

Chapter 21

Evolutionary Social Psychology

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Based merely on the scents of shirts worn recently by unknown men, women can, to a significant degree, assess the men's physical attractiveness—but only while ovulating. When worried about catching colds, people show greater prejudices against those who are disabled, obese, or foreign. When romantic inclinations are temporarily intensified, men—but not women—become more creative, confrontational, and nonconformist. Encountering a stranger with attitudes similar to one's own automatically activates thoughts of kinship. Pregnant women are more ethnocentric than their non-pregnant counterparts, but only during the first trimester. And upon viewing an opposite-sex face resembling one's own, people judge that person to be a desirable friend but undesirable sexual partner—to be trustworthy but not lustworthy.

These empirical findings, and many others like them, are difficult to explain—even post hoc—with most conventional social psychological theories. Yet, each was predicted from analyses of the psychological implications of human evolutionary biology (e.g., DeBruine, 2005; Gangestad & Thornhill, 1998; Griskevicius, Cialdini, & Kenrick, 2006; Navarrete, Fessler, & Eng, 2007; Park & Schaller, 2005; Park, Schaller, & Crandall, 2007). In addition to facilitating the discovery of diverse, sometimes counterintuitive, and often complex phenomena, an evolutionary perspective on social psychology also integrates these phenomena with one another and with a host of other findings, too. Evolutionarily informed empirical inquiries have produced deeper understandings of classic social psychological phenomena ranging from attraction to aggression, conflict to cooperation, person perception to prejudice, social cognition to social influence. The evolutionary approach has also served to open the field to phenomena long ignored, such as kin relations and child rearing—phenomena central to social life in the real world. The result is a comprehensive view of human social behavior

governed by a coherent set of rigorously logical general principles (Buss, 2005; Cosmides, Tooby, & Barkow, 1992; Crawford & Krebs, 2008; Gangestad & Simpson, 2007).

In this chapter, we review the current state of evolutionary social psychology. We begin with a brief primer on exactly what evolutionary social psychology is and is not, articulating its assumptions and the tools it provides for inquiry into social cognition and behavior. We then present an overview of what we call the *affordance management system*—a conceptual framework that articulates, in general terms, the manner in which many evolved psychological mechanisms influence cognition and behavior as individuals negotiate the many threats and opportunities inherent in social life. We proceed to review many different lines of evolutionarily informed research on a wide range of social psychological phenomena. This review highlights the many novel and nuanced hypotheses that have been deduced within an evolutionary framework, and illustrates the generative and integrative power of evolutionary logic when applied to the study of social psychology. We then address broader questions. We explore the relationships among evolved adaptations, development, learning, and culture. We discuss several epistemic and methodological issues that attend inquiries in evolutionary social psychology (and common misunderstandings that arise from these issues). We identify promising directions for future research. Finally, we reconsider the utility that an evolutionary perspective offers to scientific inquiry into social behavior.

WHAT IS EVOLUTIONARY SOCIAL PSYCHOLOGY?

Evolutionary psychology isn't a theory, model, or hypothesis. Rather, evolutionary psychology is a set of

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metatheoretical assumptions that govern how scientists approach conceptual and empirical inquiry into psychological phenomena (Buss, 1995; Ketelaar & Ellis, 2000). These assumptions (e.g., that cognition is the product of an underlying physiology, and that human physiology has been shaped by a long history of biological selection pressures) are scientifically noncontroversial, and are based on a vast empirical database within the biological sciences more broadly. When applied to the conceptual landscape of social psychology, these assumptions focus scientific inquiry on specific kinds of research questions and generate specific kinds of answers to those questions. These assumptions also provide a set of logical tools that, when applied rigorously, can be used to deduce specific theories, models, and hypotheses about social psychological phenomena. It is these theories, models, and hypotheses (not the metatheory of evolutionary social psychology) that offer specific predictions for social psychological phenomena, and that are directly tested by empirical evidence.

Thus, evolutionary social psychology is logically analogous to cognitive social psychology. Just as the cognitive sciences provide a metatheoretical context (and a set of conceptual tools) that can be used to derive hypotheses about social psychological phenomena, the evolutionary sciences provide a metatheoretical context (and a somewhat different set of conceptual tools) that can be used to derive hypotheses about social psychological phenomena. The analogy is apt in other ways, too: Just as the metatheory of cognitive science generates multiple, and sometimes competing, theories about social psychological phenomena, so too does the metatheory of evolutionary science. Just as the advent of the cognitive approach to social psychology was greeted with skepticism decades ago, so too has been the advent of evolutionary psychological inquiry. And, just as the cognitive revolution eventually reshaped the landscape of social psychology, the findings generated thus far by the evolutionary perspective suggest that it, too, has the potential to further revolutionize inquiry into social behavior (Kenrick, Schaller, & Simpson, 2006).

Because its metatheoretical assumptions are rooted in the biological sciences (rather than the traditional social sciences), evolutionary social psychology is sometimes viewed as exotic, and sometimes even as threatening to the basic assumptions of social psychology. In fact, an evolutionary approach is entirely consistent with the defining themes of social psychology. Evolutionary social psychology is emphatically focused on the *power of the situation*, assuming that the proximate impetus to action typically lies in the immediate social context. Evolutionary social psychology is also an *interactionist* perspective, recognizing that thoughts, feelings, and behavior emerge as an interactive function of variables pertaining to the person (e.g., specific

motives, strategies, and capacities) and the situation (e.g., salient contextual cues connoting specific threats or opportunities within the immediate social context). It is explicitly interactionist in another way, too: An evolutionary perspective rejects any simplistic “nature *versus* nurture” approach to the causes of social behavior. Rather, it acknowledges, and seeks to unpack, the fascinating and complex relationships among evolved mechanisms, developmental processes, learning, and culture. Given these features, evolutionary analyses rarely generate hypotheses about inflexible, rigid forms of behavior. Instead, these hypotheses often explicitly articulate how evolved psychological adaptations imply predictably *flexible* responses to cues in the immediate environment. Finally, evolutionary social psychology generates hypotheses about mediating processes—about how particular cues in the social environment heuristically imply particular threats and opportunities, activate particular cognitive and affective mechanisms, and thereby incline individuals toward particular behaviors.

In other ways, however, evolutionary approaches move beyond traditional social psychological approaches. Evolutionarily informed deductions typically begin by identifying specific domains of fitness-relevant behavior (e.g., coalition formation, child-rearing, mate acquisition) and specific problems pertaining to each domain (e.g., how to avoid social exclusion, how to enhance parental commitment to offspring, how to identify a mate who maximizes one’s own reproductive potential). The resulting deductions are *domain specific*: Psychological mechanisms that govern social inference and behavior in one social domain may be very different from those that govern inference and behavior in other, superficially similar, domains. The focus on recurrent fitness-relevant problems also encourages attention not only to specific underlying processes (e.g., the automatic activation of attitudes), but to the specific *contents* of those processes (e.g., the automatic activation of specific attitudes—rather than others—that are functionally relevant to particular fitness-relevant problems). The result is a set of hypotheses that are often more highly specific and nuanced than those deduced from other conceptual perspectives.

IMPORTANT ASSUMPTIONS AND CONCEPTUAL TOOLS

Some individual organisms have characteristics that enable them, compared to other individuals, to more successfully exploit the prospects and avoid the perils presented by their local ecologies. As a consequence, these organisms are more successful at transmitting their genes into future generations. Over many generations of differential reproductive success, this process—*natural selection*—produces

populations possessing those characteristics that previously conferred relative reproductive fitness (Darwin, 1871). Natural selection applies to all living species, including humans, and has shaped the ways contemporary humans think about and interact within their social worlds. In this section, we highlight some key evolutionary concepts and their implications for understanding human social psychology.

Reproductive Fitness Is the Coin of the Realm

People are purpose-driven. They have goals, and their actions can be understood as attempts, conscious or not, to achieve these goals. Open nearly any contemporary social psychology journal and you will read about how people's thoughts, feelings, and behavior are driven by the goals to get along with others, conserve mental resources, maintain internal consistency, enhance self-esteem, or satisfy some other need or motive or goal.

Evolutionary approaches also begin with the tacit assumption that social behavior ultimately serves some function. The ultimate function of behavior is reproduction—the perpetuation of genes into subsequent generations. Evolutionary perspectives on psychological processes consider the implications that those processes—and the behaviors they produce—have for reproductive fitness.

This does not mean that reproductive fitness is a conscious goal. Reproductive fitness is not usually a psychological goal state at all (conscious or nonconscious). At an evolutionary level of analysis, behavior is functional not in the sense of being purpose-driven, but in the sense that these behaviors (and the psychological mechanisms that produce them) had positive implications for reproductive fitness in the past. This evolutionary understanding of “function” is entirely compatible with psychological approaches to function emphasizing motives, needs, and goals. Behaviors that are functional in an evolutionary sense (because they conferred reproductive fitness in ancestral environments) are typically driven—consciously or unconsciously—by more proximate goals (of the sort typically articulated by social psychological theories).

Reproduction may be the ultimate function of behavior, but this does not mean that each episode of behavior effectively promotes reproductive success. Evolutionary adaptations are not perfect (as we discuss more fully below), and behaviors inconsistent with reproductive fitness are inevitable. Such behaviors are often of considerable interest to evolutionary psychologists. Just as the study of cognitive errors and biases can provide insights into the proximate goals that underlie human cognition, the study of fitness-inconsistent behaviors may provide clues to the evolution of the psychological mechanisms that produce these puzzling

behaviors (e.g., Campero-Ciani, Corna, & Capiluppi, 2004; Kenrick, Keefe, Bryan, Barr, & Brown, 1995).

To assert that psychological mechanisms were designed by evolution to promote reproductive fitness is sometimes misunderstood to imply that all behavior is ultimately about sex. It's not. Successful reproduction typically requires solutions to a large number of problems (e.g., self-protection, acquisition of resources) and sub-problems that have nothing directly to do with copulation, *per se*. Any psychological process that bears on the solution to this broader set of problems may have enormous consequences for reproductive fitness.

Indeed, even individuals who never reproduce directly may nonetheless increase their reproductive fitness through a variety of indirect means. Reproductive fitness is defined not by the mere production of offspring but by the successful reproduction of genes. Actions that have implications for the survival and reproduction of close genetic relatives therefore have indirect implications for one's own reproductive fitness (the concept of *inclusive fitness*; Hamilton, 1964). Under predictable conditions, for instance, some birds actually fare better by helping their siblings raise a clutch than by mating on their own (Trivers, 1985). People may also enhance their own reproductive fitness by facilitating the survival and reproduction of close kin (Burnstein, Crandall, & Kitayama, 1994; Faulkner & Schaller, 2007; Hrdy, 1999). Consequently, evolutionary processes apply not only to the small set of behaviors bearing directly on sex and mating, but to all of human social cognition and behavior.

Adaptations Solved Problems

Adaptations are features of an organism that were naturally selected because they enhanced the reproductive fitness of its predecessors in ancestral environments. Adaptations solved recurring problems. Some solved problems related to movement (e.g., wings, legs); some solved problems related to the acquisition of nutrients (e.g., the giraffe's long neck, digestive enzymes in saliva). In this chapter, we focus on (a) adaptive problems defined by the recurring threats and opportunities presented by human *social* ecologies, and (b) the cognitive, emotional, and behavioral mechanisms that evolved to help ancestral humans solve them.

What kinds of recurring problems did early humans face? There is considerable overlap in the various answers that have been offered to that question (e.g., Bugental, 2000; Kenrick, Li, & Butner, 2003). Like most animals, humans must solve problems of self-protection (from non-human predators and human rivals), disease avoidance (including that posed by human-human pathogen transmission), and mate attraction. Like other animals that invest heavily

in offspring, humans must also solve problems related to child rearing. Like the (relatively few) mammals that include long-term pair-bonding as a predominant mating strategy, humans must solve problems related to mate retention. And like other social animals, humans must solve the (sometimes competing) problems of coalitional cooperation, exchange of resources, and status-seeking.

These broad classes of problems can each be divided into hierarchically linked sub-problems. For instance, to solve the problem of successful social exchange, individuals must solve sub-problems that include identification of individuals with traits that facilitate or hinder successful exchange, detection of actual acts of non-reciprocation, and the discouragement of such acts (e.g., Cosmides & Tooby, 2005; Cottrell, Neuberg, & Li, 2007; Fehr, Fischbacher, & Gächter, 2002). To solve the problem of mate selection, individuals must also solve a myriad of sub-problems, including the ability to discriminate between individuals according to their fertility, parental potential, genetic quality, and degree of kinship (e.g., Gangestad & Simpson, 2000; Kenrick & Keefe, 1992; Lieberman, Tooby, & Cosmides, 2007). Most adaptations are designed to solve these kinds of specific sub-problems.

Adaptations Are Functionally Specialized and Domain-Specific

An assumption underlying most evolutionary approaches is that natural selection results in a large number of relatively specialized, problem-specific psychological mechanisms. For instance, rather than having a single all-purpose “survival system” that addresses the problems of extracting nutrients from food and moving those nutrients throughout the body, people possess functionally distinct (albeit linked) digestive, circulatory, and respiratory systems. These domain-specific systems are themselves made up of functionally distinct structures that perform necessary sub-tasks (e.g., the digestive system’s salivary glands, stomach, and intestines). Similarly, rather than having a single “social survival system” that addresses all fitness-relevant problems presented by social ecologies (problems of status attainment, coalition formation, child-rearing, and the like), the human psyche is made up of functionally distinct (albeit linked) cognitive, emotional, and behavioral mechanisms—each adapted to a set of specific fitness-relevant challenges.

This view—that adaptations are functionally specialized—contrasts with explanatory perspectives invoking “domain-general” principles, such as some general desire to seek reward. Domain-general principles may appeal to parsimony, but an abundance of research on human cognition raises serious problems for these domain-general approaches. Just as there are multiple, functionally distinct visual systems, learning systems, and memory systems (e.g., Kanwisher,

McDermott, & Chun, 1997; Klein, Cosmides, Tooby, & Chance, 2002; Moore, 2004, Sherry & Schacter, 1987), it is becoming increasingly clear that there are also multiple, functionally-distinct systems for responding to the multiple, conceptually distinct prospects and perils of social life (Ackerman & Kenrick, 2008; Barrett & Kurzban, 2006; Kurzban & Aktipis, 2007; Pinker, 1997; Schaller, Park, & Kenrick, 2007; Tooby & Cosmides, 1992).

Many psychologists traditionally presumed that the mind emerges free of content and constraint—a “blank slate” to be written upon by experience and learning (Pinker, 2003). On the contrary, functionally specialized systems are domain-specific: They possess some amount of content that directs and constrains which information in the world “counts” as relevant input information and which outcomes potentially serve as solutions to the adaptive problem confronted. Research on associative learning illustrates this key point. Only certain stimuli get conditioned to nausea, and the particulars depend on the organism’s evolutionary history and typical ecology. Rats, which have poor vision and rely on taste and smell to find food at night, condition nausea to novel tastes but not to novel visual stimuli (Garcia & Koelling, 1966). In contrast, quail, which have excellent vision and rely on visual cues in food choice, condition nausea easily to visual cues but not to taste (Wilcoxon, Dragoin, & Kral, 1971). The same principles apply to people. A fearful response is more easily conditioned to objects that posed a significant threat throughout humans’ evolutionary past (e.g., snakes) than to objects that cause many more deaths in current-day environments (e.g., electrical outlets and automobiles) but that did not exist in ancestral ecologies (Öhman & Mineka, 2001). Similarly, people are faster and more accurate at detecting objects that posed threats in ancestral environments than at detecting objects that pose threats only in modern environments (New, Cosmides, & Tooby, 2007).

Evidence of evolved functional specificity has become increasingly common within the social psychological literature. We will review a wide range of such findings.

Adaptations Are Imperfect in Evolutionarily Sensible Ways

Biases, errors, and poor decisions are sometimes, naively, taken as evidence that the psychological processes underlying them could not have evolved, because evolution presumably would have created a better, smarter, less error-prone system. This is not so. Evolved psychological mechanisms are inevitably imperfect, for several reasons.

First, biological evolution is slow. Changes in gene frequencies within populations occur more slowly than changes in the environments inhabited by the organisms that house those genes. This is particularly the case for

humans, who reproduce slowly but alter their environments rapidly and significantly. Recall that, to the extent that any psychological mechanism has evolved, it did so as an adaptation to selection pressures that existed over long periods of time in ancestral environments (sometimes known as the *environment of evolutionary adaptedness*, or *EEA* for short; Bowlby, 1969). Some of these historical environments had similar features to the ones humans currently reside in (e.g., families, neighbors, threats from outgroups). However, the EEA for other adaptations may differ substantially from contemporary human ecologies. For example, the small, kin-based coalitional groups that characterized much of human history are different in many respects from the large, urban, ethnically heterogeneous societies within which many humans live today. To the extent there are differences between ancestral and contemporary environments, psychological *adaptations* (to ancestral social ecologies) may not currently be *adaptive* (in contemporary social ecologies).

Second, given the way natural selection works, it is unlikely that any evolutionary adaptation will operate perfectly within any environment, even within the specific environment in which it was selected. Natural selection is not a creative process, per se; it does not generate new, ideal solutions to fitness-relevant problems. Instead, it is a winnowing process; it selectively eliminates from populations those genes (and their phenotypic expressions) that, compared to other genes (and their expressions), are less reproductively fit. What evolves within a population is rarely as perfect as what might have been created by a forward-thinking, omniscient intelligent designer. Existing adaptations are simply relatively less flawed than the biologically constrained set of alternatives from which blind processes of natural selection had to “choose.”

Third, evolved psychological mechanisms were selected because, multiplied across instances and across individuals, they enhanced reproductive fitness more than did alternative mechanisms. One might usefully think of evolved psychological mechanisms as if-then *decision rules*, or *stimulus-response heuristics*, in which specific sets of psychological inputs (e.g., perceptions, inferences) trigger specific sets of psychological outputs (e.g., cognitive, emotional, or behavioral responses). Consider, for instance, the tendency for the perception of an angry face to trigger an avoidant response. Averaged across many instances, this stimulus-response heuristic likely led to better fitness outcomes than did alternative stimulus-response associations. Of course, in some specific instances, this heuristic may be counterproductive (when, for example, the apparently angry person doesn't actually pose a threat).

The types of errors and biases generated by evolved, stimulus-response psychological mechanisms tend to be

fitness-seeking (Gigerenzer, Todd, & the ABC Research Group, 1999; Haselton & Nettle, 2006). To respond to some stimulus in an adaptive fashion (e.g., to avoid a dangerous rival or approach a promising mate), one must first identify that stimulus (i.e., categorize a person as a dangerous rival or a promising mate). Such categorizations depend on imperfect, often superficial, cues, creating a classic *signal-detection problem*. At the simplest level of analysis, two distinct kinds of errors may occur: A false positive error (e.g., classifying a benign individual as dangerous) or a false negative error (e.g., classifying a truly dangerous person as benign). Because cues are imperfectly diagnostic, errors are inevitable, and any systematic attempt to minimize the likelihood of false positive errors inevitably increases the likelihood of false negative errors, and vice versa. How are these signal detection dilemmas resolved? The logic of reproductive fitness implies that psychological mechanisms will be biased in favor of whichever error (either false positive or false negative) leads, in the long run, to less deleterious outcomes for reproductive fitness.

This fundamental principle has a nickname: The *smoke detector principle* (Nesse, 2005). A smoke detector (the kind that homeowners install in their ceilings) may be calibrated to minimize (irritating) false positives, or to minimize (fatal) false negatives. Not surprisingly, they are deliberately (and wisely) calibrated to minimize the more costly false negative error, which inevitably results in the occasional irritating false positive. Analogously, natural selection has shaped perceptual, cognitive, and emotional systems to minimize the likelihood of making whichever form of error is most harmful to reproductive fitness. Consequently, these mechanisms have predictable biases, and regularly favor the alternative, less costly, form of error.

This fundamental logical insight underlies many evolutionary analyses of social psychological phenomena (e.g., Haselton & Nettle, 2006; Kurzban & Leary, 2001; Park, Schaller, & Van Vugt, 2008; Schaller & Duncan, 2007). One prominent example is *error management theory* (Haselton & Nettle, 2006). This theory helps explain why men misperceive women to be more sexually available than they actually are, and why women show a rather different bias in their perceptions of men (Haselton & Buss, 2000; Maner et al., 2005). Analyses of inference errors people regularly make (and do not make) can be an invaluable means of testing theories and hypotheses. We discuss many such biases below.

THE AFFORDANCE MANAGEMENT SYSTEM

The specialized adaptations making up the human psyche were designed by natural selection to manage the threats and

opportunities afforded by the ecologies early humans and their ancestors inhabited. These threats and opportunities can collectively be called “affordances” (Gibson, 1979; McArthur & Baron, 1983; Zebrowitz & Montepare, 2006). This set of coordinated adaptations can therefore be considered an *affordance management system*. The simple template depicted in Figure 21.1 characterizes the basic contours of this system.

To illustrate, imagine walking alone down a dark, deserted street in an unfamiliar city. Suddenly you hear footsteps approaching rapidly from behind. Not knowing the source of the sounds, you may categorize it as a threat to your physical safety. This perception of threat rapidly initiates a suite of coordinated, self-protective responses—sensory vigilance toward the assumed threat, a rush of adrenaline, implicit activation of threat-relevant semantic concepts (“Danger!”), increased blood flow to large muscles in your legs and arms (and away from your digestive system), and a strong behavioral inclination to escape—all of which facilitate the likelihood that you flee. This example illustrates several key principles that characterize the affordance management system.

Cues Connote Affordances

Effective affordance management requires psychological mechanisms that translate perceptual stimuli (e.g., sounds, smells, morphological features) into fitness-relevant categorical inferences (e.g., threat to physical safety, mating opportunity, etc.). Many research programs in evolutionary psychology attempt to articulate specific cues likely to imply specific affordances. Specific characteristics of other people heuristically imply infectious disease, for instance (Schaller & Duncan, 2007). Other specific cues heuristically

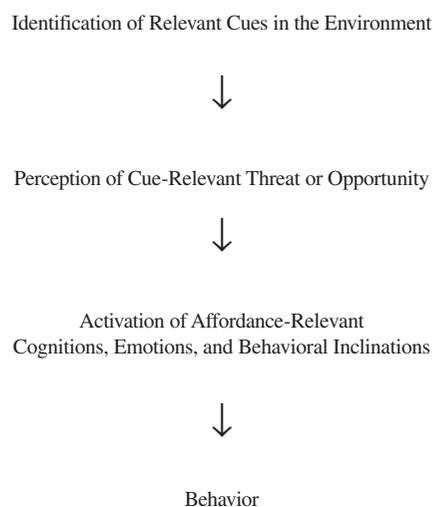


Figure 21.1 Affordance Management System.

connote kinship (Park et al., 2008). Still other cues heuristically connote fertility (Kenrick & Keefe, 1992). And so on. The implicit message, of course, is that in order to predict an individual’s response to any social situation, one must attend not only to the superficial details of that situation but also to the fitness-relevant threats or opportunities that those details imply.

Thinking (and Feeling) Is for Doing

Perceptual, cognitive, and affective processes are integral to the affordance management system. But the eventual outcome is behavior—doing something. This emphasizes the fundamental axiom that thinking is for doing (S. T. Fiske, 1992). Feeling is for doing, too. These premises are particularly salient within the evolutionary approach, because cognitions and emotions cannot, by themselves, have any direct influence on reproductive fitness; natural selection can only operate on actual motor behavior (or the lack of it). Consequently, to understand why people think and feel different things in different situations, it is important to consider the implications of thought and feeling for the actual behavior likely to result.

The Focus Is on Function

The linkages between processes—cue perception, affordance categorization, response suites, and behavior—are *functional* linkages. They are coordinated to facilitate solving the problem implied by the initially perceived cue. For instance, although you *could* respond to the perception of approaching footsteps by contemplating a snack and licking your lips, you are unlikely to do so—because food fantasizing and lip licking were unlikely to have served fitness under analogous circumstances in ancestral worlds. Inherent to an evolutionary approach, and to the idea of an affordance management system, is the assumption that human social cognition and behavior is *motivated* social cognition and behavior.

Content Matters

In light of the functional nature of psychological mechanisms, an evolutionary approach implies that cognitive, affective, and behavioral systems must not only make gross distinctions between things that are good and bad (or requiring approach versus avoidance), but must also make much finer qualitative distinctions (Kenrick & Shiota, 2008). Many events may be evaluative unpleasant—a rapidly approaching stranger, the death of a child, a thief escaping with your bag of groceries—but they are unpleasant in fundamentally different ways, with different

functional implications. Cognitive, affective, and behavioral responses must be calibrated to differentiate among them in textured ways so as to produce focused, functionally specific solutions. Thus, when evolutionary logic is applied to social psychological phenomena, it typically yields hypotheses not only about underlying processes but also, crucially, about *content*, too—and in ways that are often extraordinarily precise about the *particular* affective, cognitive, and behavioral responses one would expect in different social situations.

Context Matters, Too

For most psychological adaptations, there is no hardwired highway that necessarily links some specific set of perceptual cues to some specific threat or opportunity inference, or that necessarily links that threat or opportunity inference to some specific feeling, cognition, and/or behavioral response. These links are probabilistic, and their strength tends to be contingent upon additional information gleaned from the immediate environment. Sudden noises produce more exaggerated fear responses among people who are in the dark (Grillon, Pellowski, Merikangas, & Davis, 1997), and snakes are more readily detected by people who feel anxious (Öhman, Flykt, & Esteves, 2001). Similarly, inferences about, and adaptive reactions to, social stimuli are sensitive to inputs from both chronic and ephemeral elements of the perceptual context. As seen throughout this chapter, evolutionary approaches provide logical tools that allow one to derive novel predictions about how specific features of the immediate social situation and specific perceiver dispositions (e.g., current goals, traits, beliefs) facilitate or attenuate specific cognitive, affective, and behavioral phenomena. This appreciation for moderation effects, of course, is consistent with social psychology's traditional theme of person-situation interactionism.

This Applies to All of Social Psychology

The affordance management system provides a broad conceptual template that can be applied across all of social psychology. In the following sections, we summarize a variety of different ways in which evolutionary thinking has been applied productively to different social psychological topic areas. The vast majority of this work—both theoretical and empirical—fits the template of the affordance management system. Table 21.1 provides a complementary summary, highlighting specific examples that illustrate the functional linkages between specific adaptive problems, the cues that reveal them, the functional responses to them, and the contextual variables that moderate the extent to which these adaptive mechanisms are engaged.

EVOLUTIONARY PERSPECTIVES ON SOCIAL PSYCHOLOGICAL PHENOMENA

The landscape of social psychology is broad. Social psychological inquiry focuses on highly automatized perceptual and memory processes as well as on highly deliberative forms of actual interpersonal behavior. It includes the study of individuals, dyads, groups, and entire cultures. Evolutionary theorizing has been applied productively across this entire scholarly landscape. We cannot review it all here. Instead, in the following sections, we provide a selective review to illustrate both the breadth and depth of this research and to illustrate the generative utility that an evolutionary approach brings to the study of social psychology.

Ultrasociality, Belongingness, and Self-Esteem

In many species, including humans, reproductive fitness is enhanced by proximity to, and alliances with, conspecifics. Compared to those who pursued a solitary lifestyle, significant fitness benefits accrued to those who lived in cooperative, highly interdependent groups (e.g., Brewer & Caporael, 2006; Leakey & Lewin, 1977). Given these fitness benefits associated with *ultrasociality* (Campbell, 1982), one would expect humans to be highly motivated to be accepted by their fellow group members—to experience a profound *need to belong* (Baumeister & Leary, 1995; Leary, this volume).

When their bodies require nutrition, people experience hunger, which motivates them to find food and eat; when people encounter threatening footsteps on the dark city street, they feel fear, which motivates them to find a safe haven. Self-esteem may serve a similar signaling function for the belongingness motive, operating as a *sociometer* that informs people whether they are falling below the threshold for social inclusion (Leary & Baumeister, 2000). On this account, high self-esteem indicates successful social inclusion; lowered self-esteem signals actual or impending social exclusion. Indeed, variation in self-esteem is linked with the degree to which one feels included and/or accepted by others (Leary, Tambor, Terdal, & Downs, 1995; Leary, Haupt, Strausser, & Chokel, 1998; Murray, Griffin, Rose, & Bellavia, 2003). Moreover, neuroimaging (fMRI) results indicate that the psychological pain of social exclusion is produced by some of the same physiological mechanisms involved in the experience of physical pain (Eisenberger & Lieberman, 2004). This finding is consistent with speculation that neural mechanisms that once served simply to indicate the threat of physical injury may have undergone additional adaptation in response to the ultrasocial landscape of human (and pre-human) populations, and thus now function to signal the threat of social exclusion as well (MacDonald & Leary, 2005).

Table 21.1 Representative Illustrations of Functional Linkages Between Specific Fundamental Social Motives, Social Affordances (Opportunities and Threats) Germane to Them, Cues that Reveal These Affordances, Functional Psychological and Behavioral Responses to Them, and the Types of Contextual Variables that Moderate the Extent to Which These Adaptive Mechanisms are Engaged.

Motive	Relevant Affordances	Relevant Heuristic Cues	Functional Response “Syndromes”	Functionally Relevant Moderating Factors
To self-protect	<p><i>Opportunities:</i> Safety provided by others.</p> <p><i>Threats:</i> Violence from outgroup members; violence from ingroup members.</p>	<p>Presence of familiar, similar others.</p> <p>Presence of unfamiliar, dissimilar, angry mates.</p>	<p>Perceive such individuals as safe; feel friendly toward them; become braver; smile; approach; offer cooperation.</p> <p>Err on side of perceiving such individuals as dangerous; experience fear; attempt to escape or join similar, familiar others to defend.</p>	<p>Located in familiar surroundings; many similar, familiar others nearby; high dispositional trust in others.</p> <p>Located in unfamiliar surroundings; darkness; past experience of being physically harmed; being female or of small stature.</p>
To attract mates	<p><i>Opportunities:</i> Availability of desirable, opposite-sex others.</p> <p><i>Threats:</i> Presence of desirable, same-sex others.</p>	<p>Opposite-sex other’s age, physical attractiveness, status, bodily symmetry, morphological abnormalities, scent, nonverbal (flirting or rejecting) behaviors.</p> <p>Same-sex other’s age, status, symmetry, masculinity/femininity, flirting behaviors.</p>	<p>Subjective lust; increase in testosterone; over-interpretation of sexual interest by men; conservative bias in evaluating signs of men’s commitment by women.</p> <p>Bias toward attending to and interpreting attractive and high status same-sex individuals as competitors; denigrating same-sex competitors; costly signaling to potential mates.</p>	<p>Relative mate value; age; restricted vs. unrestricted sexual strategies; current ovulatory status; histocompatibility.</p> <p>Relative mate value; male-female ratio of available mates; status-linked distribution of resources; unpredictability of resource availability.</p>
To retain mates	<p><i>Opportunities:</i> Long-term parental alliances.</p> <p><i>Threats:</i> Sexual infidelity, Mate-poaching.</p>	<p>Other’s expressions of love, intimacy, commitment; other’s and own age and apparent fertility.</p> <p>Partner’s flirtation behaviors; presence of nearby, high mate-value, opposite-sex individuals.</p>	<p>Own expressions of love, intimacy, commitment; feelings of love; enhanced attention to other’s needs; diminished concern with equity between mates; bias toward viewing mate favorably, other potential partners less favorably.</p> <p>Jealousy; mate-guarding; enhanced vigilance and memory for desirable members of other sex; aggression against mate or suspected mate-poacher.</p>	<p>Shared children; own mate value; own resources; availability of desirable alternative mates.</p> <p>Relative mate value; own resources; availability of desirable alternative mates; ovulatory status.</p>

To care for offspring	<p><i>Opportunities:</i> Enhanced reproductive fitness.</p> <p><i>Threats:</i> Especially high costs imposed by children.</p>	<p>Apparent relatedness of child; physical similarity of child.</p> <p>Apparent (un)relatedness of child; physical (dis)similarity of child; child's health; health, age, and other qualities of one's other children.</p>	<p>Vigilance to child and nearby unfamiliar others; feelings of parental love; resource provision without expectation of reciprocity.</p> <p>Enhanced attention to one's other children, or to alternative mate; withholding of resources; child abuse, infanticide.</p>	<p>Oxytocin levels; gender; number of other children of one's own, siblings, or nieces/nephews; age of child; availability of tangible resources.</p> <p>Degree of paternal uncertainty, step-parenthood; age of child; number of other children of one's own, siblings, or nieces/nephews.</p>
To form and maintain cooperative alliances	<p><i>Opportunities:</i> Share resources, receive material support, enhanced self-protection, access to mates.</p> <p><i>Threats:</i> Exposure to disease, cheating/free-riding, incompetence, excessive demands.</p>	<p>Familiarity; past acts of reciprocity, trustworthiness; other's adherence to group norms; facial characteristics signaling trustworthiness.</p> <p>Subjective "foreignness" of others; unfamiliarity of other; other's acts of cheating, norm violation.</p>	<p>Feelings of trust and respect; commitment to other; willingness to share, reciprocate; work with others to achieve group goals; adherence to group norms.</p> <p>Hypersensitivity to unfair exchanges, disease-linked cues, or rejection cues in others; sensitivity to existing social norms; feelings of moral disgust, fear, and anger; stigmatization and other forms of informal and formal social control; tit-for-tat interactional strategies.</p>	<p>Coalitional identity or investment; gender; "collectivistic" cultural context and proximity to kin networks; dispositional trust in others; need for belongingness, social approval.</p> <p>Own inclinations to cheat; personal vulnerability to disease; location (central vs. peripheral) within group network.</p>
To seek status	<p><i>Opportunities:</i> Status-enhancing alliances, improved access to resources and (for males) mating opportunities.</p> <p><i>Threats:</i> Loss of status, social regard, status-linked resources and mates.</p>	<p>Nonverbal status-conferring displays (e.g., eye-contact, bodily orientation, etc.) by others; shifts in exchange rules; others willingness to invest in oneself.</p> <p>Nonverbal dominance displays by others; shifts in exchange rules; lack of apparent respect from others.</p>	<p>Public displays of resources, abilities (costly signaling), dominance, self-efficacy, inclinations toward leadership; sensitivity to cues implying one's own position in hierarchy and to presence of others with similar concerns.</p> <p>Embarrassment, shame; vigilance toward those higher in status hierarchy and toward those on their way up; join with related others of similar status to try to overthrow current high status; denigrate others.</p>	<p>Current status level; presence of potential familial coalitional partners; presence of desirable (female) mates.</p> <p>Current status level; public vs. private nature of interactional context; optimism, self-efficacy.</p>

From the evolutionary perspective, thinking and feeling are for doing: It is not enough to feel the sting of rejection, but one must also do something to redress the deficit. One strategy is to actively avoid and punish those doing the rejecting, and the literature on social exclusion indicates that the aversive state of exclusion precipitates various kinds of antisocial behavior (e.g., Leary, Twenge, & Quinlivan, 2006; Twenge, Baumeister, DeWall, Ciarocco, & Bartels, 2007). Strategies for re-establishing social connections, however, are likely to solve the problem of exclusion more effectively than aggression, which can trigger increased rejection. Consistent with this reconnection hypothesis, when people are threatened with social exclusion, they tend to express greater interest in making new friends, increase their desire to work cooperatively with others, and form more positive first impressions of new potential interaction partners (Maner, DeWall, Baumeister, & Schaller, 2007).

Although the above research is consistent with certain evolutionary analyses, the kinds of nuanced hypotheses we highlighted in our opening paragraph haven't yet emerged within this arena. For instance, it seems likely that the need to belong may currently be conceptualized too broadly; other evolutionary views would suggest, instead, greater modularity—that there are distinct sets of problems and opportunities linked to relationships with kin, friends, and one's broader coalition (e.g., Ackerman, Kenrick, & Schaller, 2007), and that these distinct needs would be attuned to different social cues, elicit different cognitive and behavioral responses, lead to different behavioral strategies, and be modulated by different person variables and ecological circumstances. Similarly, recent evidence suggests that self-esteem may be sensitive not only to social acceptance and rejection, but also to other cues as well, depending on sex and prominent current goals (e.g., appearance, status, others' assessments of one's mate value, etc.; Anthony, Holmes, & Wood, 2007; Johnson, Burk, & Kirkpatrick, 2007; Penke & Denissen, 2008).

Social Attention, Perception, and Person Memory

From an evolutionary perspective, it makes little sense to cognitively process just any information, but to selectively process information that was highly relevant to ancestral reproductive fitness (Kenrick, 1994). Individuals quick to attend to and process rapidly approaching angry men, for example, would have likely outreproduced their inattentive and slower-witted neighbors.

Simply put, cognitive processing should be selective, and selective in particular ways. The mind should, as a default, expend its energy processing the kinds of information that implied threats and opportunities in ancestral social environments—for instance, angry male faces,

physically attractive members of the opposite sex, and crying children. Moreover, the informational grist selected by the cognitive mill should be sensitive to whatever evolutionarily relevant goal states are especially salient.

Consider the benefits of being beautiful, and its implications for visual attention. Physically attractive people are liked more, paid more, and are assumed to possess many desirable characteristics (Feingold, 1992). Evolutionary analyses suggest, however, that—depending on the context—attractive individuals may afford either opportunities *or* threats to reproductive fitness; this, in turn, has implications for the prediction of visual attention to (or away from) physically attractive individuals. Some of these implications are demonstrated in a set of highly nuanced findings from a series of studies by Maner, Gailliot, Rouby, and Miller (2007). Attractive opposite-sex targets were especially likely to hold attention of perceivers for whom the fitness-relevant problem of acquiring a mate was highly salient and who were also inclined toward an “unrestricted” (e.g., relatively promiscuous) mating style. No such attentional advantage was directed at opposite-sex targets in general, nor did attractive opposite-sex targets hold the attention of individuals with a more “restricted” approach to mate-seeking. What about attention to attractive *same-sex* targets? They were especially likely to hold the attention of perceivers for whom the fitness-relevant goal of retaining current mates was highly salient and who were also dispositionally inclined to employ a zealously protective and vigilant strategy of guarding mates from same-sex rivals. No such attentional advantage was directed at either same-sex or attractive targets in general, nor did attractive same-sex targets hold the attention of individuals less inclined toward mate-guarding. This pattern of textured findings illustrate that social attentional processes are attuned to the affordances implied by the perceptual environment, and that these affordances are defined jointly by the fitness-relevant goals of perceivers and the fitness-relevant features of the persons perceived.

This is just one example. There is a burgeoning body of evolutionarily informed empirical research documenting similar forms of process specificity in individuals' attention to their social environment (e.g., Becker, Kenrick, Guerin, & Maner, 2005; Duncan, Park, Faulkner, Schaller, Neuberg, & Kenrick, 2007; Fox, Russo, Bowles, & Dutton, 1991; Maner, DeWall, & Gailliot, 2008; Öhman & Mineka, 2001).

Similarly nuanced findings emerge in research that focuses not on social attention, per se, but on the detection of specific features in others' faces. Recall that an adaptive behavioral response to social exclusion is behavioral reconnection with potentially rewarding others (Maner et al., 2007). It follows that the experience of social exclusion should enhance individuals' ability to detect facial

expressions that signal affiliative potential and to accurately discriminate these expressions from other facial expressions. This is indeed the case (Pickett & Gardner, 2005). For example, socially excluded individuals show a substantial increase in the ability to discriminate between real smiles and fake smiles (Bernstein, Young, Brown, Sacco, & Claypool, 2008). Another example reflects the fact that adult males and females have historically differed in their capacity to do physical harm, and in their tendencies toward aggression versus succorance. One implication of this sex difference—that men are more likely to afford aggression, women more likely to afford helpfulness—is that there may be an adaptive bias to detect anger in the faces of men and more affiliative expressions in the faces of women. Indeed, perceivers more quickly and accurately identify male faces as *angry*, but female faces as *happy*; conversely, angry expressions facilitate the identification of faces as male, whereas happy expressions facilitate identification of faces as female. Additional results reveal that this phenomenon cannot be readily attributed to learned stereotypes about men and women: When androgynous computer-generated faces are dressed in male versus female clothing, for example, they are perceived as stereotypically masculine or feminine, but not as correspondingly angry or happy (Becker, Kenrick, Neuberg, Blackwell, & Smith, 2007).

Content specificity of this sort emerges not only in perceivers' perception of actual information on others' faces, but also in the *mis*perception of information that isn't actually there. White perceivers for whom self-protection goals (but not other goals) are highly salient erroneously "see" anger (but not other negative emotions) in the neutrally expressive faces of Black men, but not in the neutrally expressive faces of White men or women, or in the faces of Black women (Maner et al., 2005). These results fit with speculation—common to many evolutionary analyses of intergroup relations (e.g., Navarrete, Olsson, Ho, Mendes, Thomsen, & Sidanius, in press; Schaller & Neuberg, 2008)—that unexpected interactions with outgroup males afforded a particularly potent threat to reproductive fitness.

The evolutionary importance of faces heuristically connoting threat also has implications for recognition memory. Consider the robust "outgroup homogeneity bias" in recognition memory: White perceivers, for example, are much more accurate at recognizing previously encountered White faces than Black faces (e.g., Anthony, Copper, & Mullen, 1992; Chance & Goldstein, 1996). An evolutionary analysis of this phenomenon suggests that the effect occurs because limited processing resources are selectively allocated to the faces of individuals who have clear fitness implications for perceivers. Since most fitness-relevant interactions have historically occurred within coalitional groups, this implies

a processing advantage for ingroup faces. However, when a facial expression implies imminent threat—as is implied by an angry facial expression—it is likely to attract processing resources regardless of ingroup/outgroup status. In fact, given the historically greater danger associated with intergroup (rather than intragroup) interactions, angry outgroup faces may be especially likely to attract the kind of processing resources that allow accurate identification later on. This implies that when White perceivers encounter angry faces (both White and Black), the usual outgroup homogeneity effect in recognition memory should be eliminated—and even reversed. It is (Ackerman et al., 2006).

Social Inference and Impression Formation

To effectively avoid a social threat or avail oneself of a reproductive opportunity, it is advantageous—and sometimes essential—to identify that threat or opportunity quickly. Just as there are evolutionary advantages associated with fast and frugal decision-making heuristics more broadly (e.g., Gigerenzer et al., 1999), there is also a need for speed in social inference. Indeed, people form trait impressions quickly, spontaneously, and with minimal cognitive effort (Carlston & Skowronski, 2005; Gilbert & Malone, 1995; Newman & Uleman, 1989).

Speedy and spontaneous impressions of others can be adaptive even if they are imperfect, as long as they are generally diagnostic of actual behavior. In fact, first impressions are often remarkably accurate given the impoverished information they are based upon (Ambady, Bernieri, & Richeson, 2000; Vanneste, Verplaetse, Van Hiel, & Braeckman, 2007; Yamagishi, Tanida, Mashima, Shimoma, & Kanazawa, 2003). For example, people are able to accurately estimate the upper-body strength of men based solely on facial photographs (Sell et al., 2009), and just 50 milliseconds are sufficient for perceivers to infer, at levels exceeding chance, a man's sexual orientation (Rule & Ambady, 2008). Such findings are consistent with speculation regarding an evolved *personality judgment instinct* (Haselton & Funder, 2006).

Not all trait impressions are equally relevant to reproductive fitness, however. Trait that best convey whether someone represents a threat or an opportunity should be most central to impression formation. The embodiment of a threat or opportunity depends upon an individual's intentions (e.g., whether someone intends harm or intends to share reproductively useful resources) and on that individual's skill at carrying out those intentions (greater skill implies greater threat and greater opportunity, depending on whether the person's intentions are nasty or nice.) Consistent with this functional analysis (Fiske, Cuddy, & Glick, 2007; Schaller, 2008), impressions of individuals (and of the social groups to which they belong) are consistently located

within a two-dimensional space anchored by the broad evaluative dimensions of interpersonal warmth and competence (Fiske et al., 2007; Judd, James-Hawkins, Yzerbyt, & Kashima, 2005; Rosenberg, Nelson, & Vivekananthan, 1968). The warmth dimension—particularly as represented by traits that emphasize trustworthiness—is especially central to impression formation (Cottrell et al., 2007; Kelley, 1950; Oosterhof & Todorov, 2008; Peeters & Czapinski, 1990).

Many initial trait impressions are inspired by superficial characteristics, and recent evolutionarily analyses have yielded empirical findings linking specific superficial cues to specific impressions and identifying the specific conditions under which these linkages are especially strong. One such line of research focuses on psychological defenses against disease transmission and their implications for impression formation. Because pathogenic diseases pose powerful fitness costs, perceivers should be sensitive to cues signaling the possibility that another person carries an infectious disease. Many of these cues are morphological anomalies. In line with the smoke detector principle, perceivers often make overinclusive inference errors, responding inferentially to many truly healthy, but superficially anomalous-looking, individuals as though they were sick. For instance, even specific physical anomalies not diagnostic of pathogen transmission—including accident-caused facial disfigurement, physical disability, and obesity—spontaneously trigger disease-connoting implicit impressions, especially among perceivers who feel specifically vulnerable to disease transmission (Park, Faulkner, & Schaller, 2003; Park, Schaller, & Crandall, 2007; Schaller & Duncan, 2007). In fact, it has been suggested that physical unattractiveness of any kind may serve as a crude heuristic cue for ill-health, and thus lead to aversive trait inferences (Zebrowitz, Fellous, Mignault, & Andreoletti, 2003).

A second illustrative line of research examines heuristic cues to kinship and the impressions these cues inspire (Park et al., 2008). Many animal species employ superficial heuristic cues such as phenotypic similarity to distinguish kin from non-kin (Hepper, 1991; Rendall, 2004). Although humans have more recently evolved additional mechanisms that improve identification of close kin (based on capacities for language and symbolic thought), human inferences also appear to be implicitly influenced by evolutionarily ancient heuristic cue-based mechanisms. One consequence is that people respond to phenotypically similar individuals in a more kin-like way, even when those individuals are total strangers. For instance, perceived facial similarity leads to impressions connoting greater liking and trustworthiness, and also—in contrast to alternative explanations suggesting that similarity implies positive evaluations of all kinds—to *reduced* sexual attractiveness (DeBruine, 2002, 2005; see

also Ackerman, Kenrick, & Schaller, 2007). Moreover, perceived attitude similarity implicitly activates semantic cognitions connoting kinship (Park & Schaller, 2005). This latter finding suggests that evolved kin-detection mechanisms may help account for the classic similarity-liking effect (Byrne et al., 1971)—an interpretation bolstered by evidence that the similarity-liking effect emerges more strongly when the similar attitudes are those that are highly heritable (Tesser, 1993), and thus more diagnostic of actual kinship.

Prosocial Behavior

Why do people act in ways that benefit others? From an evolutionary perspective, there are many answers to this question; we explore a few of them here.

Kinship

Kinship provides one foundation for understanding the evolution of prosocial behavior, and for predicting variability in prosocial behavior across different circumstances. The logic of inclusive fitness (Hamilton, 1964) implies that, to the extent another individual is a close genetic relative, any action that directly enhances that individual's reproductive fitness indirectly enhances one's own fitness as well. This forms the basis of a process through which a particular form of altruism—nepotism—may have evolved. Evidence of nepotistic altruism is found widely across the animal kingdom (Greenberg, 1979; Holmes & Sherman, 1983; Suomi, 1982), including humans. Compared with dizygotic twins, for instance, monozygotic (identical) twins are more cooperative in mixed-motive games (Segal & Hershberger, 1999). In other contexts, too, people are more inclined to help genetically closer kin, and this tendency is exaggerated under conditions that have more direct implications for the kin member's actual reproductive fitness (Burnstein, Crandall, & Kitayama, 1994; Neyer & Lang, 2003; Stewart-Williams, 2008).

The evolved psychology of kinship also has important implications for prosocial behavior among total strangers. As with many other animals, ancestral humans were often unable to directly identify kin—one cannot “see” genes—but instead inferred kinship implicitly on the basis of superficial cues such as familiarity and similarity (Lieberman et al., 2007; Park et al., 2008). One implication of readily employing such cues is that persons may heuristically respond prosocially to individuals who appear either familiar or highly similar in some way—even when they know, rationally, that the individuals are total strangers. For instance, just as facial similarity promotes trust (DeBruine, 2002), it also promotes cooperative behavior in a public goods game (Krupp, DeBruine, & Barclay, 2008).

A variety of other cues may also heuristically imply kinship. Several different lines of evolutionary theorizing converge in suggesting that friendship may be a cue connoting kinship, and that this may especially be the case among women. Consistent with this analysis, women—but not men—behave just as benevolently toward friends as they do toward actual kin (Ackerman et al., 2007). Emotions may also serve as heuristic cues. Empathy likely evolved as part of a functional system for aiding kin in distress, and thus kinship may be implicitly connoted by the emotional experience of empathy—even when the empathy is elicited by non-kin (Hoffman, 1981; Krebs, 1987; Park et al., 2008). This suggests that the well-known relation between empathy and helping behavior among strangers may be rooted, in part, in the evolved psychology of kinship and kin-recognition.

Reciprocal Exchange

In exchange for the benefits people receive from fellow group members, they are obligated to provide benefits to them. Although some of the specific rules of social exchange vary across societies, the norm of reciprocal exchange is universal (Brown, 1991; A. Fiske, 1992). Fitness benefits for sharing emerge at both group and individual levels of analysis: By sharing resources, the individual helps other members of the group survive, and accrues credit for the future when his or her own luck may be down (Hill & Hurtado, 1989). Moreover, generous sharing enhances an individual's status within the group, and such status portends significant benefits of its own, including access to future group resources and enhanced mate value (Griskevicius et al., 2007).

From a purely economic perspective, one might expect prosocial behavior toward an unrelated individual only when a person was confident that others would, in fact, reciprocate. In fact, however, people often share resources with total strangers with whom they have no reciprocal alliances and will never interact again. Trying to explain such seemingly irrational behavior is an active domain of interdisciplinary inquiry (e.g., Henrich et al., 2005). An evolutionary perspective on social cognition helps resolve this issue. When making behavioral decisions, individuals respond not merely to rational assessments but also to heuristic cues (e.g., a sense of familiarity) that connote, imperfectly, potential reciprocity. In addition, the vast majority of interactions in ancestral environments involved coalitional group members who would, in fact, reciprocate. Therefore, following the smoke detector principle, psychological mechanisms that govern prosocial behavior between unrelated individuals may well have evolved in such a way to err on the side of assuming reciprocity (an assumption that helped maintain and promote social bonds) rather than non-reciprocity (an assumption that would have

undermined social bonds, thereby generating a broader set of costs). If so, mechanisms that evolved to promote reciprocal exchange and cooperation will be overinclusive, leading to many acts of prosocial behavior that, in reality, are unlikely to ever to be reciprocated (Burnham & Johnson, 2005; Johnson, Price, & Takezawa, 2008).

An evolutionary perspective has also recently been applied to better understand an aspect of exchange that appears puzzling from a simple economic perspective—the fact that people sometimes reject offers of help from others. Such behavior is less puzzling, however, when one realizes that offers of benefits from others often come—explicitly or implicitly—with associated costs and obligations. How the trade-offs between the benefits of receiving help versus the costs of accepting it depend importantly on the recipient's current goals and the salient aspects of the social context relevant to those goals (Ackerman & Kenrick, 2008).

Stigmatization

Any implicit trust in coalitional ingroup members (the assumption that they will reciprocate and share) has a flip side: Groups are vulnerable to the invasion of “cheaters” and “free-riders”—individuals who strategically avail themselves of others' benevolence while failing to reciprocate or otherwise hold up their end of the implied exchange relationship. There is an enormous interdisciplinary literature on this problem, and on the evolved cognitive and behavioral strategies that might help solve the problem. One line of work has direct implications for the psychology of stigmatization, indicating that there may be evolved psychological mechanisms (and complementary cultural norms) that promote *altruistic punishment*—the willingness to punish (and potentially socially exclude) free-riders, even if doing so requires the expenditure of valuable resources oneself (e.g., Fehr & Gächter, 2002; Henrich et al., 2006).

A large body of research supports the hypothesis that there are specialized cognitive adaptations that function to identify others who intentionally violate norms of social exchange (Cosmides & Tooby, 2005)—the necessary first step in the stigmatization of these individuals. More broadly, evolutionary theorizing has identified a number of different threats that individuals may pose to the successful operation of cooperative groups (e.g., inability to reciprocate, carrying of contagious disease, counter-socialization of children, challenge to accepted authority structures), and that form the basis of different forms of social stigmatization (Kurzban & Neuberg, 2005; Neuberg, Smith, & Asher, 2000). From this perspective, many acts of stigmatization and social exclusion may be viewed as altruistic acts of prosocial policing and punishment.

Aggression

Like altruistic behaviors, aggressive behaviors should be viewed as possible manifestations of conditional strategies that evolved to facilitate survival and reproduction (Campbell, 2005; Duntley, 2005). Across many animal species, aggression serves a number of fitness-relevant goals, including control over territorial boundaries, division of limited resources, and defense of offspring against predators (Scott, 1992). Evolutionary analyses of human aggression take a similar conceptual approach (Buss & Duntley, 2006; Kirkpatrick, Waugh, Valencia, & Webster, 2002). Further, because of the substantial fitness costs that often attend aggressive acts (e.g., risk of injury and retaliation), most evolutionary analyses presume people are likely to behave aggressively only when other strategies for reaching goals have failed (Dabbs & Morris, 1990; Wilson & Daly, 1985). Thus, rather than treating aggression as a single psychological construct, it is helpful to consider different fitness-relevant problems that might be solved via aggressive behavior, and to identify the multiple, domain-specific mechanisms and variables that may precipitate different forms of aggressive behavior within different social contexts.

This evolutionarily informed approach to aggression has led to a number of productive lines of research on various specific forms of aggression, such as violence against stepchildren, spousal homicide, rape, and infanticide (e.g., Daly & Wilson, 1984, 1996, 2005; Wilson & Daly, 1992; Thornhill & Thornhill, 1992). It has also led to nuanced predictions and novel empirical discoveries bearing on the specific contexts within which specific psychological variables, such as self-esteem, predict aggression (e.g., Kirkpatrick et al., 2002).

One line of inquiry has focused on male aggression as a strategy for acquiring mating opportunities. The evolutionary principle of differential parental investment implies that females, compared to males (who are required to invest relatively less in offspring), maximize fitness outcomes by exercising considerable discrimination in choosing mates. Consequently, men find themselves in the position of competing with each other for the opportunity to mate with highly selective women. Two strategies could accomplish this end. One is to display characteristics highly prized by women (e.g., traits connoting good genes, resources, status, etc.; Miller, 2000). The other strategy is to beat out the competition directly (e.g., fighting one's way to the top of the local dominance hierarchy). In both cases, the capacity for physical aggression confers reproductive fitness to men (Alcock, 1993). Indeed, there is a dramatic sex difference in physically violent behavior, and this holds across human societies and across historical time periods (Archer, 2000;

Campbell, 2005; Daly & Wilson, 1988; see Bushman & Huesmann, this volume).

If aggression provides a means of meeting this very specific reproduction-relevant goal (mating), then aggression should be facilitated or inhibited depending on the extent to which that mating goal is salient. Cross-species comparisons reveal that as species become more polygynous (with some males likely to attract no mates while others attract many), males become more violent (Buss & Duntley, 2006). Within many different species, male aggressiveness increases just before the mating season, when territories and females are being contested (Gould & Gould, 1989). Developmental analyses of human aggression reveal conceptually similar findings. Boys increase dominance displays at puberty, which is also when evidence of successful competitiveness (such as being a sports star) results in greater popularity with girls (Weisfeld, 1994). And men are most violent in their late teens and twenties, the developmental phase during which they are most vigorously competing for mates (Daly & Wilson, 1988). Once a male has attracted a long-term mate, aggression decreases (Palmer, 1993). Much of this behavioral variation is the consequence of variation in testosterone, which not only regulates male sexual activity but is also implicated in the development of muscle mass, competitiveness, status-striving, and violence (Dabbs & Dabbs, 2000; Mazur & Booth, 1998; McIntyre et al., 2006).

The link between mating motives and status concerns varies not only developmentally, but also moment to moment, depending on the immediate context. This, too, has consequences for aggressive behavior: Under specific conditions in which either status or mating motives are temporarily activated, men—but not women—show an exaggerated tendency to engage in direct physical aggression (Griskevicius, Tybur, Gangestad et al., 2009). This same research indicated that women typically responded to status or mating motives with indirect aggression, rather than having an immediate public interchange with their opponent. Furthermore, women's aggression can be triggered by resource threats, especially when these have implications for their offspring (Campbell, 1999, 2005; Griskevicius, Tybur, Gangestad et al., 2009).

Sexual Attraction and Mate Selection

Differential reproduction is at the heart of natural selection, and much research in the biological sciences focuses on the evolution of features that attract members of the opposite sex. The resulting insights have informed many studies of human sexual attraction and mate selection, and many empirical findings in this literature are difficult to

explain without the logical tools provided by an evolutionary perspective.

One body of evolutionary research has revealed the importance of bilateral symmetry to the subjective perception of physical attractiveness. In many animal species, symmetry is associated with developmental stability and reproductive success, implying that symmetry may be a useful heuristic cue connoting “good genes” (Moller & Thornhill, 1998). Individuals’ own reproductive fitness is enhanced by choosing mates with good genes (increasing the likelihood of producing healthy and reproductively fit offspring). Symmetry is subjectively attractive to humans, too: People perceive symmetrical faces to be healthier and more attractive than asymmetrical faces (Jones, Little, Penton-Voak, Tiddeman, Burt, & Perrett, 2001; Mealey, Bridgstock, & Townsend, 1999; Rhodes, Zebrowitz, Clark, Kalick, Hightower, & McKay, 2001; Thornhill & Gangestad, 1999a).

The attraction to symmetry is not limited to face perception. Bodily symmetry is also a likely indicator of good genes, and women appear to be especially attuned to selectively favor more symmetrical men as sexual partners (Gangestad & Thornhill, 1997). Women are sensitive to a variety of cues that correlate with bodily symmetry, including a man’s skill at rhythmic dancing (Brown et al., 2005), and even olfactory cues (perceived simply from the scent of a man’s unwashed t-shirt; Thornhill & Gangestad, 1999b). Further, women appear especially attracted to men with “good genes” under conditions in which these genes have the greatest functional implications for female reproductive fitness—when women are especially liable to become pregnant (Gangestad, Thornhill, & Garver-Apgar, 2005). For instance, when presented with men’s unwashed t-shirts, women in the most fertile phase of their ovulatory cycles are especially likely to prefer the scent of symmetrical men (Thornhill & Gangestad, 1999b).

Prior to the application of evolutionary theorizing to the social psychology of attraction, it was largely unknown that female social cognition and behavior varies predictably across the ovulatory cycle. Other evidence indicates that women in the most fertile phase of their cycle show an increased interest in men who possess genes that would enhance the immune system competence of potential offspring (Garver-Apgar, Gangestad, Thornhill, Miller, & Olp, 2006). Ovulating women also show an increased preference for men with masculine sex-typed features (such as a deep voice or taller stature), which also are hypothesized to serve as signals of underlying genetic quality (e.g., Johnston, Hagel, Franklin, Fink, & Grammer, 2001; Pawlowski & Jasienska, 2005; Penton-Voak, Little, Jones, Burt, Tiddeman, & Perrett, 2003; Puts, 2005). Another such finding revealed that ovulating women are relatively more interested in extramarital affairs with masculine men,

especially if their current partners are relatively unattractive (Pillsworth & Haselton, 2006).

Whereas that line of research has necessarily focused on female preferences, other lines of evolutionarily informed research have compared the mating behaviors and mate preferences of men and women. Much of this work is informed by the evolutionary implications of *differential parental investment* (Trivers, 1972). Throughout evolutionary history, female mammals have been obligated by physiology to make a large investment in offspring, both prior to birth (during gestation) and afterwards (during nursing). Male mammals have not. The maximum number of offspring a female can potentially produce is, therefore, relatively small compared to the maximum number that a male might produce. The implication is that female reproductive fitness has historically been facilitated by a relatively choosy approach to sexual relations. In addition, for species with helpless offspring such as humans, female reproductive fitness has been enhanced when mating with a male who commits resources to the care of a child after it is born. This further implies a female priority on monogamous relationships, and a preference for mates who have the capacity and willingness to expend resources on offspring care. In contrast, and in keeping with their relatively minimal obligate parental investment, male reproductive fitness has historically been facilitated by a somewhat more unrestricted approach to sexual relations, and by a preference for mates whose physical features heuristically connote fertility.

An enormous body of empirical evidence has tested, and supported, these predicted sex differences. Men generally show a greater interest than women in casual sexual relationships (Buss & Schmitt, 1993; Clark & Hatfield, 1989; Li & Kenrick, 2006). Compared to men, women hold higher standards for potential romantic partners, especially for sexual relationships (Kenrick, Groth, Trost, & Sadalla, 1993; Kenrick, Sadalla, Groth, & Trost, 1990). Women generally place a higher priority on variables that connote a mate’s ability to commit resources to offspring (e.g., wealth, status), whereas men generally place a higher priority on variables that connote a mate’s fertility (e.g., youth, facial attractiveness; Badahdah & Tiemann, 2005; Buss & Schmitt, 1993; Hanco, Master, & Sabini, 2004; Li & Kenrick, 2006; Wiederman, 1993). These effects emerge across many different cultures (Buss, 1989; Kenrick & Keefe, 1992; Schmitt, 2005; Schmidt et al., 2003). It is worth noting that these sex differences emerge most strongly under conditions in which individuals must prioritize. Without constraints on their choices, both men and women prefer mates who are both attractive and resource-rich; when forced to compromise, however, women prioritize a mate’s status over his physical appearance, whereas men prioritize a mate’s attractiveness over her wealth (Li, Bailey, Kenrick, & Linsenmeier, 2002).

These consequences of differential parental investment emerge not only on straightforward assessments of sexual behavior and mate preferences; they also have more subtle effects. Research on counterfactual thinking reveals that when asked about their regrets in life, men are more likely to wish they had slept with more partners, whereas women wish they had tried harder to avoid getting involved with losers (Roese, Pennington, Coleman, Janicki, Li, & Kenrick, 2006). Predictable biases in person perception emerge as well. Women tend to be skeptical about a man's commitment even when it may be sincere, whereas men are biased to perceive sexual desire in a woman even when it may not be there (Haselton & Buss, 2000). And, of course, context matters: Men's tendency to project sexual interest onto women emerges especially when romantic goals are highly salient to the men and the women are physically attractive (Maner et al., 2005).

By drawing on the evolutionary logic of reproductive fitness, it is also possible to make many nuanced predictions about mate preferences that are difficult to deduce from alternative perspectives. For instance, the male preference for relatively youthful mates might be predicted by stipulating the existence of a social norm encouraging men to date younger women (Eagly & Wood, 1999). Although such an alternative might account for the finding that 45-year-old men are attracted to women in their 20s, it cannot account for the fact that men in their 20s are attracted to women their own age, nor for the fact that teenage boys are actually attracted to somewhat *older* women (Buunk, Dijkstra, Kenrick, & Warntjes, 2001; Kenrick, Gabrielidis, Keefe, & Cornelius, 1996; Otta, Queiroz, Campos, daSilva, & Silveira, 1998). Nor can it account for the fact that those differences are found across cultures and historical time periods, actually becoming more pronounced in societies not subject to Euro-American sex-role norms (Kenrick & Keefe, 1992; Kenrick, Nieuweboer, & Buunk, 2010). The entire set of findings, however, was explicitly predicted by the hypothesis that men have an evolved preference for mates whose features connote fertility and fits with a broader nomological network of evolution-based findings (Kenrick, 2006b; Kenrick & Li, 2000).

Of course, there is also considerable variability within the sexes, both in mate preferences and in sexual strategies more generally (Simpson & Gangestad, 1991). An evolutionary metatheoretical perspective suggests that within-sex variability may be attributable, in part, to the same underlying physiological mechanisms that account for differences between sexes. At a proximal level of analysis, many evolved sex differences are likely to result from different levels of androgens—such as testosterone, which masculinizes the body (and therefore the brain). Individual differences in testosterone, in both men and women, would

therefore be expected to influence mating behavior and mate preferences. This is the case (Regan & Berscheid, 1999).

Mating strategies and mate preferences also vary cross-culturally (Buss, 1989; Kenrick, Nieuweboer et al., 2010; Schmitt, 2005). Although such cross-cultural variation is sometimes offered as evidence against an evolutionary explanation (e.g., Eagly & Wood, 1999; Wood & Eagly, 2002), the logical tools offered by an evolutionary approach actually provide the basis for multiple (and sometimes competing) hypotheses about specific ecological variables that have specific implications for fitness-relevant costs and benefits associated with different mating preferences, and thus have clear implications for cross-cultural differences. There is now abundant evidence supporting evolutionarily informed predictions about cross-cultural differences in mating behavior, including evidence casting doubt on alternative explanations based on sociocultural variables alone (e.g., Gangestad, Haselton, & Buss, 2006; Schaller & Murray, 2008; Schmitt, 2005). Employed rigorously, the logical tools of evolutionary psychology not only predict universal tendencies, but can also predict deviations from these tendencies that occur under unique ecological circumstances.

Evolutionary inquiry into these cultural differences reflects a broader body of work that has arisen in the literature on human evolution and sexual behavior. This body of research has emerged from the recognition that, in terms of implications for reproductive fitness, there are *trade-offs* that arise when choosing to employ a mating strategy that emphasizes relatively unrestricted casual sexual liaisons versus a strategy that emphasizes relatively monogamous committed relationships (Buss & Schmidt, 1993; Gangestad & Simpson, 2000; Kenrick et al., 2003). The particular nature of these trade-offs (i.e., the ratio of reproductive costs and benefits) may vary considerably according to the specific contexts that individuals find themselves in. These contexts may be relatively enduring, with implications for chronic individual differences in mating preferences and mating strategies. Consequently, there has arisen an important line of research examining *socio-sexual orientation* and its implications for social cognition and interpersonal behavior (e.g., Bleske-Rechek & Buss, 2001; Duncan et al., 2007; Simpson & Gangestad, 1991, 1992). These contexts may also be temporary, with the implication that individuals may be adaptively equipped to flexibly employ different strategies, and to prioritize different features of potential mates, under different mating contexts. There has therefore arisen another important line of research examining the ways in which social cognition and behavior varies depending on whether individuals—both men and women—find themselves in

a *short-term* or *long-term* mating context, and on other variables that influence the reproductive trade-off between short-term and long-term mating (Buss & Schmidt, 1993; DeBruine, 2005; Fletcher, Tither, O'Loughlin, Friesen, & Overall, 2004; Gangestad & Simpson, 2000; Kenrick, Sundie, Nicastle, & Stone, 2002; Li & Kenrick, 2006; Puts, 2005; Regan, Medina, & Joshi, 2001; Shackelford, Goetz, LaMunyon, Quintus, & Weekes-Shackelford, 2004).

Long-Term Romantic Relationships

For the vast majority of mammals, the adult male contributes little more than sperm to his offspring. Humans are different. Long-term relationships (with both parents often contributing substantially to offspring care) are common in human populations, and these committed dual-parent relationships have beneficial consequences for the reproductive fitness of offspring (Geary, 2000). Given these fitness benefits, it's not surprising that an evolutionary perspective has been brought to bear on many different social psychological phenomena pertaining to long-term romantic relationships.

One body of research focuses on psychological adaptations that promote commitment to existing romantic relationships. These adaptive mechanisms include positive biases favoring existing partners over potential alternatives (Johnson & Rusbult, 1989; Miller, 1997). For instance, compared with individuals who are not in committed relationships, those who are in long-term relationships often perceive alternative mates as less physically and sexually desirable (Simpson, Gangestad, & Lerma, 1990). Moreover, when feelings of romantic love are psychologically salient, people selectively reduce their visual attention to attractive members of the opposite sex (Maner, Rouby, & Gonzaga, 2008).

These cognitive and attentional biases may be rooted, at a physiological level of analysis, in hormonal changes that accompany commitment to long-term romantic relationships. For instance, compared to men in short-term sexual relationships, those in long-term relationships have relatively lower levels of testosterone (Gray, Chapman, Burnham, McIntyre, Lipson, & Ellison, 2004). In addition, oxytocin appears to play an important role in the experience of companionate love, and in the formation and maintenance of long-term romantic attachments (Brown & Brown, 2006; Carter, 1998; Diamond, 2004). Oxytocin is also secreted when mothers nurse infant children and appears to play an important role in the forging of mother-child attachments. Given this neuroendocrinological similarity, it has been suggested that long-term romantic attachments may be facilitated by some of the same cognitive, affective, and neurophysiological systems that evolved to

facilitate adaptive attachments between mammalian mothers and their infants (Bowlby, 1969; Hazan & Shaver, 1994; Zeifman & Hazan, 1997). This does not mean, of course, that these two forms of attachment are equivalent. Because parent-child bonds and adult romantic bonds solve different adaptive problems, there are important differences in the decision biases governing attachments to children and lovers (Kenrick, 2006a).

Another body of research has focused on psychological responses to a partner's real or imagined infidelities. Individuals typically express strong negative reactions to the thought that their partner might flirt or have sex with another. Jealousy is found across a wide variety of cultures and is commonly implicated in spousal assault and homicide (Buss, 1994; Buunk & Hupka, 1987; Daly, Wilson, & Weghorst, 1982). The logic of differential parental investment implies predictable sex differences in the experience of jealousy. Consistent with this analysis, jealous women pay more attention to a potential rival's beauty, whereas jealous men attend more to a rival's social dominance (Dijkstra & Buunk, 1998). A sex difference is also predicted in the extent to which jealousy is aroused by sexual infidelity versus emotional infidelity (i.e., the formation of a close emotional attachment to a mating rival). A female mate's sexual infidelity is expected to be especially upsetting to men, because it raises the possibility that they might unwittingly invest resources in a biologically unrelated child. In contrast, a male mate's emotional infidelity is expected to be especially upsetting to women, as it raises the possibility that her mate might redirect his resources to children who aren't her own. Some have argued that, because the survival of human infants ancestrally required a close bond between both parents, both sexes should be similarly upset by sexual and emotional infidelity (DeSteno, Bartlett, Braverman, & Salovey, 2002; Harris, 2003). Consistent with the logic of differential parental investment, however, the predicted sex differences emerge across studies done in multiple countries and with multiple methods (Buss, Larsen, Westen, & Semmelroth, 1992; Buunk, Angleitner, Oubaid, & Buss, 1996; Pietrzak, Laird, Stevens, & Thompson, 2002; Sagarin, Becker, Guadagno, Nicastle, & Millevoi, 2003; Shackelford, LeBlanc, & Drass, 2000; Wiederman & Allgeier, 1993). Although there is continuing debate about the exact nature of sex differences in jealousy, a number of findings using different methods converge to support an evolutionary model (Sagarin, 2005).

Offspring Care

From an evolutionary perspective, the formation and maintenance of romantic relationships serves the ultimate

function of producing offspring and sustaining those offspring until they are successful reproducers themselves. The investment of resources in children involves trade-offs, however. According to *life-history theory*, all animals (including humans) divide their resources between (1) their own survival and somatic development, (2) mating effort, and (3) parenting effort (Kaplan & Gangestad, 2007; Kenrick & Luce, 2000; Stearns, Allal, & Mace, 2008). Decision rules about how to allocate those resources are predicted to have evolved in such a way as to be sensitive to cues and circumstances connoting the relative fitness benefits and costs associated with specific allocation priorities. Therefore, the extent that a parent will invest resources in caring for a child (rather than in attempts to produce additional children, for instance) is expected to depend upon many additional variables, including the availability of resources, the child's needs, the child's apparent reproductive potential, the existence of other offspring, and—for men especially—the extent one is confident the child is one's own.

There is now a large body of research supporting specific predictions based on this analysis. For instance, mothers give more to offspring who are healthy and withhold from those with a lower probability of reproductive success (Hrdy, 2000). Children with greater reproductive potential are more likely to receive help under life-and-death circumstances (Burnstein et al., 1994). The actual or apparent genetic relatedness of offspring also influences the extent to which parents invest in them. Parents provide more nurturant care to actual biological offspring than to stepchildren (Daly & Wilson, 1998; Tooley, Karakis, Stokes, Ozanne-Smith, 2006). And men provide better care to children to whom they bear a physical resemblance, a superficial cue that heuristically implies confidence in their paternity (Apicella & Marlowe, 2004; Burch & Gallup, 2000; Platek et al., 2004).

The effects of parental uncertainty extend to the investment of resources in grandchildren and other relatives, too. For instance, a maternal grandmother knows with a high degree of certainty that her daughter is hers and that her daughter's children are truly her daughter's. In contrast, a paternal grandfather is considerably more uncertain; he cannot be sure that his ostensible son is truly his, nor that his son's ostensible children are truly his son's. These variations in parental uncertainty are reflected in the extent that individuals invest resources (e.g., money, emotional support) in their grandchildren and other relatives: Higher degrees of parental uncertainty result in lower investment (Laham, Gonsalkorale, & von Hippel, 2005; Michalski & Shackelford, 2005; Pollet, Nettle, & Nelissen, 2007; Webster, 2003). These effects are further moderated by additional variables bearing on reproductive fitness (e.g., Laham et al., 2005; Webster, 2003).

Social Influence

Research on social influence covers a wide range of topics, including the study of conformity, obedience to authority, compliance, and persuasion (see Hogg, this volume). Textbooks often treat these different topics (and the phenomena identified with each) as conceptually independent, united merely by the superficial fact they are examples of social influence. In contrast, an evolutionary approach reveals deep conceptual commonalities underlying these ostensibly distinct phenomena. In so doing, it provides a unique explanatory perspective (and generates novel hypotheses) that answer fundamental research questions about social influence processes.

Classic studies of social influence—for example, those by Sherif, Asch, and Milgram—are often viewed as surprising evidence that individuals are not as independent and free-thinking as they might wish to believe. From an evolutionary perspective, however, people's obedient and conformist tendencies are not so surprising (Campbell, 1975). Historically, hierarchical status structures appear to have offered many competitive advantages to groups (Sidanius & Pratto, 1999). It seems reasonable to presume that deference to authority figures has historically conferred fitness advantages, providing an evolutionary basis not only for obedience, but for authoritarian attitudes more broadly (Kessler & Cohrs, 2008).

Conformity, too, has multiple evolutionary roots. Conforming to the actions of others reduces the likelihood of social exclusion, which is likely to benefit reproductive fitness. Moreover, in most stable ancestral ecological contexts, behaving like others was likely to have led to fitness-enhancing decisions, thereby selecting for mimicry, imitation, and other manifestations of conformity (Coultas, 2004; Henrich & Boyd, 1998; Kessler & Cohrs, 2008). These two lines of fitness-relevant logic indicate evolutionary foundations for “normative” and “informational” influence, respectively. These evolutionary analyses also suggest a conceptual linkage between classic social influence phenomena with other kinds of phenomena entirely, such as the tendencies toward highly automatic behavioral mimicry (Lakin, Jefferis, Cheng, & Chartrand, 2003) and implicitly accepting others' assertions to be true (Gilbert, 1991).

People are more susceptible to social influence under some situations than others, and an evolutionary approach is useful for understanding this cross-situational variability. Our analysis of belongingness needs suggests that conformity will especially pronounced under conditions in which the risk of social exclusion is exaggerated, such as when one's own attitudes and actions deviate from group norms; this is the case (Snyder & Fromkin, 1980). Moreover, if conformity has a positive impact on fitness, then the natural

tendency toward conformity will be amplified under circumstances that represent immediate threats to one's fitness. Indeed, conformity to salient norms is enhanced when death or fear-inducing physical threats are made salient (Gailliot, Stillman, Schmeichel, Maner, & Plant, 2008; Griskevicius, Goldstein, Mortensen, Cialdini, & Kenrick, 2006). Cross-cultural evidence is consistent with this analysis as well: In geographical regions historically characterized by a higher prevalence of pathogenic diseases, there have emerged cultural value systems that most strongly encourage conformity to behavioral norms (Fincher, Thornhill, Murray, & Schaller, 2008).

The evolutionary perspective also provides conceptual leverage for predicting the characteristics of those individuals that people are most likely to imitate, obey, conform to, or otherwise be influenced by. Conformity may be an evolutionarily adaptive behavioral strategy, in general, but it is especially adaptive to selectively imitate the actions of prestigious individuals (Henrich & Gil-White, 2001). Prestige is a fluid concept; the specific features that confer prestige may vary across different cultural contexts. It is clear, however, that people endowed with higher levels of prestige-connoting traits—for example, expertise, attractiveness, or fame—exert greater influence in a variety of ways (Heath, McCarthy, & Mothersbaugh, 1994; Henrich & Gil-White, 2001; Kamins, 1989; Milgram, 1974; Wilson & Sherrell, 1993).

Finally, although the fitness benefits of conformity may generally outweigh the benefits associated with deviance, deviance may nonetheless have specific kinds of fitness benefits that, under specific and predictable circumstances, may trump those associated with conformity. In ancestral populations, only a minority of males had access to female reproductive resources, and males' reproductive fitness was substantially influenced by their ability to distinguish themselves from other males competing for access to the same females. In such a competitive mating context, blending in with the crowd may have been disadvantageous, and presenting oneself as distinctive and different is likely to have led to greater reproductive fitness. This implies that, whereas conformity may be the default behavioral strategy among both men and women, men (but not women) will show anti-conformity tendencies under specific circumstances in which mating motives are salient. Recent experimental findings support this logic (Griskevicius et al., 2006).

Group Dynamics

Most evolutionary analyses focus specifically on reproductive fitness at the level of the gene or the individual organism, and there is rarely much logical need to consider groups

as an additional level of analysis. It can be argued, however, that in highly interdependent ultrasocial species such as *Homo sapiens*, individuals' outcomes have manifold consequences for all other individuals in their social groups and, reciprocally, the group's outcomes have substantial implications for fitness at the levels of individuals and the genes making them up. Consequently, evolutionary frameworks that consider the logical relations between outcomes at the levels of genes, individuals, and groups might provide useful tools for understanding intra-group dynamics. *Multilevel selection theory* (Sober & Wilson, 1998) provides one such conceptual framework, emphasizing the impact that group-level outcomes have on the reproductive fitness of individuals (and genes) within the group. This framework has been used to generate hypotheses and empirical discoveries bearing on brainstorming, distributed cognition, cooperative behavior, and social dilemmas (O'Gorman, Sheldon, & Wilson, 2008; Sheldon & McGregor, 2000; Wilson, Van Vugt, & O'Gorman, 2008).

There is also a wide-ranging body of literature stimulated by the observation that group living affords specific kinds of coordination problems to solve (Kameda & Tindale, 2006). One illustrative example is provided by recent evolutionary analyses of leadership (Van Vugt, 2006; Van Vugt, Hogan, & Kaiser, 2008). The psychology of leadership can best be understood within a context that considers the evolved psychology of followership, too. Evolutionary analyses have also yielded hypotheses about the particular characteristics of leaders that are appealing under different kinds of circumstances. For instance, masculine facial morphologies (connoting higher levels of testosterone, competitiveness, and aggression) are more highly desired in political leaders during times of war versus peace (Little, Burriss, Jones, & Roberts, 2007). In addition, whereas there is a preference for male leaders to manage potential intergroup competition, there is a preference for female leaders to manage potential *intragroup* competition (Van Vugt & Spisak, 2008)—perhaps because females tend to be more concerned with preserving within-group unity (Eagly & Johnson, 1990; Geary, 1998).

A third line of research has applied evolutionary insights to the complex dynamical processes through which norms emerge within groups (e.g., Kameda, Takezawa, & Hastie, 2003; 2005; Kenrick et al., 2003). This work not only contributes to an understanding of group processes and group outcomes, but also to an understanding of the origins of culture—a topic we discuss in somewhat more detail below.

These applications of evolutionary theorizing to group dynamics are all relatively recent, and they offer hope for a revival of social psychological interest in the study of group dynamics. Despite its centrality to social psychology, interest in group dynamics has not been in the mainstream

for some time (Moreland, Hogg, & Hains, 1994; Sanna & Parks, 1997; Steiner, 1974). The application of evolutionarily informed theorizing in this domain may help reverse that trend. Just as the study of sex-differences (which, after an initial flurry of popularity, had become somewhat marginalized in the absence of rigorous theorizing) was re-energized by the introduction of evolutionary theorizing (e.g., Buss, 1995; Kenrick, 1994), so too an evolutionary approach has the potential to bring the study of group dynamics back into vogue.

Intergroup Prejudices and Intergroup Conflicts

Although traditional social psychology often speaks simply of “prejudice” as though it were a single, unitary thing, an evolutionary approach—emphasizing particularized domain-specific adaptations—suggests that it may be more appropriate to speak of *prejudices*, plural. For instance, prejudices predicated on gender or on sexual orientation may be psychologically distinct from one another and from prejudices based on facial disfigurement. Even within the more specific context of intergroup relations, there appear to be multiple, evolutionarily distinct mechanisms that produce discrimination between ingroup and outgroup, and in doing so, produce psychologically distinct intergroup prejudices (Cottrell & Neuberg, 2005; Neuberg & Cottrell, 2006). From this perspective, the nature of prejudices is predictable from a functional analysis of emotions and the threats they are designed to address. For instance, people prejudiced against gay men tend to perceive them as posing threats to health and values; consequently, their prejudices are characterized by physical and moral disgust, and their discriminatory inclinations heuristically focus on avoiding close physical contact and keeping gay men out of positions of social policy and socialization influence. In contrast, people prejudiced against African Americans (especially African American men) tend to perceive them as posing threats to physical safety; consequently, their prejudices contain a stronger component of fear, and their discriminatory inclinations focus on strategies of self-protection.

Several lines of research proceed from the premise that small coalitional groups provided early humans with access to many fitness-relevant opportunities and also with protection from many kinds of fitness-relevant perils. This provides an evolutionary foundation for the psychology of social identity and its implications for ingroup favoritism (Brewer & Caporael, 2006). By emphasizing the point that coalitional social structure (rather than mere group categorization) lies at the heart of intergroup cognition, this approach implies that contemporary categorical distinctions (e.g., perceptual discrimination according to racial or ethnic categories) can be

psychologically eliminated by cross-cutting categorizations that are more immediately coalitional in nature (Kurzban, Tooby, & Cosmides, 2001); people respond to coalitions and the threats and opportunities they pose, not to race *per se*. Another implication is that any perceived threat to one’s coalitional ingroup—even if the threat does not originate in a coalitional outgroup—may lead to exaggerated ingroup favoritism (e.g., Navarrete, Kurzban, Fessler, & Kirkpatrick, 2004).

Another line of research begins with the recognition that hierarchical group structures may confer relatively positive fitness outcomes to group members. The evolutionary implication—articulated by *social dominance theory* (Sidanius & Pratto, 1999)—is that humans may be characterized by psychological adaptations that favor the establishment and maintenance of dominance hierarchies. These adaptations may produce effects at the cognitive and behavioral level of analysis, and also at a societal level, in the creation of institutions that legitimize and reify existing dominance hierarchies (e.g., Mitchell & Sidanius, 1995). Different kinds of prejudices (e.g., sexism, racism) may be viewed, in part, as manifestations of these cognitive mechanisms and social institutions. People who are dispositionally favorable to social dominance hierarchies are likely to show these prejudices at especially high levels (Pratto, Sidanius, Stallworth, & Malle, 1994), and these prejudices may be especially likely to emerge under circumstances within which dominance considerations are temporarily paramount (Guimond, Dambrun, Michinov, & Duarte, 2003; Pratto, Sidanius, & Levin, 2006).

Additional evolutionary research programs focus less on the nature of ingroups and more on outgroups and the specific fitness costs associated with intergroup contact. One line of inquiry draws on evidence that, historically, intergroup contact was likely to be associated with an increased chance of interpersonal aggression and physical injury. One might thus expect the evolution of adaptations that dispose individuals to associate outgroup members with traits connoting aggression, violence, and danger, and to do so especially under conditions in which perceivers feel especially vulnerable to danger. For instance, when people (especially those who chronically perceive the world to be a dangerous place) are in the dark, they are more prone to the implicit activation of danger-connoting stereotypes of ethnic outgroups (Schaller, Park, & Faulkner, 2003; Schaller, Park, & Mueller, 2003). Evolutionary analyses often generate very specific predictions, and that is the case here: The darkness-stereotyping finding was specific to stereotypes relevant to physical safety threat (e.g., aggressive); no such effect is observed on equally negative stereotypes irrelevant to physical safety (e.g., ignorant). In fact, in real-life intergroup conflict situations, an increased

sense of vulnerability may actually lead to more positive outgroup stereotypes along trait dimensions connoting competence, while simultaneously leading to more negative stereotypes along trait dimensions connoting warmth and trustworthiness—a constellation of stereotypic traits that most clearly implies an actual fitness-relevant threat (Schaller & Abeyesinghe, 2006).

The threat of interpersonal violence is not the only fitness-relevant cost associated with intergroup contact. Historically, intergroup contact was associated with increased exposure to pathogenic diseases (Schaller & Duncan, 2007). It follows that a functionally specific form of intergroup prejudice is likely to be exaggerated when people perceive themselves to be especially vulnerable to infection. This is indeed the case. People who perceive themselves to be more vulnerable to disease show stronger implicit cognitive associations linking outgroups to danger, but not to negativity in general (Faulkner, Schaller, Park, & Duncan, 2004). Xenophobia and ethnocentrism are also predicted by disease-relevant individual difference variables (Faulkner et al., 2004; Navarrete & Fessler, 2006), and by naturally occurring circumstances (such as the first trimester of pregnancy) in which individuals' immune functioning is temporarily suppressed (Navarrete, Fessler, & Eng, 2007). Empirical results such as these are impossible to explain with traditional theories of prejudice that focus primarily on processes pertaining to social categorization, social identity, and realistic conflict. They follow directly from hypotheses deduced within an evolutionary framework, however.

Several of these evolutionary perspectives imply sex differences in prejudice and intergroup conflict (e.g., Van Vugt, De Cremer, & Janssen, 2007; Yuki & Yokota, 2009). For instance, dominance hierarchies have historically been especially pertinent to male reproductive fitness. Social dominance theory thus implies that, compared to women, men are more chronically concerned with the maintenance of social dominance hierarchies, and should exhibit especially strong prejudices toward others who threaten one's own status in an existing dominance hierarchy (e.g., Sidanius, Pratto, & Brief, 1995). Also, historically, intergroup contact occurred primarily between males. This implies that men are especially likely to perceive outgroup members as a threat and that, among men, these prejudicial perceptions are especially likely to be triggered by contextual cues connoting vulnerability to harm. Evidence from several studies supports this implication (Schaller & Neuberg, 2008). Finally, outgroup men (compared to outgroup women) were especially likely to inflict mortal wounds ancestrally—a phenomenon true in modern societies, as well—thereby suggesting that male (compared to female) outgroup members will be especially likely to trigger danger-connoting cognitive associations. This also

appears to be the case (Maner et al., 2005; Navarrete et al., 2009).

The Affordance Management System Revisited

This body of research, of which we have only glossed the surface, illustrates the value of thinking about psychological mechanisms in terms of the specific kinds of adaptive problems they solve—problems related to, for instance, self-protection, coalition maintenance, mate selection, child rearing, and other challenges to reproductive fitness. The adaptive, problem-solving nature of psychological mechanisms is revealed by the functionally specialized, domain-specific manner in which they are engaged. Interpersonal attraction, for instance, is not a single construct. There are very different forms of attraction, and they are governed by very different psychological principles in very different adaptive contexts. In contexts that emphasize the adaptive value of coalitions and cooperative behavior, individuals are especially attracted to people who seem familiar or physically similar; in sexual contexts, however, familiarity and physical similarity are repellant instead (Ackerman et al., 2007; DeBruine, 2005; Lieberman et al., 2007).

This brief review has illustrated, in a variety of ways, how evolved psychological mechanisms are sensitive to predictable categories of cues in the perceptual environment—cues that heuristically connote very specific opportunities or threats. These cues are often very subtle (the scent of symmetry, for instance; Thornhill & Gangestad, 1999b), and their discovery as important social psychological variables emerged only after psychologists equipped themselves with the logical tools of evolutionary inquiry. These fitness-relevant cues—even very subtle ones—trigger predictable, functionally specific cascades of affect, cognition, and behavior. For instance, superficial cues connoting female fertility trigger (among male perceivers, but not female perceivers) very specific consequences on attention and memory, as well as on more overt judgments and behavior (Becker et al., 2005; Duncan et al., 2007; Kenrick & Keefe, 1992).

Psychological adaptations are imperfect, but in evolutionarily sensible ways, and thus help to explain many of the inferential biases and prejudices that are of central interest to social psychologists. The evolutionary consequences of differential parental investment, for instance, manifest not only in sex differences in mate preferences, but also in the fact that men (but not women) often misperceive sexual interest in the faces of attractive opposite-sex others, whereas women (but not men) often erroneously assume that their suitors are cads (Haselton & Buss, 2000; Maner et al., 2005). The substantial fitness costs associated with infectious diseases lead perceivers not only to respond aversely to individuals who actually are diseased, but also

to predictable prejudices against a variety of objectively healthy individuals who just happen to appear morphologically, behaviorally, or culturally anomalous (Faulkner et al., 2004; Park et al., 2003; 2007).

Content matters. Psychological adaptations respond to specific cues, and these cues trigger the activation of highly specific affective states and associative knowledge structures with highly specific contents. In the realm of prejudice, for instance, particular categories of fitness-relevant threat are associated with very particular prejudices—defined by particular emotional responses and by very particular kinds of negative stereotypes but not by other, equally negative, stereotypes (Cottrell & Neuberg, 2005; Schaller, Park, & Faulkner, 2003).

Context matters too. Evolved stimulus-response associations are highly sensitive to the intrapersonal context created by perceivers' own preexisting dispositions and goals, and by immediate ecological circumstances within which perceivers find themselves. The scent of a symmetrical man is sexually attractive to women, but primarily under circumstances in which those women are most prone to become pregnant (Thornhill & Gangestad, 1999b). Facial cues connoting female fertility are especially likely to draw and hold men's attention, but primarily among men with a dispositional tendency toward unrestricted mating (Duncan et al., 2007). White people misperceive anger in the faces of African American men, especially under conditions in which self-protective motives have been made temporarily salient (Maner et al., 2005). Morphological, behavioral, and cultural anomalies trigger disease-connoting prejudices especially among perceivers who are, or merely perceive themselves to be, especially vulnerable to infection (Faulkner et al., 2004; Navarrete et al., 2007; Park et al., 2007). These psychological phenomena are malleable—not despite being the products of evolution, but *because* they are the products of evolution.

Finally, the implications of underlying evolutionary principles apply across the entire landscape of social psychology. Adaptations that facilitate kin-recognition have implications not only for person perception, but also for altruism, aggression, mate selection, and offspring care (Apicella & Marlowe, 2004; DeBruine, 2005; Lieberman et al., 2007; Park et al., 2008). Adaptations that facilitate avoidance of physical harm have implications for phenomena as superficially distinct as person memory, intergroup prejudice, and conformity (Ackerman et al., 2006; Griskevicius, Goldstein, et al., 2006; Schaller, Park, & Faulkner, 2003). Adaptations that serve the ultimate function of sexual selection have implications for topics as ostensibly irrelevant to mating as altruism, aggression, conformity, and creativity (Griskevicius, Cialdini, & Kenrick, 2006; Griskevicius et al., 2006, 2007, 2009).

LINKAGES TO DEVELOPMENT, LEARNING, AND CULTURE

Many people assume that evolutionary theories of social behavior imply a hardwired genetic determinism, a diminished role of developmental and learning processes, and an absence of cultural differences. None of these assumptions are correct.

Development

The human genotype is not a blueprint depicting the phenotypic features of people; rather, it is more like a recipe book, providing instructions for the assembly and generation of those phenotypic characteristics. This assembly process is more commonly referred to as development. Developmental processes are fundamental to any evolutionary approach to human behavior (Bjorklund & Pellegrini, 2002; Geary, 2006; Marcus, 2004).

There is no simple inflexible relation between a gene and its role in the assembly of phenotypic features (Carroll, 2005; Ridley, 2003). Genes may or may not be expressed. Even if they are expressed, the exact location and timing of their expression may vary considerably. Gene expression may vary depending on the presence of other pieces of genetic code. Gene expression may vary depending on the gene's immediate physiological environment (e.g., hormone levels within the developing organism). And gene expression may vary depending on features of the physical and social environment within which the organism itself is located. For instance, genetically identical butterflies may take on entirely different appearances depending on local climatic conditions during development (Beldade & Brakefield, 2002) and, among some species of fish, ecological variables such as social density and local sex ratio influence the expression of genes that govern whether the developing organism ultimately becomes male or female (Godwin, Luckenbach, & Borski, 2003). Among humans, qualities of the family environment influence the expression of genes that precipitate sexual maturation (Ellis, 2004). Phenotypic plasticity of this sort is itself adaptive, given that a particular phenotypic trait may or may not confer relative fitness advantages, depending on the local ecological circumstances.

This principle of adaptive phenotypic plasticity applies not only to the development of physiological features, but also to the development of behavioral tendencies as well. This evolutionary logic has been applied toward the understanding of individual differences in attachment style (Bowlby, 1969), mating strategies (Bjorklund & Shackelford, 1999; Gangestad & Simpson, 2000), kin recognition (Lieberman et al., 2007), and many other phenomena central to social cognition and social behavior.

Learning

Learning mechanisms provide means through which information about chronic developmental environments are acquired. Learning mechanisms also provide means through which organisms acquire information about temporary contexts, thus allowing them to flexibly (and functionally) adjust behavioral responses. Because the fitness benefits of learning are enormous, it is no surprise that so many different learning mechanisms have evolved (Moore, 2004).

Particularly relevant to many social psychological phenomena is the concept of prepared associative learning—the evolved tendency to acquire specific fitness-relevant associations more quickly and efficiently than other (less fitness-relevant) associations. As noted earlier, there is extensive evidence that people are biologically prepared to acquire a fear response to stimuli (such as snakes) that represented significant sources of threat in ancestral environments (Öhman & Mineka, 2001). Analogously, there is evidence that people are especially efficient at learning, and especially slow to unlearn, fearful responses to coalitional outgroups (Olsson, Ebert, Banaji, & Phelps, 2005). This effect is specific to perceptions of male (but not female) outgroup members, a finding that is consistent with speculation that male outgroup members historically posed an especially substantial fitness threat (Navarrete et al., 2009).

Prepared learning of this sort can operate through non-social associative mechanisms, but social learning is implicated too. Rhesus monkeys, for instance, learn to fear snakes simply from observing other monkeys' fearful reactions to them (Cook & Mineka, 1990). It is likely that social learning mechanisms contribute to the extraordinarily efficient learning of fitness-relevant interpersonal impressions and prejudices as well (Schaller, 2006).

Cross-Cultural Variability

Humans inhabit many different cultural environments. These different cultural contexts create different developmental circumstances and different learning environments. Evolved mechanisms would thus be expected to manifest differently across different human cultures. Evidence of cross-cultural differences is therefore entirely compatible with an evolutionary perspective on human social behavior (Buss, 2001; Kenrick et al., 2003; Norenzayan & Heine, 2005; Norenzayan, Schaller, & Heine, 2006; Schaller, 2007).

In fact, evolutionary theorizing can be extraordinarily useful as a means of predicting the origins of cross-cultural differences in the first place. Here the concept of *evoked culture* is important: Cultural differences may themselves reflect differences in the extent to which evolved psychological mechanisms are expressed differently under different

ecological circumstances (Gangestad, Haselton, & Buss, 2006; Schmitt, 2005; Schmitt et al., 2003; Tooby & Cosmides, 1992). One sustained program of research has focused on regional differences in pathogen prevalence and its implications for the origins of many cultural differences, including in food preparation (Sherman & Billing, 1999), parenting practices (Quinlan, 2007), marriage systems (Low, 1990), and mate preferences (Gangestad & Buss, 1993; Gangestad et al., 2006). Research employing an evolutionary cost/benefit analysis has also provided evidence that regional variability in pathogen prevalence may have contributed to the emergence of worldwide differences in extraversion and other basic dispositional tendencies (Schaller & Murray, 2008) and to cultural differences in individualism, collectivism, and other fundamental value systems (Fincher et al., 2008; Thornhill, Fincher, & Aran, 2009).

It's worth making one last point here. Researchers and others often posit a role for socialized norms and culture as “alternatives” to evolutionary explanations. This will rarely be correct. Particular norms and culture sometimes collaborate in creating behavior (e.g., by potentially altering the expression of evolved inclinations) and are sometimes phenomena themselves to be explained by evolutionary processes. Moreover, positing a particular norm or cultural process as an alternative to an evolution-inspired hypothesis (e.g., that males are socialized to prefer younger women as mates) begs the question of why that particular norm exists as opposed to its opposite. The nature *versus* nurture debate has been roundly rejected in the biological sciences as assuming a false dichotomy; it makes no more sense to pursue that dichotomy in the psychological sciences.

THINKING STRAIGHT ABOUT THEORY AND RESEARCH IN EVOLUTIONARY SOCIAL PSYCHOLOGY

The general principles underlying evolutionary hypotheses have been tested extensively across many different animal species and are well established (Alcock, 1993; Daly & Wilson, 1983; Trivers, 1985; Wilson, 1975). Evolutionary approaches have resulted in the rigorous deduction of many novel hypotheses about social cognition and behavior. Some of these have generated compelling empirical support, some have been refuted, and others have yet to be fully tested. Evolutionarily informed hypotheses in psychology are subjected to the same high standards of empirical evidence as any other hypotheses. Despite their heuristic and integrative successes, evolutionary inquiries about social psychological phenomena have elicited especially high levels of skepticism and controversy. Some of this controversy is driven by misconception, misinterpretation, and ideology;

some is driven by the fact that evolutionary hypotheses can involve extra layers of inference compared to more proximate hypotheses (Alcock & Crawford, 2008; Conway & Schaller, 2002; Cosmides, Tooby, Fiddick, & Bryant, 2005; Daly & Wilson, 2005; Kurzban, 2002). We briefly discuss the most common issues and questions raised about evolutionary inquiry in the psychological sciences.

The Epistemic Status of Evolutionary Psychological Hypotheses

The paleontologist Stephen Jay Gould argued that many evolved characteristics have no adaptive function whatsoever, and so—despite the enormous success of the adaptationist research program in evolutionary biology (Alcock, 2001; Williams, 1966)—criticized evolutionists for adopting an adaptationist perspective on animal behavior. As part of this critique, he famously characterized adaptationist explanations as “just-so stories”—fanciful speculations that “do not prove anything” (Gould, 1977, p. 26). The “just-so story” accusation has been regularly trotted out by critics of evolutionary approaches to human psychology as well, typically as a shorthand means of asserting that evolutionary analyses are untestable, or are merely post-hoc explanations for common knowledge, or both.

Both critiques are logically unfounded. We noted at the outset that the evolutionary approach to social psychology isn't a specific theory or a hypothesis, but is instead a metatheoretical framework within which specific theories and hypotheses can be deduced. That important epistemic distinction is blurred by critics who suggest that evolutionary explanations are untestable (Ketelaar & Ellis, 2000). As we have reviewed above, the metatheoretical assumptions and logical tools of evolutionary inquiry have led to numerous highly specific hypotheses about social psychological phenomena, and these hypotheses are exactly as testable—exactly as falsifiable—as other hypotheses in the psychological sciences. Similarly, it is abundantly clear that evolutionary analyses do far more than simply provide post-hoc accounts for common knowledge. We have reviewed a large number of empirical discoveries that have emerged as a result of evolutionary inquiry. Some of these findings (just like other social psychological findings) may be consistent with intuition and lay observation. But many more are so nuanced, complex, or counterintuitive that they are unlikely to be part of any common knowledge (such as the links between ovulation and social behavior). Nor were they found within the scientific literature until they were revealed as the result of empirical inquiry guided by evolutionary theorizing.

This is not to say that there aren't additional epistemic and methodological complexities that attend evolution-

ary social psychology. There are. Compared to traditional social psychological theories (which merely specify sets of psychological processes), theories that draw on evolutionary theorizing (and thus also specify the evolutionary origins of those psychological processes) introduce an additional level of logical inference at which additional kinds of alternative explanations must be entertained (Conway & Schaller, 2002). There are many empirical strategies for dealing with these additional inferential complexities (Simpson & Campbell, 2005). The use of multiple methods is especially important. The most compelling support for any alleged social psychological adaptation is likely to draw on results from standard psychological experiments in conjunction with results from cross-species analyses, cross-cultural surveys, brain imaging, genetic analyses, and other diverse methods of inquiry (Schmitt & Pilcher, 2004). In addition, simple findings rarely yield fully compelling conclusions. Whereas alternative explanations may be readily found for main effects (e.g., a sex difference in mate preferences), alternative explanations can often be ruled out by more complex findings (e.g., a sex difference that appears and disappears under very specific conditions predicted by the logic of inclusive fitness). Deliberate attempts to deduce and test more complex interactions can therefore lead to especially compelling empirical findings.

A somewhat different epistemic issue is rooted in scientists' inability to directly observe ancestral environments and to measure the constraints they posed on reproductive fitness. Skeptics sometimes wonder whether one can deduce plausible theories and hypotheses in the absence of such observations and measurements. The answer is yes. Considerable bodies of archeological, anthropological, and biological evidence have yielded many confident conclusions about the ecologies of ancestral humans; these inferences (about group sizes, infectious diseases, homicide rates, etc.) form the basis for the deduction of many hypotheses bearing on social psychological phenomena. In addition, many evolutionary hypotheses can be informed by information that actually is measurable in contemporary environments, including evidence obtained from contemporary small-scale societies and comparative evidence from many other mammalian species. For instance, comparative evidence has been instrumental in guiding theory and research on attachment processes (Fraley, Brumbaugh, & Marks, 2005). Also, contemporary cross-cultural and comparative evidence indicates with a high degree of certainty that ancestral females played a much more substantial role than ancestral males in bearing and nurturing children. From that inference alone, the principles of differential parental investment can be presumed to apply to the evolution of human beings (Geary, 2000). As the chapter has illustrated, this has further implications for

the deduction of an enormous number of specific hypotheses bearing on social cognition and behavior.

The Logical Implications of Evolved Psychological Mechanisms

People sometimes think that, if human behavior is influenced by evolved adaptations, then people would never act against their own interests. This is wrong. As discussed above, evolved mechanisms are not foolproof and, like financial investments, operate on expected average payoffs. Psychological tendencies that are adaptive in the long term may still sometimes produce instances of costly and even maladaptive behavior. Such actions may also reflect environmental influences against which there are no evolutionary safeguards, because the environmental feature was rare or nonexistent in ancestral environments (e.g., birth control, easily available potent psychotropic drugs). Finally, of course, it is important keep in mind that evolutionary processes operate in the service of genetic replication, not in the service of the organisms that house those genes (Dawkins, 1976). Ostensibly maladaptive behaviors may produce hidden benefits for one's genes. Aggression, for example, occasionally leads to the aggressor's death, but aggressive tendencies may historically have resulted in net reproductive benefits (especially among men). And, as the enormous literature on the evolution of altruism reveals, selfish genes need not result in selfish people.

Another common misunderstanding is that if a psychological phenomenon is the result of evolved mechanisms, then the phenomenon itself must be evident at birth. This is actually rarely the case. Although the presence of a psychological phenomenon in infants may, in some cases, contribute compelling evidence of an innate predisposition, this is by no means necessary evidence. As we have discussed, developmental processes (including learning processes) are essential to the emergence of many evolved psychological phenomena, and much of this development occurs postpartum. Sexual maturation provides one obvious example: The onset of human puberty is a genetically programmed event, but does not occur until after a developing person has reached a particular size and physical condition. More broadly, many evolved adaptations require environmental input before they are expressed phenotypically. Even if a psychological phenomenon is absent at birth, it may still reflect the operation of adaptations.

It is also sometimes assumed that, because many evolved psychological mechanisms manifest in highly automatized stimulus-response associations, evidence of automaticity is necessary to support an evolutionary interpretation. As a corollary, it is sometimes assumed that if a phenomenon is moderated by manipulations of cognitive load, then the phenomenon cannot reflect an evolved adap-

tation (DeSteno, Bartlett, Braverman, & Salovey, 2002). These assumptions are wrong, and fail to consider the different ways in which different adaptations may manifest at a psychological level of analysis (Barrett, Frederick, Haselton, & Kurzban, 2006). Both automatic as well as more effortful cognitive responses may be produced as a result of evolved mechanisms.

Finally, there is the gross misconception that evolutionary influences on human behavior imply genetic determinism—that individuals' thoughts, feelings, and actions are inflexibly governed by their genes. This misconception may emerge from the fact that genes are associated with some relatively inflexible physical features (eye color, for example). But genes also encode for the development of many highly flexible traits as well. Even overt physical characteristics can change dependent on ecological variations (e.g., Godwin et al., 2003). Genetically endowed cognitive and behavioral flexibility is a central feature of the adapted mind. As our review of the social psychological literature reveals, evolved mechanisms play an important role in directing individuals' attention to fitness-relevant information in their immediate ecological context and thus enable these individuals to respond adaptively, and flexibly, to those circumstances.

So, are evolution-inspired hypotheses untestable? No. Are such hypotheses merely post hoc accounts of common sense knowledge? No. Does the inability to directly observe ancestral environments preclude the generation of well-grounded evolution-inspired hypotheses? No. Does an evolutionary perspective presume that people never act against their apparent best interest? No. Must a mechanism be observable at birth to be considered an evolved adaptation? No. Is evidence of automaticity necessary to claim that a psychological mechanism has evolved? No. And does the evolutionary approach imply that human thought and behavior are biologically determined, inflexibly controlled by genes? Emphatically, no.

FUTURE DIRECTIONS

Underlying Mechanisms

Like most social psychological inquiries, evolutionary social psychological research focuses on social cognition and social behavior. It is assumed that these cognitive and behavioral outcomes are the product of adaptations that have a physical manifestation—in the anatomy of the nervous system, the neurotransmission of neurotransmitters, the release of androgens into the bloodstream, and so forth.

Recent advances in brain imaging techniques (e.g., fMRI) reveal that specific anatomical structures are implicated in sexual attraction, social exclusion, self-esteem,

intergroup prejudice, and many other fitness-relevant social psychological responses (e.g., Eisenberger & Lieberman, 2004; Fisher, Aron, Mashek, Li, & Brown, 2002; Harris & Fiske, 2006; Heatherton, Macrae, & Kelley, 2004; Phelps et al., 2000). Research in neuroendocrinology reveals relations between endocrine activity and specific kinds of cognitive and behavioral responses. Sex hormones, for instance, influence not only sexual behavior but many other forms of social behavior as well. Variation in testosterone levels has been associated with aggression, expressive behavior, empathic mimicry, and intellectual performance under conditions of stereotype threat, among many other social psychological outcomes (Archer, 1991; Dabbs, Bernieri, Strong, Campo, & Milun, 2001; Hermans, Putman, & van Hong, 2006; Josephs, Newman, Brown, & Beer, 2003). Other hormones matter, too. For instance, women's estradiol levels predict their preference for facial cues of men's testosterone (Roney & Simmons, 2008), women's progesterone levels predict sensitivity to fearful and disgusted facial expressions that suggest the presence of nearby threats (C. Conway et al., 2007), and oxytocin is implicated in feelings of interpersonal trust and attachment in close relationships (Insel & Young, 2001; Kosfeld et al., 2005). And the study of neurotransmitter systems is also obviously relevant. Dopamine and serotonin transporter systems have each been implicated in a wide range of social behaviors with consequences for reproductive fitness (e.g., Knutson, Wolkowitz, & Cole, 1998; Melis & Argiolas, 1995).

A fruitful avenue for future research in evolutionary social psychology is to more explicitly explore the role of evolution in designing anatomical structures and neurochemical processes that give rise to social cognition and behavior. The benefits will be reciprocal: Evolutionary explanations for social psychological phenomena will benefit from a more rigorous anchoring in the "meat" of the mind; the study of social neuroscience will benefit from the rigorously functional perspective that is provided by the evolutionary sciences (Duchaine, Cosmides, & Tooby, 2001).

Evolutionary explanations imply events that operate at multiple levels of analysis, including a genetic level. Although it is not necessary to articulate genetic mechanisms to conduct rigorous research in evolutionary social psychology, it can potentially be useful to do so—especially as advances in behavior genetics and functional genomics begin to reveal specific genes (and their context-contingent expressions) implicated in fitness-relevant behaviors. Ample evidence now links specific alleles expressed in the dopamine and serotonin transporter systems (e.g., different variants of the DRD4 allele, and of the 5-HTTLPR allele) to a variety of traits bearing on social cognition and social behavior (e.g., Ebstein, 2006; Munafo, Yalcin, Willis-Owen, & Flint, 2008; Schinka, Busch, & Robinchaux-Keene, 2004), and

the expression of these genes is moderated by specific elements of an individual's social environment (e.g., Taylor et al., 2006). As discoveries in behavioral genetics and functional genomics yield new information about specific genes and their relation to social psychological phenomena—and about the specific environmental circumstances that lead these genes to be expressed—there will emerge fruitful opportunities to employ genetic mechanisms as means of articulating the important connection between human evolutionary origins and social psychological outcomes.

Broader Applications

An emerging subdiscipline of psychology (with links to other biological, social, and cognitive sciences) addresses questions at the intersection of evolutionary and cultural psychology and, in so doing, identifies evolved psychological mechanisms that may have contributed to the origins of culture (Norenzayan, Schaller, & Heine, 2006). Specific lines of inquiry have focused, for instance, on the evolved psychology underlying moral norms and religious practices (e.g., Atran & Norenzayan, 2005; Krebs & Janicki, 2004; Weeden, Cohen, & Kenrick, 2008). Evolutionary analyses—particularly those that consider how different cognitive and behavioral tendencies are likely to have different implications for reproductive fitness under different ecological circumstances—are also proving useful for explaining the origins of cross-cultural differences (e.g., Fincher et al., 2008; Gangestad et al., 2006; Kenrick, Nieuweboer et al., 2010; Schaller & Murray, 2008; Schmitt, 2005; Schmitt et al., 2003). These lines of inquiry are still young, and additional work must address other cultural differences and other ecological pressures that may influence the manner in which universal human capacities are expressed. Additional work must also address the exact mechanisms through which ecological variability produces cultural variability. Different ecologies may promote differential selection of genes, differential expression of common genes, differential activation of common neural structures, differential constraints on social learning, and so forth. Elucidation of these mechanisms will constitute an important part of future research in evolutionary cultural psychology.

There are also exciting developments in the integration of evolutionary social psychology and economics. Evolutionary analyses within the fields of biology and anthropology often rely on economic models (e.g., Henrich et al., 2006), and this work overlaps considerably with social psychological research on mixed-motive games and decision making (e.g., Kahneman & Tversky, 1991; Van Vugt & Van Lange, 2006). Social psychologists and economists alike have typically applied domain-general decision models to these problems,

overlooking the important implications likely to result from the fact that very different decision rules often apply when interacting with strangers, relatives, romantic partners, children, and other functionally distinct categories of people (e.g., Clark & Mills, 1993; Fiske & Haslam, 1996). The application of evolutionary analyses—based on domain-specific consequences for reproductive fitness—potentially yields novel implications for the computation of expected utility and novel predictions about the decisions people are likely to make when presented with economic decisions and mixed-motive dilemmas (Kenrick, Griskevicius et al., 2009; Kenrick, Sundie, & Kurzban, 2008).

Emerging literatures also highlight additional applications of evolutionary social psychology—applications to study of crime and punishment, for instance, and to politics and public policy (Crawford & Salmon, 2004; Duntley & Shackelford, 2008). Social psychology has always had powerful implications for the study of—and potential solutions to—social issues. These implications may be made even more powerful through a rigorous application of an evolutionary approach to social psychology.

FINAL COMMENTS

The most useful theories (and those that are least likely to be wrong) are those that are logically coherent and deductively rigorous. Evolutionary approaches bring with them many sophisticated tools that ensure deductive rigor (e.g., the strict computational logic of evolutionary game theory, inclusive fitness theory, and means of mathematically modeling the relative fitness outcomes associated with different behavioral strategies).

Useful theories must also be generative, producing novel, testable hypotheses (Lakatos, 1970; Ketelaar & Ellis, 2000). Darwin's theory of evolution by natural selection is arguably the most generative scientific theory of all time. And when these basic evolutionary principles are applied to human behavior, they can be used to deduce psychological theories that have proven to be extraordinarily generative as well, including theories pertaining to reasoning processes (Cosmides & Tooby, 2005), person perception (Zebrowitz & Montepare, 2006), interpersonal relationships (Buss & Schmitt, 1993; Gangestad & Simpson, 2001), and more. Evolutionarily informed theories in social psychology have yielded many novel—and often very subtle and non-obvious—hypotheses bearing on a wide range of topics, including not only those that are straightforwardly linked to human evolution, but also many that are not. Many of these novel hypotheses involve predictive constructs (e.g., likelihood of conception, ambient darkness) that are straightforwardly derived from

evolutionary analyses but lie well outside the conceptual architecture of traditional psychological theories. Further demonstrating the value of the approach, other novel evolutionary hypotheses focus on finer-level outcomes well beyond the specifications of traditional conceptualizations (e.g., specific emotional reactions rather than general prejudice; short-term versus long-term mate value rather than general level of attraction).

Another important criterion for evaluating scientific theories is explanatory coherence (Thagard, 2000). An evolutionary perspective reveals deep conceptual connections between many different, and superficially unrelated, forms of social behavior. For example, evolved kin recognition mechanisms provide conceptual links between phenomena as superficially different as altruistic behavior, the similarity-liking effect, and incest avoidance, and the theory of differential parental investment has implications for domains as diverse as altruism, aggression, conformity, and creativity. An evolutionary approach can conceptually integrate many of social psychology's "mini-theories," forging a less piecemeal, more conceptually coherent understanding of social behavior.

An evolutionary approach also integrates findings across different levels of analysis and description, connecting phenomena at the individual level of analysis (e.g., attentional processes) with phenomena at the population level (the evolution of the mechanisms that produce those attentional processes). Evolutionary explanations connect empirical observations of ongoing cognitive processes with very different kinds of facts and speculations about pre-human ancestors, primate relatives, and life on Earth more broadly. Therefore, an evolutionary approach to social psychology provides a unique means of integrating social psychological findings with a much broader set of scientific findings within the biological, historical, cognitive, and social sciences (e.g., behavioral ecology, paleontology, linguistics, anthropology). In contrast to some of psychology's subdisciplines (such as sensation and perception), social psychology has traditionally fallen closer to the social sciences than the biological sciences, with its findings being of greater interest to sociologists and political scientists than to colleagues in the natural sciences. But that is changing, following the emergence of evolutionary social psychology and parallel developments in social neuroscience. This bodes well for the long-term vitality of social psychology.

ENVOI

Humans are animals. As such, human brains, like the brains of all animals, evolved via natural selection to solve the

types of recurring fitness-relevant problems that our ancestors faced long ago. Perhaps more important, people are *social* animals. The problems faced by our ancestors thus included not only those faced by all animals (e.g., resource acquisition, self-protection, mating), but also those specific to social life (e.g., affiliation and coalition maintenance, status-seeking, intergroup conflict). These assertions should be uncontroversial. Yet the discipline of social psychology, which has dedicated itself to the exploration of human social life, traditionally disregarded the fact of this evolved nature in its attempts to uncover the principles and facts of social behavior. This was a mistake. Three decades ago, one of us encountered more than one senior social psychologist who vehemently denigrated “grand theories” and advocated instead for the value of “mid-level” theories—as if seeking the former would be akin to Icarus’s folly. In light of impressive conceptual and empirical advances in recent years, it is our sense that any folly lies instead in ignoring the demonstrably most powerful, integrated set of ideas in the natural sciences—evolutionary theory—in social psychology’s efforts to truly understand the fascinating complexities of human behavior.

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