

Evolutionary Psychology: A How-To Guide

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Researchers in the social and behavioral sciences are increasingly using evolutionary insights to test novel hypotheses about human psychology. Because evolutionary perspectives are relatively new to psychology and most researchers do not receive formal training in this endeavor, there remains ambiguity about “best practices” for implementing evolutionary principles. This article provides researchers with a practical guide for using evolutionary perspectives in their research programs and for avoiding common pitfalls in doing so. We outline essential elements of an evolutionarily informed research program at 3 central phases: (a) generating testable hypotheses, (b) testing empirical predictions, and (c) interpreting results. We elaborate key conceptual tools, including task analysis, psychological mechanisms, design features, universality, and cost-benefit analysis. Researchers can use these tools to generate hypotheses about universal psychological mechanisms, social and cultural inputs that amplify or attenuate the activation of these mechanisms, and cross-culturally variable behavior that these mechanisms can produce. We hope that this guide inspires theoretically and methodologically rigorous research that more cogently integrates knowledge from the psychological and life sciences.

Keywords: evolutionary psychology, social psychology, cross-cultural psychology, misconceptions, universality

Theories in evolutionary psychology are commonly viewed with greater skepticism than more traditional psychological theories. These considerations, coupled with the fact that it is essential to be intellectually persuasive to succeed in the scientific environment, might tempt the pragmatic scientist to play it safe—to avoid dabbling in multilevel theories that specify models of historical origins. Giving in to this temptation, however, would surely have unhealthy consequences for the advancement of psychological science.

—Conway and Schaller (2002, p. 160)

In recent years, behavioral scientists from diverse backgrounds have shown increased interest in evolutionary perspectives. This rise in evolutionary thinking reflects a growing interest across the psychological and behavioral sciences in understanding the influence of selection and other evolutionary forces on human psychology. This is evidenced by greater emphasis on evolutionary theories in leading handbooks of personality psychology (Buss, 2009; Buss & Penke, 2015) and social psychology (Buss & Kenrick, 1998; Neuberg, Kenrick, & Schaller, 2010), special issues dedicated to an evolutionary approach to the psychological sciences (e.g., Gangestad & Tybur, 2016), edited volumes and social psychology textbooks integrating evolutionary principles (Schaller, Simpson, & Kenrick, 2006; Simpson & Kenrick, 1997), and the publication of more evolutionarily oriented introductory psychology textbooks (e.g., Gray, 2010).

Despite mounting scientific interest, ambiguity persists about the application of evolutionary psychological principles. There are several sources of conceptual confusion that may be particularly important. First, ironically, there is evidence that humans possess evolved cognitive mechanisms that impede an accurate understanding of the logic of

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evolutionary theory (Legare, Lane, & Evans, 2013; Shtulman & Schulz, 2008). Second, technical principles of evolutionary theory appear deceptively simple at first glance, but in fact require mastery of a formidable body of key concepts. The combination of these two obstacles suggests that more rigorous training in evolutionary theory is necessary to properly conduct research consistent with evolutionary principles. However, most psychologists receive little or no such training. To our knowledge, no psychology graduate program in the United States requires even a single course in evolutionary biology. Collectively, these issues point toward the utility of an accessible, systematic guide that researchers can use to generate and test evolutionary psychological hypotheses.

The Stages of Research

As with all psychological research, evolutionarily informed research involves (a) generating hypotheses, (b) empirically testing predictions based on those hypotheses, and (c) interpreting study results. However, research that seeks to be consistent with evolutionary principles must also incorporate several additional features at each stage of research. We organize this article around these distinct phases of research, outlining the elements that well-designed evolutionary research must share with all well-designed psychological research, as well as detailing key features unique to an evolutionary approach.

First, however, we discuss the hierarchical structure of evolutionary psychology, because this structure entails several key concepts that are a necessary foundation for properly applying evolutionary principles at the distinct phases of research.

The Hierarchical Theoretical Structure of Evolutionary Psychology

Evolutionary theory provides a framework for understanding the distal causal processes responsible for creating functionally organized organic mechanisms, such as those of the human brain and mind. However, it is not a psychological theory itself. Rather, it can be used to produce “middle-level theories” (Buss, 1995) from which specific hypotheses can be generated. These hypotheses, in turn, can be used to generate specific testable empirical predictions about the mind’s information-processing mechanisms and the behavioral outputs that they produce.

From Evolutionary Theory to Middle-Level Theories

The central principle of natural selection is that, over time, genes that more successfully promote their own replication increase in frequency relative to competing genetic variants. When this core principle is applied to specific domains of life, such as mating, parenting, or other kin relationships, it yields *middle-level theories*.

For example, the middle-level theory of kin selection (Hamilton, 1964) is an extension of the core principle of selection to the context of altruism among kin. The key insight of kin selection theory is that a gene can increase its own replicative success through direct reproduction, but also by promoting the reproduction of other bodies likely to carry copies of itself. Because genetic relatives carry copies of one’s genes, the preconditions necessary for the evolution of altruism can be met if this altruism is directed toward one’s genetic relatives. Hamilton (1964) generated the middle-level theory of kin selection by applying the central evolutionary principle of selection to the domain of altruism and kin relationships.

From Middle-Level Theories to Specific Hypotheses

Researchers can use middle-level theories such as kin selection to generate multiple *hypotheses*. Kin selection theory specifies that altruistic behavior can be favored by selection if the benefit of that behavior to the target (B), weighted by the genetic relatedness between altruist and target (r), is greater than the cost of the behavior to the altruist (C ; Hamilton, 1964). Formally, this is given as $rB > C$.

This formula illustrates that the degree of genetic relatedness between two individuals is an important determinant of whether a given situation meets the $rB > C$ criterion. Identifying kin of differing degrees of genetic relatedness would thus have been an important adaptive problem. This reasoning leads to the *kin recognition hypothesis*: that selection favored the evolution of psychological mechanisms



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designed to estimate the degree of relatedness between self and target (e.g., DeBruine, 2002; Lieberman, Tooby, & Cosmides, 2003, 2007).

Researchers can then use this broad hypothesis, which is based on the middle-level theory of kin selection, to generate more specific hypotheses. For example, the broad kin recognition hypothesis has led to numerous specific hypotheses about the mechanisms by which humans might have evolved to detect kin. In the case of detecting siblings, researchers have proposed several classes of cues recurrently linked to genetic siblingship in ancestral conditions. These include (a) environmental cues such as physical proximity (e.g., cohabitation), (b) social cues such as observing a neonate nursing from one's own mother (i.e., maternal perinatal association [MPA]), (c) linguistic cues such as those embedded in kin classification systems, and (d) phenotypic cues such as physical resemblance. *Each* of these four proposed classes of cues represents a distinct hypothesis about evolved sibling recognition mechanisms.

From Hypotheses to Predictions

Researchers can then use hypotheses to generate *testable empirical predictions*. For example, Lieberman et al. (2003, 2007) hypothesized that humans' sibling detection mechanisms are designed to (a) produce elevated estimates of relatedness when one observes a newborn nursing from one's own mother, and (b) in the absence of the MPA cue, increase estimates of relatedness as a function of cohabitation. Lieberman et al. hypothesized that these elevated estimates of relatedness, in turn, lead to greater altruistic motivation. Based on these hypotheses, Lieberman and col-

leagues advanced the following *testable predictions*: (a) older siblings will exhibit greater altruism toward younger siblings if they have observed them nursing from their own mother, (b) older siblings who have *not* observed such nursing will exhibit greater altruism toward younger siblings with whom they have cohabited longer, and (c) younger siblings will exhibit greater altruism toward siblings with whom they have cohabited longer.

These predictions were generated based on specific hypotheses, which in turn were inspired by the middle-level theory of kin selection, which was itself generated on the basis of evolutionary theory. A key implication of the hierarchical theoretical structure of evolutionary psychology is that the application of a simple insight at a broad level—such as that of a middle-level theory like kin selection—can yield rich and diverse downstream hypotheses and a priori predictions readily testable in empirical research. Middle-level evolutionary theories guide the generation of hypotheses unlikely to be produced in their absence, and have great heuristic value for discovering novel psychological phenomena (Table 1; see also Buss, 2015).

Hypothesis Generation

Like all scientific research, evolutionary psychological research may be theory-driven or observation-driven. A theory-driven “top-down” approach often entails identifying ancestral conditions that would have impacted individuals' survival or reproduction, and then describing psychological mechanisms capable, in principle, of solving the problems posed by those conditions. This contrasts with a “bottom-up” approach, in which a researcher begins by observing a phenomenon, and then generates testable hypotheses about the psychological mechanisms that could be responsible for producing the observed phenomenon (Buss, 1995).

Theory-Driven, Top-Down Approach

A top-down approach involves two steps. First, a researcher identifies a specific survival- or reproduction-related problem present in ancestral human environments (see the “Knowledge about ancestral environments” section). Second, the researcher articulates the specific psychological equipment that could, in principle, have helped solve that adaptive problem. This includes sensory, perceptual, and physiological systems that detect cues to the problem (inputs); computational machinery that processes these cues (algorithms); and behaviors, emotions, and cognitions mobilized by these computations in order to solve the relevant problem (outputs).

Step 1: Identify an adaptive problem. Adaptive problems refer to conditions that would have had a recurrent impact on ancestral humans' survival or reproduction (Tooby & Cosmides, 1988). Adaptive problems for humans



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span many domains: avoiding predators, resisting infection, negotiating status hierarchies, attracting a mate, preventing infidelity, protecting offspring, seeking retribution, finding nutritious food, managing one's reputation, and many more. Solving these problems may have (a) been necessary for survival or reproduction; (b) not been strictly necessary for survival or reproduction, but removed an impediment to survival or reproduction; or (c) afforded a more effective or economical means of improving survival or reproduction relative to other existing alternatives. All adaptive problems share the following key feature: The genes of the individuals who solved that problem had greater replicative success than the genes of those who did not solve that problem. A critical first step in a top-down approach is thus to identify an adaptive problem—a task for which psychological researchers have multiple tools at their disposal.

Knowledge about ancestral environments. Despite our necessarily incomplete knowledge of ancestral environments, well-established data from disciplines such as anthropology, geology, primatology, and biology—as well as the fact that physical laws are unchanging (Tooby & Cosmides, 1992)—enable us to know a great deal about human ancestral environments. For instance, the structure and distribution of tools and fossilized bones provide insight into ancestral locomotion, social structures, and diet (Harcourt-Smith & Aiello, 2004; Richmond & Strait, 2000). Samples of ancient soils and geological data offer information about ancestral climates (e.g., Vieites, Nieto-Román, & Wake, 2009). Research on the etiology of disease reveals ancestral infectious threats (Williams & Nesse, 1991). We know that ancestral humans walked upright, lived in small groups, were omnivorous, reproduced sexually, used tools, and

learned skills and norms from group members, and that women gestated and lactated but men did not. As Tooby and Cosmides (2005) point out:

It is certain that our ancestors, like other Old World primates, nursed; had two sexes; chose mates; had color vision calibrated to the spectral properties of sunlight; lived in a biotic environment with predatory cats, venomous snakes, and spiders; were predated on; bled when wounded; were incapacitated from injuries; were vulnerable to a large variety of parasites and pathogens; and had deleterious recessives rendering them subject to inbreeding depression if they mated with siblings. (pp. 23–24)

Each of these facts embodies key information about the evolution of our species because each influenced human survival and reproduction. Consequently, researchers have used these observations to generate hypotheses about the human mind's evolved information-processing programs. Psychologists interested in pursuing evolutionarily informed research programs can harvest “low-hanging fruit” by identifying even seemingly mundane adaptive problems faced by ancestral humans.

Applying middle-level theories to ancestral human conditions. Only a subset of the conditions that ancestral humans faced actually posed adaptive problems. Identifying this subset is facilitated by middle-level theories, which specify the criteria that enhance survival or reproduction in different domains of life. Middle-level theories reveal adaptive problems by describing the specific ways in which ancestral conditions impacted survival and reproductive success.

The middle-level theory of *parental investment*, for example, specifies the conditions influencing the relative success of different mating strategies. Under conditions in which offspring production requires little investment, being less choosy about one's mates and mating with a larger number of partners can pay greater reproductive dividends than being comparatively more discriminating. Conversely, when substantial investment is required to produce offspring, the costs of injudicious mating decisions increase. Under these conditions, it is more reproductively beneficial to be more selective and to more carefully allocate one's limited reproductive resources (Trivers, 1972).

In humans, men and women differ considerably in the minimum parental investment required to successfully produce and rear offspring. Women alone gestate, give birth, and lactate, making the minimum parental investment higher for women than for men. Consequently, injudicious mating decisions are typically more costly for women than for men. Ensuring the suitability of a mating partner is therefore a more pressing adaptive problem for women.

This application of parental investment theory to recurrent ancestral conditions—in this case, sex differences in human reproductive biology and obligatory parental invest-



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ment—illustrates that middle-level theories help identify important adaptive problems. Indeed, one of the most powerful benefits of an evolutionary perspective is its heuristic value in leading researchers to new insights in domains once regarded as familiar.

Useful heuristics for identifying specific adaptive problems. Even with the help of middle-level theories, the space of potential adaptive problems is large and the task of identifying a specific adaptive problem can be daunting. Here, we introduce three categorization heuristics that can be used to carve up the space of potential adaptive problems and aid in this task.

Must-solve versus beneficial. This heuristic describes a useful distinction between (a) problems that the organism *must* solve in order to survive and reproduce, and (b) problems that did not *necessarily* have to be solved, but whose solution would nonetheless have increased the organism's fitness (Tooby & Cosmides, 1992).

The *must-solve* category reflects those problems that, if not solved, would have single-handedly resulted in the organism failing to survive and reproduce. This category includes the most immediately obvious problems such as locating and securing nutritious, nontoxic food to eat; avoiding predators; avoiding lethal infectious diseases; and finding, attracting, and successfully reproducing with a fertile mate.

The *beneficial* category may be less immediately obvious. Examples of problems in this category include detecting the compatibility of a potential mate's immune system with one's own; preventing and detecting infidelity in romantic relationships; cooperating with kin and nonkin for mutual benefit; and rejecting, ostracizing, or punishing individuals

who steal, free-ride, or exploit others. Within this category, useful classes of problems for researchers to think about include (a) improving the performance of an extant adaptive solution (e.g., increasing visual acuity in an already functional visual system); (b) increasing the economy of an existing adaptation, such as by decreasing its costs (e.g., downregulating the production of testosterone when the benefits of this hormone are exceeded by its immune-compromising costs); (c) increasing the reliability of the development of an adaptation (i.e., rendering an adaptation less susceptible to environmental perturbations during ontogeny); (d) increasing the number of cues that the adaptation takes as input (e.g., "decrease in display or quality of physical affection" and "reluctance to disclose how personal time is spent" as distinct cues to one's mate's infidelity; Shackelford & Buss, 1997); and (e) increasing and diversifying the repertoire of outputs that an adaptation can produce to improve the functional match between behavior and the specific cause of the problem (e.g., different behavioral responses, such as mate vigilance vs. derogation of intra-sexual rivals, in response to different cues to the threat of one's mate's infidelity; Buss, 1988).

The value of the *must-solve versus beneficial* heuristic is to aid researchers in developing psychological hypotheses by reminding them of the vast space of adaptive problems, including those that are less obvious—but not necessarily less important—in driving the evolution of psychological adaptations.

How can a researcher employ this heuristic? Consider aggression in humans, which encompasses adaptive problems ranging from intrasexual competition and warfare to protecting kin, mates, and allies. Each of these subdomains of aggression would have presented ancestral humans with important adaptive problems.

To use the *must-solve versus beneficial* heuristic, the researcher can first ask, What aggression-related problems must have been solved to enable an ancestral human to survive and reproduce? This question immediately suggests one crucial adaptive problem: not falling victim to lethal aggression. A key first step in solving this adaptive problem is to identify potential aggressors. To do this, the organism must detect cues to aggression. Based on this line of reasoning alone, the researcher already has generated the hypothesis that humans may have evolved psychological mechanisms designed to detect probabilistic cues to aggression. Indeed, a growing body of research suggests that the human mind is sensitive to such cues, including nonobvious features such as individuals' facial width-to-height ratio (see Carré & McCormick, 2008).

Similarly, the researcher can consider aggression-related problems that did not strictly *need* to be solved, but whose solution would nonetheless have benefitted an organism's fitness. For example, competition for social status would have been associated with some individuals employing ag-



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gressive (even if not nonlethal) strategies. Employing cost-benefit analyses here can yield nuanced hypotheses about the design features of the psychological adaptations that evolved to deal with the adaptive problem of such aggressive conspecifics. Specifically, an aggression researcher could consider the shifting costs and benefits to the organism of failing to detect cues to such aggression when (a) the organism is injured or its ability to physically defend itself is otherwise impaired, and (b) when the organism is in the presence of vulnerable kin, or (c) alternatively, in close proximity to physically formidable kin or allies. A researcher can use this idea—that the costs and benefits of different responses to aggression would have been context-dependent—to generate the novel hypothesis that a key design feature of humans' psychological adaptations for dealing with aggressive conspecifics is sensitivity to these contextual cues.

Threat versus opportunity. A *threat* is a feature or characteristic of the physical, ecological, or social environment with the potential to compromise an individual's survival or reproduction. These "hostile forces of nature" (Darwin, 1859) include threats from (a) the abiotic environment, such as droughts or extremes of temperature; (b) other species, such as predators or parasites; and (c) other humans, including hostile out-groups and dangerous rivals from one's in-group (Darwin, 1859; Ghiglieri, 2000).

An *opportunity*, on the other hand, represents a previously unexploited situation that, if taken advantage of, could enhance survival or reproduction. For example, at many stages of human evolution, there were previously unexploited food sources whose procurement required new forms of cooperation, tool making, or innovations such as

cooking with fire, which can transform previously inedible items into valuable nutrition, as well as increase ease of digestion and absorption of nutrients (see Wrangham, 2009). Attending to these "opportunities" can lead to hypotheses, predictions, and findings that might otherwise remain undiscovered.

Which adaptive problems would have driven the evolution of adaptations? Adaptive problems that generate strong selective pressures are those that drive the evolution of adaptations. The *strength* of an adaptive problem would have depended on two factors: (a) the *magnitude* of its impact on survival or reproduction, and (b) the *frequency* at which it was faced. These two factors would have varied continuously across adaptive problems, but for illustrative purposes, here we dichotomize them into high versus low impact and frequent versus infrequent.

High-impact, high-frequency adaptive problems. An adaptive problem that was both frequently faced and heavily impacted fitness, such as the need to eat, would have generated extraordinarily strong selection pressures. Humans and other animals have a large repertoire of adaptations that impel them to seek food, discriminate between nutritious and non-nutritious food items, and avoid ingesting pathogenic substances (e.g., Rozin, 1976; Tybur, Lieberman, & Griskevicius, 2009). And if such substances make it past this first set of motivational and behavioral filters, humans have additional defenses designed to expel them (e.g., gagging, nausea, vomiting).

High-frequency, high-impact adaptive problems often drive the evolution of complex and sophisticated mechanisms. However, adaptive problems do not need to be *both* frequently faced and have a large impact on fitness to drive the evolution of psychological adaptations. Both high-frequency but low-impact, and low-frequency but high-impact, adaptive problems can lead to the evolution of adaptations.

Low-impact, high-frequency adaptive problems. Some adaptive problems are faced frequently, but each instance has only a small impact on survival or reproductive success (Duntley & Buss, 2011). For example, a bite from a common ectoparasite such as a mite typically results in only a negligible loss of blood. This adaptive problem is thus low in its magnitude of fitness impact. However, the prevalence of ectoparasites in human living conditions suggests that humans faced this low-impact problem frequently (Rantala, 1999). Consequently, if a genetic variant associated with increased deterrence of ectoparasites were to arise, it would offer frequent low-magnitude fitness benefits. Even if the reproductive success of this gene were only 1% greater than competing genetic variants, the novel mutation could nonetheless spread throughout the population to the exclusion of all other genetic variants (Nilsson & Pelger, 1994).

High-impact, low-frequency adaptive problems. Adaptive problems that *did* have a profound impact on survival or

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Table 1
Adaptive Problems and Psychological Adaptations

Domain	Adaptive problem	Psychological adaptation	References	
Ecological Threats	Dangerous animal aversion	<ul style="list-style-type: none"> Specialized attentional systems for tracking animals Systems for identifying still animals as asleep or dead 	New, Cosmides, & Tooby (2007) Barrett & Behne (2005)	
	Avoiding dangerous heights	<ul style="list-style-type: none"> Descent illusion 	Jackson & Cormack (2007)	
	Pathogen avoidance	<ul style="list-style-type: none"> Disgust toward cues of illness in conspecifics Disgust toward vectors (insects, maggots, rodents) 	Schaller & Park (2011)	
	Poisonous animal aversion	<ul style="list-style-type: none"> Specialized snake and spider fears Specialized snake and spider attentional systems 	Rakison & Derringer (2008) Ohman, Flykt, & Esteves (2001)	
Nutrition	Toxin avoidance	<ul style="list-style-type: none"> Disgust toward spoiled and contaminated foods Use of spices in cooking Single-trial food aversion learning 	Tybur, Lieberman, & Griskevicius (2009) Sherman & Billing (1999) Cashdan (1998)	
	Mating	Mate selection for "Good genes"	Gildersleeve, Haselton, & Fales (2014) Grammer & Thornhill (1994)	
Mating	Fertility	<ul style="list-style-type: none"> Ovulation-based shifts in mate preferences Attraction to facial symmetry 	Smith et al. (2006) Buss (1989)	
	Commitment & investment	<ul style="list-style-type: none"> Attraction to femininity (males) Preferences for youth (males) Preferences for older mates (females) Attraction to willingness to invest in children (females) 	La Cerra (1995) Buss (1989)	
	Detering infidelity	<ul style="list-style-type: none"> Mate guarding behavior Sex-differentiated jealousy 	Buss (1988) Buss, Larsen, Westen, & Semmelroth (1992)	
	Mating with multiple partners (males)	<ul style="list-style-type: none"> Preference for sexual variety (males) Lowered standards in short-term mating (males) 	Schmitt, Alcalay, Allik, et al. (2003) Kenrick, Groth, Trost, & Sadalla (1993)	
	Kinship	Directing care toward relatives	<ul style="list-style-type: none"> Discriminative parental solicitude Preferences for facial resemblance Greater altruism toward more closely related kin 	Daly & Wilson (1980) Saad & Gill (2003) Lieberman et al. (2007)
		Incest avoidance	<ul style="list-style-type: none"> Disgust toward mating with kin Specialized kin-detection systems 	Lieberman et al. (2007)
	Cooperation	Avoiding non-cooperators	<ul style="list-style-type: none"> Specialized cheater-detection mechanisms Anger and punishment directed toward defectors 	Cosmides & Tooby (1992) Krasnow, Cosmides, Pedersen, & Tooby (2012)
		Aggression & Conflict	<ul style="list-style-type: none"> Strength- and attractiveness-dependent anger Specialized formidability assessment mechanisms Stranger anxiety coinciding with independent locomotion Auditory looming bias 	Sell, Tooby, & Cosmides (2009) Zilioli et al. (2015) Boyer & Bergstrom (2011) Neuhoff (2001)

reproduction would also have led to the evolution of psychological adaptations. Even adaptive problems that were never faced during an individual's *entire lifetime* can drive the evolution of psychological adaptations. We emphasize this critical, but strongly counterintuitive, point: Adaptive problems with a large impact on fitness did *not* need to be faced by a majority of ancestral individuals in order for *all* modern humans to possess psychological adaptations designed to deal with those problems.

To demonstrate how a low-frequency, high-impact adaptive problem can lead to the evolution of adaptations, we used NetLogo (Wilensky, 1999) to conduct a simulation of the selection pressures generated by the rare, but high-impact, adaptive problem of homicide (e.g., Buss, 2015). In our simulation, individuals foraged for finite food resources that provide the energy necessary for survival and reproduction. Once individuals secured sufficient metabolic resources to produce offspring, they reproduced. Overall population size was constrained by a finite food supply and mortality: Individuals died if they reached a critically low level of metabolic resources, reached 50 years of age, or were murdered. For each individual, the likelihood of being murdered was extraordinarily small: a 0.02% annual likelihood. Murder therefore presented an extremely low-frequency, but high-magnitude, adaptive problem.

We then introduced a small population of individuals who were identical to the others except for a single mutation. The initial population frequency of this mutation was just 1%. With such a small population, the random force of genetic drift would usually drive this mutant gene to extinction in the long run. Indeed, when the mutation conferred no selective advantage, it went extinct in 100% of model runs. However, when the mutation conferred immunity to murder—and therefore solved this high-impact, low-frequency adaptive problem—very different outcomes emerged. In 57% of runs, the frequency of the murder-immunity gene rapidly rose from 1% to over 99% in the population. That the murder-immunity trait evolved to be *species-typical*—present in virtually every member of the population—is particularly striking because those individuals who were susceptible to murder faced less than a 1% chance of being murdered over the course of their entire lifetime.

More than 99% of the population *never* faced the adaptive problem of homicide—and yet the antihomicide adaptation evolved to be present in virtually *every* member of the species. This simulation demonstrates a key evolutionary principle: Even a very rare adaptive problem (e.g., homicide, cuckoldry, attack from a large predator) faced by a very small subset of the population can lead to the evolution of an adaptation possessed by *all* members of the species (see, e.g., Buss, 2015).

It is worth noting that our simulation demonstrates both this critical point, as well as the more general utility of mathematical modeling and simulations in developing evo-

lutionary psychological hypotheses. Complex social and strategic problems can have many potential solutions depending on the specific environmental and social contexts that emerge (e.g., see Axelrod & Hamilton, 1981). When the potential solutions to a given adaptive problem are numerous and their relative merits complex, evolutionary end states may be too difficult to identify intuitively. In such computationally complex situations, simulations and modeling can be invaluable tools.

Step 2: Propose an adaptation. A researcher's next step is to propose a psychological adaptation capable of solving the relevant problem. Task analysis is a powerful tool for systematically generating a priori hypotheses. Evolutionary task analysis begins by specifying the relevant end state—the solution of the adaptive problem—and proceeds by detailing the specific psychological steps and machinery (e.g., sensory, perceptual, cognitive, affective, behavioral) capable, in principle, of producing that end state (Marr, 1982).¹

Lieberman et al. (2003, 2007) provide a model example of an evolutionary task analysis. They reasoned that arriving at the end states of avoiding incest and directing altruism toward kin requires detecting cues indicative of kinship, distinguishing kin from nonkin based on these cues, and regulating sexual attraction and behavioral altruism accordingly. This task analysis guided research toward previously unknown (a) cognitive mechanisms that detect cues reliably correlated with genetic relatedness in ancestral environments; (b) kinship-estimating algorithms that hierarchically organize cues, assigning greater priority to those that more reliably indicated genetic relatedness; (c) affective mechanisms that deter incest and motivate altruism toward kin; and, at the end of these processes, (d) behavioral outputs that solve the adaptive problem.

To carry out a task analysis, a researcher should ask this indispensable question: What psychological machinery and behavioral outputs would help solve this adaptive problem? In answering this question, it is important to consider a wide range of perceptual, cognitive, emotional, and behavioral features that, together, could constitute an effective solution to the adaptive problem. A comprehensive analysis poses this question at each stage of processing: detecting important environmental information (the “input” stage), algorithmic processing of those inputs (the “internal computation” stage), and the thoughts, emotions, physiological responses, and behaviors that the mechanism produces (the “output” stage).

¹ This process is helpful both for generating hypotheses about psychological adaptations and for dramatically reducing the possible set of hypotheses, because only a sharply delimited subset of features could, in principle, produce the relevant end state. The researcher therefore can rule out all hypotheses that fail to produce an end state that successfully solves the adaptive problem under consideration.

The importance of postulating specific design features.

The psychological equipment and procedures that enable the solution of the adaptive problem are the adaptation's *design features*. These are the elements of the machinery whose functional coordination—with each other and with the environment—enables the organism to solve the adaptive problem. Proposing a candidate adaptation entails proposing the specific design features that constitute it.

This task may include (a) identifying the social, cultural, or other environmental inputs that the mechanism is expected to process; (b) describing the algorithmic processing of these inputs (e.g., prioritizing cues with greater predictive validity; e.g., Burnstein, Crandall, & Kitayama, 1994; Gigerenzer, 2008; Lieberman et al., 2007); and (c) predicting the mechanism's psychological, physiological, or behavioral outputs. Researchers should then specify as many precise empirical predictions about observable psychological phenomena as possible based on these proposed design features.

This detailed specification of the psychological machinery is critical for four reasons. First, the specification is necessary to confirm that the proposed adaptation could plausibly solve the adaptive problem. Second, predicting numerous, specific design features enables a researcher to design studies that test for their existence, and thereby test for the existence of the adaptation itself. Third, specifying the psychological processes renders the hypothesized psychological adaptation empirically testable, and, consequently, falsifiable. Fourth, this detailed specification is necessary in order to submit alternative hypotheses to discriminative tests and adjudicate between them.

Schaller's, Tybur's, and others' work on disease avoidance (e.g., Schaller, Miller, Gervais, Yager, & Chen, 2010; Tybur et al., 2009) offers an excellent example of research that specifies multiple design features of a hypothesized adaptation and tests for their existence. The human disease-avoidance system consists of perceptual, physiological, emotional, and behavioral components that are coordinated to solve the adaptive problem of avoiding infection. These systems are finely tuned to detect the presence of pathogen vectors, including feces, bodily effluvia, skin lesions, and substances with high parasite loads (e.g., dead bodies, rotting meat). The presence of these pathogenic substances triggers a suite of psychological, physiological, and behavioral changes that reduce the likelihood of infection. These include the emotion of disgust (e.g., Tybur et al., 2009), increased production of proinflammatory cytokines as a proactive immunological defense (Schaller et al., 2010), avoidant motor responses (Mortensen, Becker, Ackerman, Neuberg, & Kenrick, 2010), and reduced extraversion and openness (Mortensen et al., 2010).

Cost–benefit analyses. Two additional programs of research on disgust and disease avoidance illustrate another useful conceptual tool: cost–benefit analyses for generating

specific predictions about the contexts likely to activate certain cognitions, emotions, and behaviors. The first example comes from Fleischman and Fessler's (2011) work on ovulation-based shifts in disease avoidance behavior. During the luteal phase of the ovulatory cycle, women experience immunosuppression, rendering them more susceptible to infection. This higher likelihood of infection translates to higher costs of being exposed to disease vectors. Because women face these greater infection-related costs during the luteal phase, Fleischman and Fessler reasoned that women should engage in enhanced disease-avoidance behavior during this phase of the ovulatory cycle. In support of their hypothesis, Fleischman and Fessler found that luteal-phase women exhibit elevated levels of a functionally coordinated suite of cognitions, emotions, and behaviors associated with reducing exposure to disease vectors.

Similarly, Al-Shawaf and Lewis (2013) employed cost–benefit analyses to generate novel hypotheses about contexts that should up- or downregulate the emotion of disgust. Because stress is a powerful immunosuppressant that increases the costs of exposure to disease vectors, Al-Shawaf and Lewis reasoned that elevated levels of stress should amplify disgust. On the other hand, because hunger signals nutritional stress, and nutritionally stressed individuals have more to gain from eating, Al-Shawaf and Lewis predicted and found that satiation is associated with increased disgust.

These programs of research on disgust and disease avoidance illustrate two important ideas. First, by proposing specific design features, it is possible to discover previously unknown psychological and behavioral processes that operate in functionally coordinated fashion to solve an adaptive problem. Second, by considering the ancestral costs and benefits (measured in the currency of survival and reproductive success) of different behaviors across different contexts, it is possible to generate nuanced a priori predictions about which contextual variables should amplify or attenuate the activation of the psychological mechanisms under investigation.

A researcher following the steps outlined here would now have completed a theoretically driven (top-down) approach to hypothesis generation. This involved identifying an adaptive problem and proposing an adaptation that could have solved this problem by specifying the proposed mechanism's design features, including the contexts in which the mechanism's activation is likely to be amplified or attenuated.

Observation-Driven, Bottom-Up Approach

The bottom-up approach shares many characteristics with the top-down approach, including identifying an adaptive problem and specifying a hypothesized adaptation. How-

ever, it includes one additional step: It begins with observing a phenomenon—psychological, physiological, or behavioral. Observations come from many sources. Some are readily familiar, such as bipedalism or the formation of status hierarchies. Others are puzzles requiring explanation, such as female orgasm (e.g., Ellsworth & Bailey, 2013). Still others are scientific findings that do not yet have a compelling scientific explanation—for example, *why* people obey authorities who command them to deliver harmful electric shocks. And some are unexpected findings not predicted by any extant theory (e.g., psychological sex differences are typically larger in cultures with higher gender equality; Guimond et al., 2007; see also Schmitt, 2015).

After observation, scientists conduct a *reverse task analysis*, asking what psychological adaptation may be responsible for producing that phenomenon and what adaptive problem that mechanism may be designed to solve. This process of reverse engineering carries the researcher to the beginning of the top-down approach—the identification of an adaptive problem. Once this adaptive problem has been proposed, it is essential that the researcher then turn around and follow the top-down approach to formulate novel, testable predictions suggested by the proposed adaptation. Without turning around and completing the top-down approach to generate novel, testable predictions, the investigation remains incomplete and the proposed explanation remains a speculation. In short, generating novel testable predictions is an integral component of a bottom-up approach.

Byproduct (incidental effect) explanations. Many psychological phenomena do *not* reflect the functional output of psychological adaptations—many phenomena reflect random noise or the *incidental effects* of adaptations (Park, 2007; Tooby & Cosmides, 1990a, 1990b; Williams, 1966). Incidental effects, or evolutionary byproducts, represent another valuable conceptual tool that researchers can use when pursuing an observation-driven, bottom-up approach. Byproducts are phenomena that exist because they are intrinsically coupled with an adaptation, despite having no function in and of themselves (Buss, Haselton, Shackelford, Bleske, & Wakefield, 1998; Tooby & Cosmides, 1990a, 1990b). At the level of physiology, the redness of blood is a byproduct of the presence of iron in hemoglobin, an adaptation essential for transporting oxygen from the lungs to the body's tissues (Symons, 1985). At the level of morphology, the human belly button is a byproduct of the umbilical cord, an adaptation that enables a pregnant woman to transfer nutrients to her fetus (Buss et al., 1998). Similarly, psychological adaptations may produce functionless outputs as incidental byproducts of their evolved information-processing design. An example that illustrates the utility of considering byproducts of evolved psycholog-

ical mechanisms comes from Kurzban, Tooby, and Cosmides's (2001) work on racial prejudice.

Incidental effects of an evolved psychological mechanism: An empirical example. Racial prejudice poses a puzzle to evolutionary researchers. The continuously graded nature of human variation and the limited extent of human dispersal during ancestral times suggest that it would have been unlikely for ancestral humans to encounter individuals of different “races.” Despite an absence of selective pressures favoring the evolution of prejudice along racial lines, racial prejudice remains one of the great ailments of modern human society.

Kurzban and colleagues (2001) provide a potential solution to this puzzle. They propose that race-based prejudices arise as nonfunctional outputs of adaptations designed to track coalition or group membership. Ancestrally, outgroups would have been statistically associated with greater threat than in-groups. Much like modern hunter-gatherer coalitions, ancestral coalitions likely formed for purposes like hunting, resource pooling, political alliances—and, critically, intergroup warfare (Tooby & Cosmides, 1988). These important, fitness-relevant functions of coalitions created the selective conditions for the evolution of psychological mechanisms that track cues to membership in such cooperative alliances. Kurzban et al. provide evidence that in modern environments, these mechanisms lead humans to mistakenly detect artificial racial “coalitions” on the basis of small differences in morphology or skin tone. However, this research also provides powerful empirical evidence that these adaptations are capable of “erasing race”—they are capable of producing categorizations that do not discriminate along racial lines (Kurzban et al., 2001). This offers just one example—a scientifically and societally valuable example—of the importance and utility of the concept of byproduct effects in a bottom-up approach.

Generating Hypotheses: Conceptual Clarifications

The reproduction of the gene, individual, or species?

From an evolutionary perspective, the theoretical focus is on how adaptive problems impact the survival and reproduction of genes, not, strictly speaking, of individuals, groups, or species. Groups and species rarely meet the conditions necessary for evolution by selection (e.g., Pinker, 2012; Williams, 1966). In sexually reproducing species such as humans, individual organisms are extinguished when they die, but the genes that contribute to the construction of physiological, morphological, and psychological mechanisms are passed on to subsequent generations.

What does “EEA” refer to? One crucial but consistently mischaracterized concept is that of *environment of evolutionary adaptedness*, or *EEA* (Tooby & Cosmides, 1992). Unfortunately, many researchers—including some evolutionary scientists—mistakenly think that EEA refers to

a specific time and place, such as the African savanna during the Pleistocene. It does not. Rather, EEA refers to the *set of selective pressures responsible for shaping a given adaptation* (Tooby & Cosmides, 1990a).

These are two radically different concepts. The erroneous characterization makes it sound sensible to discuss *just one* EEA. The correct characterization of EEA as the recurrent set of selection pressures that shaped a particular adaptation highlights the fact that each adaptation has its own *distinct* EEA. There is no single “human EEA.” There is a distinct EEA for *each* adaptation.

To illustrate a correctly conceptualized EEA, consider humans’ psychological aversion toward incest. The EEA of incest aversion mechanisms refers to the selective pressures that favored incest-aversion adaptations. These would have included the need to find a reproductively viable mate, small-group living in close proximity to genetic relatives, and severe negative fitness consequences of genetic inbreeding. This set of conditions is not tied to any particular physical ecology, and extended well beyond the African savanna and the Pleistocene.

Hypothesis Generation: Key Points

The reader has now collected a set of conceptual and methodological tools useful for both observation- and theory-based hypothesis generation. These tools include (a) the correct characterization of an adaptation’s EEA, (b) heuristics for identifying important adaptive problems, (c) task analysis, and (d) the specification of the design features that constitute a psychological adaptation and enable it to solve its relevant adaptive problem. With these tools in hand, we turn to hypothesis testing.

Testing Evolutionary Psychological Hypotheses

The central evidentiary criterion for testing adaptation hypotheses is *special design*—functional design to solve a specific adaptive problem (see Williams, 1966). Fortunately, in the hypothesis generation stage, the researcher already proposed psychological design features (sensory, perceptual, cognitive, affective, behavioral) that are functionally specialized to solve a specific adaptive problem (Pinker, 2005; Tooby & Cosmides, 1992; Williams, 1966). Consequently, appropriate tests of an adaptation hypothesis do not require special materials, methods, or measures. Rather, testing an adaptation hypothesis simply entails testing for evidence of these psychological features.

Evolutionary psychological hypotheses posit that “certain evolutionary pressures led to certain psychological structures” (Conway & Schaller, 2002, p. 154). Such hypotheses can be evaluated by testing for evidence of these psychological structures. This testing can proceed through standard methods of investigation in psychology, including labora-

tory experiments, questionnaires, cross-cultural comparisons, observational techniques, and physiological measures (Buss, 2015). Some evolutionary researchers employ additional conceptual and empirical tools not typically in a psychologist’s toolkit (e.g., paleoarchaeological studies, phylogenetic analyses, cross-species comparative studies). However, a researcher without these tools should not be dissuaded—these additional methods can be useful supplements, but are not strictly necessary. The typical psychologist’s toolkit is already well equipped to test adaptation hypotheses.

To illustrate this point, consider human sex differences in parental investment and variance in reproductive success. Women shoulder the greater minimum obligatory investment in offspring (e.g., gestation, childbirth, and nursing; Trivers, 1972) and thereby incur greater costs from injudicious mating decisions. Moreover, the fitness benefits that ancestral men would have reaped by mating with multiple women would have been greater than the benefits to ancestral women of mating with multiple men. This has led to the evolution of choosier and more discriminating mating strategies among women relative to men (Buss, 2003; Trivers, 1972). A variety of different sources and methodologies demonstrate that

compared to women, men express a greater desire for a variety of sex partners, let less time elapse before seeking sexual intercourse, lower their standards dramatically when pursuing short-term mating, have more sexual fantasies and more fantasies involving a variety of sex partners, experience more sexual regret over missed sexual opportunities, have a larger number of extramarital affairs, and visit prostitutes more often. (Buss, 2012, p. 200)

This collection of findings highlights several key characteristics of hypothesis testing in evolutionary psychology. First, support for a proposed adaptation comes from empirical evidence of its predicted design features, including features at multiple levels of psychology, such as *motivation* (e.g., desire for sexual variety), *cognition* (e.g., frequency of sexual fantasies), *emotion* (e.g., regret about missed sexual opportunities), and *behavior* (e.g., shorter intervals before pursuit of sexual intercourse, extramarital affairs). Second, convergent evidence from distinct studies, especially those employing a variety of methods and doing so across cultures (e.g., Schmitt, Alcalay, Allensworth, et al., 2003; Schmitt, Alcalay, Allik, et al., 2003), offers an even stronger test of an adaptation hypothesis. Third, these methods are already familiar elements of psychologists’ methodological toolkits.

To provide a powerful test of a hypothesis, researchers can generate predictions not only about what they expect to see but also about what they expect *not* to see. That is, if a researcher’s hypothesis suggests that a particular information processing mechanism should be activated under Condition X but not under Condition Y, finding empirical

confirmation of both the “positive” and the “negative” prediction constitutes stronger support than merely finding evidence for the “positive” prediction. Similarly, if a researcher’s hypothesis suggests that a particular psychological mechanism will respond to one set of inputs but not another, a strong test of the hypothesis would involve demonstrating both predicted effects—the mechanism’s response to one set of cues *and* the mechanism’s lack of response to the other set. More generally, if a researcher wants to demonstrate that a psychological mechanism or process is nonrandomly designed to achieve a functional outcome, one of the strongest demonstrations a researcher can provide is evidence that it responds when it is expected to and that it also *does not* respond when it is expected not to.

In sum, clear, strong tests of adaptation hypotheses do not require unique methods distinct from those used in the rest of psychological science.² Rather, the key in testing adaptation hypotheses lies in testing for evidence of the hypothesized mechanism’s design features. Fortunately, these tests can be readily conducted with methods and measures that are already a mainstay of psychologists’ methodological toolkit.

Interpreting Results

Hypothesis testing in evolutionary research is held to the same standard as that of all sciences: Hypotheses should be confirmed or disconfirmed based on the degree of fit between prediction and observation, and the cumulative weight of evidence across multiple studies. Because an adaptation hypothesis requires specification of the proposed mechanism’s design features, evaluating such a hypothesis requires assessing the fit between the predicted design features of the proposed adaptation and empirically observed psychological phenomena.

Alternative Explanations

All observed findings are open to alternative explanations, including multiple evolutionary explanations that are in competition with one another. Research on women’s ovulation-based shifts in mating psychology (e.g., Gangestad, Thornhill, & Garver-Apgar, 2005) nicely illustrates this idea.

The “dual mating strategy hypothesis” (Gangestad et al., 2005) proposes that women have psychological adaptations that can motivate them to seek long-term mateships with men willing to commit to and invest in them, and pursue short-term mating opportunities with men of high genetic quality during the fertile phase of the ovulatory cycle. Research guided by this hypothesis has demonstrated that (a) women’s preferences for men exhibiting cues to underlying genetic quality (e.g., symmetry, masculinity) increase

at ovulation (e.g., Gildersleeve, Haselton, & Fales, 2014), (b) these shifts are less pronounced among women whose current mates exhibit high levels of these cues (Pillsworth & Haselton, 2006), (c) women dress more revealingly at ovulation (Haselton, Mortezaie, Pillsworth, Bleske-Rechek, & Frederick, 2007), and (d) men’s mate guarding increases when their partners are ovulating (Haselton & Gangestad, 2006).

This is just a subset of the considerable empirical support that the dual mating strategy hypothesis has received. However, there are compelling alternative explanations that could plausibly account for the extant data. These alternative evolutionary explanations fall into two classes: alternative function and incidental byproduct effects.

Alternative function. Researchers should consider how adaptations other than the one postulated could conceivably solve the adaptive problem, and how an observed phenomenon might be the output of an adaptation designed to solve a different adaptive problem than the one under consideration (Conway & Schaller, 2002).

A viable alternative hypothesis for women’s ovulation-based shifts in mating psychology is that these shifts reflect the output of female adaptations to “mate switch” when their mate value is highest—at peak fertility (Buss & Shackelford, 2008). Women desire long-term mates with markers of robust genetic quality. Because such men are in high demand, they can be difficult for most women to obtain for long-term mateships. This idea is central to the logic of both the dual mating strategy hypothesis and the alternative mate-switching hypothesis. Where these hypotheses diverge is in their proposed solutions to this adaptive problem.

The dual mating strategy hypothesis argues that ovulatory shifts represent an adaptive compromise: Women may, under certain circumstances, pursue long-term mateships with less genetically robust men, but engage in sexual liaisons with men of higher genetic quality. Because women’s likelihood of conception is highest at ovulation, the benefits of short-term mating with men of high genetic quality—namely, conceiving a child who inherits his father’s high quality genes (Thornhill, Gangestad, & Comer, 1995)—are also highest at ovulation.

The mate-switching hypothesis, on the other hand, contends that ovulatory shifts are the output of adaptations designed to lead women to attempt to “trade up” to high-quality long-term mates. Because women’s mate value is highest at peak fertility (which occurs near ovulation), the likelihood of successfully “trading up” is highest at ovulation. The ability of the mate-switching hypothesis to account for ovulatory shifts in female mating psychology

² See Confer et al. (2010) for a discussion of why methods and measures such as identifying specific genes or measuring current reproductive rates are neither necessary nor sufficient for establishing adaptation, and can be actively misleading.

limits the degree to which these shifts can be interpreted as *discriminative* support for the dual mating strategy hypothesis.

This captures two key points. First, theoretically and methodologically sophisticated evolutionary research must contend with alternative adaptation hypotheses. Second, during the hypothesis generation phase, it is crucial to generate hypotheses about an adaptation's design features. It is only when researchers identify and test the divergent predictions generated from the dual mating strategy and mate switching hypotheses that they will be able to adjudicate between these alternatives.

Incidental byproduct explanations. Adaptation hypotheses and byproduct hypotheses can sometimes account for the same set of findings. Ovulation-based shifts in female mating psychology again offer an illustrative example. Several byproduct hypotheses have been proposed to account for these ovulatory shifts. Here we focus on one plausible hypothesis.

Ovarian hormones are reliable indices of female fecundity (e.g., Sen & Hammes, 2010; Singh, 1993). Estradiol, the hormone that rises in concentration immediately before and after ovulation in humans, decreases in many mammalian species when environmental conditions are too poor for successful reproduction (Ellison, 1994). It has been proposed that women modulate mating effort as a function of estradiol levels, as a means of limiting reproductive attempts to contexts likely to be associated with successful nursing and child rearing (Roney, 2009). The key function of this proposed adaptation is to increase mating effort during high-fertility cycles relative to low-fertility cycles—that is, to modulate mating effort *across* cycles. However, because (a) the mechanism takes women's estradiol levels as input, and (b) these levels are highest at ovulation *within* a given cycle, this adaptation designed to produce between-cycle shifts may incidentally yield within-cycle shifts, including increased attraction to masculine and symmetrical men at ovulation (Roney, 2009). More broadly, this byproduct account illustrates that processes that evolved to solve one adaptive problem can sometimes appear quite similar to processes hypothesized to solve a different adaptive problem.

Researchers should therefore interpret study results not only with respect to their own hypothesis and predictions but also in the context of competing adaptation and byproduct effect hypotheses. Drawing out the specific predictions expected under each hypothesis enables a researcher to design studies that more clearly adjudicate between competing hypotheses.

Sociocultural explanations. Imagine that a researcher finds compelling evidence consistent with an adaptation explanation for a particular psychological phenomenon. Does this imply that socialization and culture are unimportant in the development of the phenomenon? Certainly not.

Evolutionary hypotheses are often in competition with another, and they *can* be in conflict with specific sociocultural explanations. However, evolutionary hypotheses are not by default incompatible with sociocultural accounts. Rather, evolutionary and sociocultural explanations are often logically compatible with one another.

To see why, consider Tinbergen's (1963) four categories of explanations, which apply to any psychological or behavioral phenomenon. Two of these fall into the *proximate* level of analysis, which deals with the immediate causes of a behavior or mental process, as well as how it developed during the individual's life span. The other two, on the other hand, fall into the *distal* level of analysis, which addresses the distant historical origins of how and why the psychological structures responsible for producing the behavior or mental process evolved in the first place. Understanding this distinction between proximate and distal levels of analysis is essential for understanding the frequently misunderstood and mischaracterized relationship between sociocultural and evolutionary hypotheses.

Sociocultural hypotheses investigate the proximate causes of psychological phenomena. They valuably contribute to our understanding of *how* a psychological mechanism works in sociocultural context, how it develops during ontogeny, and *what* specific social, cultural, and other environmental inputs activate the mechanism. Adaptation hypotheses, on the other hand, investigate distal causes of a psychological phenomenon in order to yield predictions about its proximate causes—understanding *why* the mechanism responsible for the psychological phenomenon evolved in the first place (distal) furnishes predictions about how the mechanism operates and what specific inputs trigger its activation (proximate).

Consequently, although sociocultural and evolutionary explanations can be in conflict, they are not necessarily so. For an adaptation explanation and a sociocultural explanation to be incompatible, the two explanations must conflict in the domain in which they overlap: To be in conflict, the adaptation hypothesis must make predictions about proximate causes of behavior that do not align with predictions made by the sociocultural hypothesis. Some evolutionary and sociocultural hypotheses do advance contradictory proximate claims, but often they do not. In such cases, they are perfectly compatible. Determining whether a particular evolutionary explanation and a particular sociocultural explanation are in conflict thus must be carried out on a case-by-case basis. The key point is that evolutionary hypotheses do not contradict sociocultural hypotheses *merely by being evolutionary in nature*.

Gender differences in mating psychology offer an illustrative example of the potential compatibility of sociocultural and evolutionary hypotheses, as well as the unfortunate historical framing of these hypotheses as necessarily in conflict. Sexual strategies theory (Buss & Schmitt, 1993) is

a prominent middle-level theory of the evolutionary origins of gender differences in mating psychology. Central to sexual strategies theory is the idea that sex differences in minimum obligatory parental investment linked to sex-differentiated mammalian reproductive biology would have created distinct selective pressures on men's and women's mating psychology. A proximate sociocultural explanation is that cultural expectations about men's and women's social roles yield these gender differences in psychology (e.g., originally proposed by Buss & Barnes, 1986; subsequently presented in modified form by Eagly & Wood, 1999). Sex differences in minimum obligatory parental investment are not incompatible with sex-differentiated cultural expectations. Even more strongly, there are persuasive arguments that an evolutionary starting point of sex differences in reproductive biology should lead to gender-specific cultural norms (see Conway & Schaller, 2002; Schaller, 1997). Unfortunately, a historical lack of understanding about the distinction between distal and proximate levels of analysis—and therefore about the potential logical compatibility of evolutionary and sociocultural hypotheses—has resulted in evolutionary and sociocultural explanations inaccurately being presented as necessarily incompatible with one another.

The assumption that a distal statement such as “natural selection played a part in shaping this mechanism” implies the proximate statement “social and cultural inputs have no effect on the development or activation of this mechanism” is common but erroneous. This error reflects a failure to distinguish between the proximate and distal levels of analysis. In fact, evolutionary explanations accord a fundamental role to social and cultural inputs both during the development of psychological mechanisms during ontogeny, and in the activation of the mechanism in its current sociocultural context (e.g., Confer et al., 2010). Not only are evolutionary and sociocultural explanations often logically compatible with one another, but their conceptual integration also bears important potential benefits for the psychological sciences. By linking models of the contemporary operation of psychological mechanisms to models of the historical origins of those mechanisms, researchers can move toward a more complete and explanatorily powerful model of human psychology (Conway & Schaller, 2002).

Cultural differences. Cultural differences in behavior or psychology are sometimes misinterpreted as evidence against adaptation. Often, the idea of a universal human nature is erroneously interpreted as implying that specific behaviors must be universal. Evolutionary reasoning does not propose this. Rather, the evolutionary psychological construct of a universal human nature³ refers to species-typical *psychological mechanisms*, not universal *manifest behavior* (e.g., Tooby & Cosmides, 1990b).

This proposal of species-typical mechanisms that process cues from the local environment leads to the expectation of

cross-cultural differences. That is, a universal adaptationist perspective predicts that systematic variability in social and cultural input should lead to systematic variability in psychological output. Cultural differences thus represent exciting opportunities to achieve a more comprehensive and contextualized understanding of psychological mechanisms. Considering universal mechanisms in tandem with systematically variable input is a powerful theoretical tool for generating a priori predictions about cultural differences in output behavior.

Gangestad and Buss's (1993) research illustrates this point. They hypothesized that because pathogens can cause morphological perturbations during development, individuals living in parasite-dense regions of the world should place greater importance on physical attractiveness in mates. Underlying this hypothesis is a cost–benefit analysis of prioritizing different attributes in potential mates. Selecting a mate with the ability to withstand pathogen exposure without impaired development is beneficial in all environments. However, selecting such a mate is more pressing in geographical regions with higher levels of pathogens than in regions with lower pathogen prevalence. This points to the hypothesis that humans' mate preference mechanisms should upregulate the importance placed on physical attractiveness in high pathogen-prevalence regions and downregulate its importance in regions with lower levels of pathogens (see Figure 1). Gangestad and Buss tested this hypothesis across 29 cultures and found that local pathogen prevalence predicted cultural variation in the importance placed on mates' physical attractiveness. As hypothesized, increased pathogen prevalence predicted greater valuation of physical attractiveness in potential mates, accounting for a full 50% of the cultural variation.⁴

Thus, culturally variable output was not only patterned in an evolutionarily predictable manner but also predicted, in advance, on the basis of evolutionary reasoning. This study illustrates that “evolutionary” is not equivalent to “cross-culturally invariant,” and represents just one example of the key idea that culturally variable input into universal psychological mechanisms can lead to culturally variable output. Further, it shows that the application of an evolutionary perspective to culturally variable socioecological conditions has the capacity to not only increase our understanding of cross-cultural diversity but also predict, in advance, previously unknown cultural differences.

³ For a detailed discussion of evolutionary genetic models, including both models that posit universal mechanisms as well as adaptation models that do not posit species-typical mechanisms, see Penke, Denissen, and Miller (2007).

⁴ Note that alternative evolutionary models may also account for this cross-cultural variation. For example, balancing selection—different selection pressures across different environments—could have selected for different psychological mechanisms in different geographical regions (see Penke et al., 2007, for a more comprehensive discussion of alternative evolutionary models).

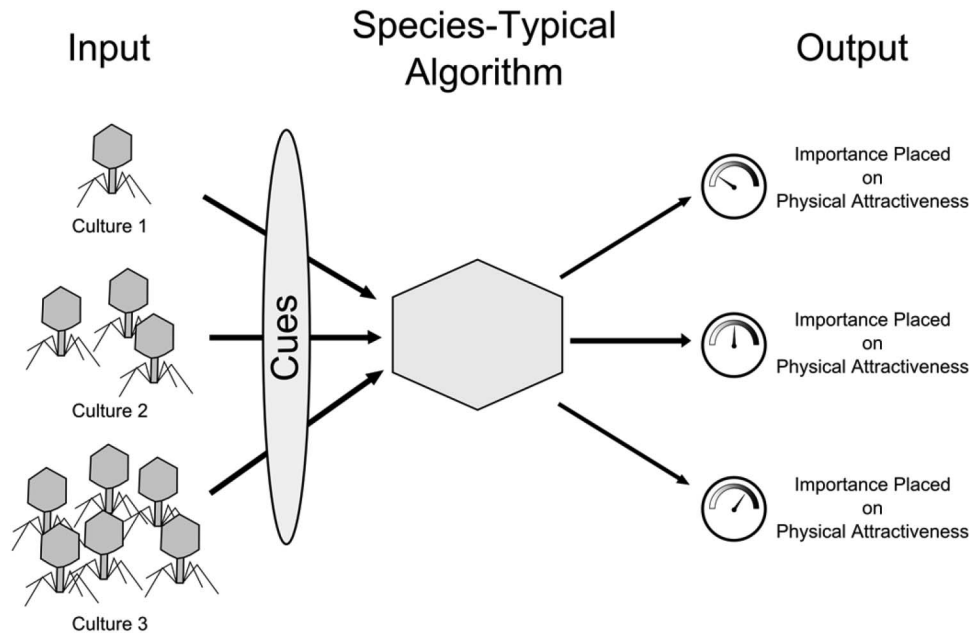


Figure 1. Species-typical mechanisms can lead to cross-cultural differences in psychology. Here, species-typical mechanisms are producing cross-cultural differences in the importance placed on physical attractiveness in potential mates as a function of local pathogen levels. The hypothesized mechanism takes cues to local pathogen levels as input and regulates the importance placed on physical attractiveness accordingly. In Culture 3, relative to Culture 1, the mechanism detects higher levels of pathogen-associated cues and up-regulates the importance placed on physical attractiveness.

In summary, we need to know both the evolutionary function that a mechanism was designed to solve as well as how the mechanism operates in variable sociocultural contexts. These represent distinct levels of analysis, and both are necessary elements in moving toward a comprehensive understanding of any psychological phenomenon (Tinbergen, 1963).

Developmental explanations. Suppose a researcher finds evidence of a hypothesized evolved psychological mechanism in adults. Is that researcher now committed to a particular developmental trajectory for that mechanism? It is a common misconception that evolutionary psychological hypotheses assume narrow developmental trajectories—for example, that mechanisms are present at birth, static, and insensitive to environmental input. This could not be further from the truth (see Confer et al., 2010).

Rather, the developmental process itself is a key focus for evolutionary psychological hypothesizing. Importantly, there are multiple compatible evolutionary developmental (“evo-devo”; e.g., see Arthur, 2002; Müller, 2007; Raff, 2000) models that offer valuable insight into research whose central topic of investigation is the development of psychological capacities or processes. For example, some evolutionary developmental models consider how constraints imposed by an organism’s life history (e.g., Kaplan & Gangestad, 2005) should result in developmental shifts in certain psychological systems and processes. Organisms

have finite energy available to dedicate to processes like growth, tissue maintenance, immune functioning, and reproduction. Energy dedicated to one process is necessarily energy that cannot be allocated to another. Researchers can use such constraints as a conceptual tool for increasing our understanding of developmental shifts in psychology. For example, after birth, humans undergo an extended period of somatic growth and brain development. This developmental period places great energetic demands on the organism and requires delaying investment in the development of other systems. However, after this prepubescent period, many of the organism’s resources can be directed away from growth and toward the development of secondary sexual characteristics, fertile menstrual cycling, and the development of the psychological systems involved in mating. This evolutionary conceptual tool of tradeoffs between the development, maintenance, and operation of different physiological and psychological systems has powerful heuristic value for generating testable predictions about human development.

A distinct but compatible model proposes that certain developmental *shifts* in psychology reflect evolved design features of the mechanisms responsible for those psychological processes. Underlying this model is the idea that organisms predictably face different adaptive problems at different life stages (Bjorklund & Pellegrini, 2000). For example, before developing the physical capacities necessary to explore their environment, children are incapable of

independently moving and encountering dangerous conspecifics. They therefore do not face this adaptive problem. Corresponding to the absence of this adaptive problem, infants generally do not exhibit stranger anxiety before the age at which they can crawl (see Boyer & Bergstrom, 2011). Importantly, however, by the time that children begin to actively explore their environment, they do reliably exhibit a fear of strangers.⁵

This conceptual tool of considering the onset of distinct adaptive problems during development has heuristic utility for understanding psychological development during other stages of the life span as well. Successfully attracting a fertile mate and taking care of infants represent distinct adaptive problems that men may face in adulthood. The physiological and psychological systems that help solve one adaptive problem may not help solve the other. For example, elevated levels of testosterone are associated with greater success in competing for mates (e.g., Gettler, McDade, Feranil, & Kuzawa, 2011), but also with inferior caretaking (Weisman, Zagoory-Sharon, & Feldman, 2014). A consideration of the shifting adaptive problems that men face as they transition from competing for mates to being fathers can be used to generate evolutionarily anchored hypotheses about the psychological shifts that men may undergo at this stage in life. Gettler et al. (2011) used this conceptual tool to hypothesize that men would exhibit elevated levels of testosterone during periods of active competition for mates, but reduced testosterone during fatherhood to facilitate child rearing and caretaking. In support of this hypothesis, Gettler and colleagues longitudinally demonstrated that (a) higher levels of testosterone predicted an increased likelihood of mating success and siring offspring, (b) fatherhood specifically (and not merely aging) was associated with a reduction in testosterone, and (c) among fathers, lower levels of testosterone were associated with greater caretaking. As this research illustrates, evolutionary models can be used to not only increase our understanding of psychological shifts during ontogeny but also generate novel, testable hypotheses about previously undiscovered facets of humans' psychological development across the life span.

These examples represent just a few of the evolutionary models at the disposal of researchers interested in development. Other evolutionary theories model certain developmental trends as a consequence of physical constraints (e.g., complex systems simply take time to develop) or as learning effects (e.g., childhood can be an ideal time to calibrate the parameters of psychological mechanisms to local conditions). Each of these distinct evolutionary models offers its own predictive and explanatory utility. These evolutionary developmental models are often mutually compatible; some may apply to some psychological mechanisms or some periods of ontogeny, but not others; and each of them offers

unique value for informing research on psychological development.

In sum, a hypothesis about a psychological adaptation does not commit the researcher to a specific stance about development. Rather, the developmental trajectory of the mechanism is an independent question, and one that is readily open to investigation by evolutionarily minded researchers. Researchers can use the conceptual tools of evolutionary developmental psychology to fruitfully tackle such important questions.

Null Results: Interpretation at Different Levels of the Theoretical Hierarchy

Empirical studies can produce null results for many reasons. These include improper conceptualization of constructs, faulty operationalization, methodological problems, or because study hypotheses are incomplete, flawed, or simply incorrect. In this section, we discuss how a researcher can draw appropriate conclusions about an adaptation hypothesis (as well as the middle-level theory that motivated it) based on null results.

A single adaptive problem can be solved in different ways, sometimes by very different adaptations. Consequently, a middle-level theory can be used to generate multiple distinct, competing evolutionary hypotheses about the adaptation that may have evolved to solve the adaptive problem in question (Conway & Schaller, 2002). Only one (or a few) of these can be correct—the set of actual solutions is smaller than the set of possible solutions. As a result, it is possible for a middle-level theory to be correct, but for some of the competing hypotheses generated from it to be false.

The fact that there are often competing evolutionary hypotheses means that there is no single hypothesis that can be regarded as “the” evolutionary hypothesis. Instead, each hypothesis proposes its own set of design features and leads to its own set of predictions. The absence of support for a specific hypothesized adaptation indeed may falsify that hypothesis, but it does not imply that *no* psychological mechanism evolved to solve the relevant adaptive problem.

There is rarely—if ever—a single critical test of a theory. The evaluation of a theory is a cumulative enterprise that can only occur through the overall weight of the evidence—multiple independent verifications or falsifications of the

⁵ Note that not only does the developmental schedule of this psychological process track the appearance of the new adaptive problem during ontogeny, but once online, the mechanism exhibits high functional specificity to deal with the relevant adaptive problem. Infanticide occurs in many primate species (Hrdy, 1977), and evidence from modern humans suggests that this threat is most pronounced when a child is with a genetically unrelated male (Daly & Wilson, 1998). The psychological mechanisms responsible for stranger anxiety carefully track these ancestral fitness threats; stranger anxiety is generally directed toward unfamiliar, unrelated men—but not women or male genetic relatives.

hypotheses generated from it (Greenwald & Ronis, 1981; Laudan, 1977; Quine, 1953). If multiple studies and methods yield disconfirming evidence for many distinct hypotheses, they cast doubt on that theory. Conversely, if multiple studies and methods yield confirmatory evidence for many distinct hypotheses, they provide support for the theory motivating those hypotheses. Ultimately, a theory should be evaluated in light of the total body of relevant evidence.

Alternative Evolutionary Approaches to the Study of Mind and Behavior

The conceptual and methodological tools we present in this article have been used to great effect in elucidating the mechanisms of mind and behavior (see Buss, 2016, for a recent compilation), but by no means do they exhaust the tools available to evolutionary scientists. Other fruitful evolutionary approaches to the study of the behavioral sciences include the use of phylogenetic and cross-species analyses (e.g., Fraley, Brumbaugh, & Marks, 2005; Vonk & Shackelford, 2012), as well as the incorporation of principles and ideas from evolutionary developmental biology, or “evo-devo” (Raff, 2000; see also Arthur, 2002; Müller, 2007). Cultural evolutionists employ the tools of cross-cultural studies and historical analysis to explore interactions between our evolved psychology and our evolving cultures in producing behavior (Henrich, 2015). Andrews and colleagues (Andrews, Gangestad, & Matthews, 2002) also advance a particularly interesting approach to testing exaptationist and byproduct hypotheses—an approach that nicely complements the one we put forward in this article.

Some alternative strategies have been collected in articles and edited volumes (e.g., Scher & Rauscher, 2003), and the interested reader is invited to consider these other investigative tools as well. In this article, we have largely focused on a set of tools that have already proven greatly successful in their theoretical richness and empirical harvest (see, e.g., Buss, 2015), but there is certainly room for conceptual and methodological pluralism in the application of evolutionary theory to the behavioral sciences.

Summary

Hypothesis Generation

As in all scientific disciplines, evolutionary psychological hypothesis generation proceeds via both theory-driven (top-down) and observation-driven (bottom-up) approaches. In the theory-driven approach, a researcher identifies an adaptive problem and proposes an adaptation that could have evolved to solve that problem. At this stage, task analysis is a powerful tool for systematically generating hypotheses about mechanisms that could, in principle, solve the relevant problem. When proposing such adaptation hypotheses,

researchers should place a special emphasis on proposing specific design features of the hypothesized mechanism. Toward this objective, researchers can consider the differential costs and benefits of the mechanism’s outputs (e.g., behaviors) across contexts to generate nuanced hypotheses about the contextual cues likely to activate or deactivate the mechanism. Identifying such context-dependent design features of the hypothesized mechanism can yield hypotheses about social, cultural, and other environmental variables that may influence the mechanism’s activation. Importantly, this can help researchers generate novel a priori hypotheses about culturally variable behaviors as the output of species-typical psychological adaptations.

In the bottom-up approach, a researcher begins by observing a psychological or behavioral phenomenon, and then engages in a reverse task analysis to determine what adaptive problem the psychological mechanism responsible for producing that phenomenon may have evolved to solve. The bottom-up approach is completed when—and *only* when—the researcher then “turns around” and generates novel testable predictions based on this hypothesized psychological mechanism.

Hypothesis Testing

Adaptation hypotheses can usually be tested using methods that are already familiar elements of psychologists’ methodological toolkits. The central criterion for testing adaptation hypotheses is *evidence of psychological processes* that exhibit functional design to solve a particular adaptive problem. Testing for evidence of these psychological phenomena can be accomplished through methods and measures familiar to all psychological researchers, such as laboratory experiments, questionnaires and surveys, cross-cultural studies, observational studies, and physiological data.

Interpretation of Results

Like all scientific hypotheses, evolutionary hypotheses should be evaluated according to the degree of fit between prediction and observation. In interpreting study results, researchers should pay special attention to alternative explanations such as competing adaptation hypotheses and incidental byproduct hypotheses.

Evolutionary hypotheses are often in competition with one another, but they are only sometimes in conflict with sociocultural explanations—despite widespread beliefs to the contrary. Sociocultural explanations typically make claims about the *proximate* causes of a psychological phenomenon, whereas evolutionary hypotheses make claims about both the distal origins of psychological mechanisms as well as the proximate causes of the phenomenon. Evolutionary and sociocultural explanations are only in disagreement when they make contradictory claims about the *proximate* causes of a psychologi-

cal phenomenon, and sometimes they do not. As such, evolutionary and sociocultural explanations are often logically compatible with one another. Importantly, their integration bears important potential benefits for the psychological sciences. By linking models of the contemporary operation of psychological mechanisms to models of the distal origins of those mechanisms, researchers can move away from the misunderstanding that these models necessarily conflict with one another and toward a more comprehensive, internally consistent, and explanatorily powerful framework for human psychology (Conway & Schaller, 2002).

Interpreting results in evolutionary psychological research requires two additional caveats: *variable output* and *multiple instantiations*. First, a finding of behavioral variability across cultures is sometimes taken to automatically rule out the hypothesis of a universal psychological adaptation. This conclusion is unwarranted. An evolutionary psychological approach emphatically does not predict universal manifest behavior. Rather, a universal adaptationist perspective posits species-typical psychological *mechanisms*. These mechanisms are expected to produce variable behavioral output in response to the socially, culturally, and ecologically variable inputs that they process. A rarely appreciated but critical point is that behavioral differences across cultures, genders, and individuals may be systematically predicted a priori based on a consideration of evolutionary psychological principles. Specifically, considering the costs and benefits of behaviors across different contexts may shed light on which contextual variables would be expected to amplify or attenuate the activation of the psychological mechanism under investigation.

Second, there are multiple ways to instantiate a hypothesis or a middle-level theory. A single hypothesis can be used to generate multiple distinct predictions, and a single middle-level theory can be used to generate distinct, even competing, hypotheses (Buss, 1995; Conway & Schaller, 2002; see also Al-Shawaf, Conroy-Beam, Asao, & Buss, 2016). For this reason, it is an error to equate verification or falsification of a particular prediction with the verification or falsification of the hypothesis that motivated it. Ultimately, the merit of a hypothesis or middle-level theory should be determined based on the cumulative body of evidence (Greenwald & Ronis, 1981; Laudan, 1977; Quine, 1953).

Conclusion

More and more researchers in the psychological and behavioral sciences are seeking to apply evolutionary psychological principles to their empirical research programs, thereby contributing to the unification of the social and behavioral sciences with the rest of the life sciences. However, because there are many missteps researchers and theorists can make, and because psychologists do not receive formal training in evolutionary principles, it is important to

provide a systematic and accessible guide for incorporating evolutionary thinking into psychological research. We hope that this guide will benefit readers and spur novel research that is theoretically and methodologically rigorous.

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