Ethology and Sociobiology*, 10: 131–144, 1989.
- Symons, D. On the use and misuse of Darwinism in the study of human behavior. In *The adapted mind: Evolutionary psychology and the generation of culture*, J. Barkow, L. Cosmides, and J. Tooby, (eds). New York: Oxford University Press, in press.
- Symons, D. *Ethology and Sociobiology*, 11, 1990.
- Tomkins, S.S. *Affect, imagery, consciousness. Vol. I*, 1962. New York: Springer.
- Tomkins, S.S. *Affect, imagery, consciousness. Vol. II*, 1963. New York: Springer.
- Tooby, J. Pathogens, polymorphism, and the evolution of sex. *Journal of Theoretical Biology*, 97: 557–576, 1982.
- Tooby, J. The emergence of evolutionary psychology. In: *Emerging Syntheses in Science*, 1985. Proceedings of the Founding Workshops of the Santa Fe Institute. Santa Fe, NM: The Sante Fe Institute.
- Tooby, J. and DeVore, I. The reconstruction of hominid behavioral evolution through strategic modeling. In Kinzey, W.G. (Ed.), *The evolution of human behavior: Primate models*, 1987. pp. 183–237. Albany: SUNY Press.
- Tooby, J. and Cosmides, L. Evolutionary psychology and the generation of culture, Part I. Theoretical considerations. *Ethology and Sociobiology*, 10:29–49, 1989a.
- Tooby, J. and Cosmides, L. The innate versus the manifest: How universal does universal have to be? *Behavioral and Brain Sciences*, 12: 36–37, 1989b.
- Tooby, J. and Cosmides, L. Evolutionary psychologists need to distinguish between the evolutionary process, ancestral selection pressures, and psychological mechanisms. *Behavioral and Brain Sciences*, 12: 724–725, 1989c.
- Tooby, J. and Cosmides, L. On the universality of human nature and the uniqueness of the individual: The role of genetics and adaptation. *Journal of Personality*, 58, 1990.
- Tooby J. and Cosmides, L. The evolutionary psychology of incest avoidance and its impact on culture. In *The adapted mind: Evolutionary psychology and the generation of culture*, J. Barkow, L. Cosmides, and J. Tooby (eds.), in press.

- Turke, *Ethology and Sociobiology*, 11, 1990.
- Vining, D. Social versus reproductive success: The central problem of human sociobiology. *Behavioral and Brain Sciences*, 9: 167–216, 1986.
- Williams, G.C. *Adaptation and natural selection: A critique of some current evolutionary thought*, 1966. Princeton: Princeton University Press.
- Williams, G.C. A defense of reductionism in evolutionary biology. *Oxford surveys in evolutionary biology*, 2: 1–27, 1985.
- Williams, G.C., and Williams, D.C. Natural selection of individually harmful social adaptations among sibs with special reference to social insects. *Evolution*, 17:249–253, 1957.
- Wilson, M. and Daly, M. The man who mistook his wife for a chattel. In Barkow, J., Cosmides, L. and Tooby, J. (Eds.), *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*. NY: Oxford University Press, in press.
- Wolf, A.P. and Huang, C. *Marriage and adoption in China 1845–1945*, 1980. Stanford, CA: Stanford University Press.
- Wright, S. *Evolution and the genetics of populations. V. I. Genetic and biometric foundations*, 1968. Chicago: University of Chicago Press.
- Wright, S. *Evolution and the genetics of populations. V. II. The theory of gene frequencies*, 1969. Chicago: University of Chicago Press.
- Wright, S. *Evolution and the genetics of populations. V. 3. Experimental results and evolutionary deductions*, 1977. Chicago: University of Chicago Press.
- Wright, S. *Evolution and the genetics of populations. V. 4. Variability within and among natural populations*, 1978. Chicago: University of Chicago Press.