Beyond the Pleistocene: Using Phylogeny and Constraint to Inform the Evolutionary Psychology of Human Mating

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Evolutionary psychologists explore the adaptive function of traits and behaviors that characterize modern Homo sapiens. However, evolutionary psychologists have yet to incorporate the phylogenetic relationship between modern Homo sapiens and humans' hominid and pongid relatives (both living and extinct) into their theorizing. By considering the specific timing of evolutionary events and the role of evolutionary constraint, researchers using the phylogenetic approach can generate new predictions regarding mating phenomena and derive new explanations for existing evolutionary psychological findings. Especially useful is the concept of the *adaptive workaround*—an adaptation that manages the maladaptive elements of a pre-existing evolutionary constraint. The current review organizes 7 features of human mating into their phylogenetic context and presents evidence that 2 adaptive workarounds played a critical role as Homo sapiens's mating psychology evolved. These adaptive workarounds function in part to mute or refocus the effects of older, previously evolved adaptations and highlight the layered nature of humans' mating psychology.

Keywords: evolutionary psychology, human mating, phylogeny, constraint, attachment

Only a few years after the publication of *On the Origin of Species* (Darwin, 1859), the scientific community and the public at large had become captivated by the possibility that humans had an evolutionary heritage that stretched back millions of years. That we are bonafide members of the animal kingdom, descended from an ancestral line that also gave rise to modern chimpanzees and bonobos, has played a central role in scientific thought ever since. Great discoveries across a variety of disciplines, from molecular biology to biological anthropology, are the direct consequences of the application of evolutionary theory to human behavior and morphology. Thanks, in large part, to the efforts of evolutionary psychologists over the past several decades (Buss & Kenrick, 1998), the role of evolutionary theorizing in explaining human behavior is unlikely to be lost on today's psychological researchers. Even researchers who do not specifically claim to study evolutionary psychology frequently develop evolutionarily inspired, functional accounts of the psychological processes they unearth. By examining how our own psychological contours reflect the sculpting hand of natural selection, we understand more about the human condition—about why we do the things we do.

Evolutionary theorizing can generate two different kinds of answers to this ultimate question of "why" an organism might exhibit a particular trait, as Tinbergen (1963) noted almost 50 years ago. One entails examining a trait's function, which helps to explain its adaptive significance, whereas the second entails examining a trait's phylogenetic history, which sheds light on its evolutionary development over time. In practice, evolutionary psychologists are primarily guided by one of the two "why" questions: the question of adaptive function. Nearly all of the major discoveries to come out of evolutionary psychology have derived from adaptationist thinking (Andrews, Gangestad, & Matthews, 2002; Buss, Haselton, Shackelford, Bleske, & Wakefield, 1998). Andrews et al. (2002) argued that the best way to determine that a particular trait is an evolved adaptation is to acquire evidence of "special design," which means, at a minimum, that the trait (a) executes a particular function with specificity and proficiency and (b) could not likely arise by means of a general-purpose learning mechanism. Today, most evolutionary psychologists search for evidence that different features of the human psyche exhibit such special design, thus permitting the conclusion that those features have been modified for a particular function by natural selection over the course of evolutionary history.

As psychologists have embraced the adaptationist program, what has become of phylogeny—the examination of a trait as it evolved over time? This second ethological question (which Tinbergen, 1963, ironically labeled "evolution") has not been as popular and is virtually absent from psychological theorizing (but see Fraley, Brumbaugh, & Marks, 2005; Maestripieri & Roney, 2006). Although a few evolutionary psychologists have made the explicit claim that phylogenetic analyses are unlikely to be useful in understanding human behavior (e.g., Thornhill, 1997; Tooby & Cosmides, 1989; but see Thornhill, 2007), more commonly phylogenetic considerations are simply ignored by evolutionary psychologists. Although adaptationism is sufficient for testing many evolutionary hypotheses (Andrews et al., 2002), I suggest that evolutionary psychology as a whole would benefit from acknowledging the specific time course of events that has characterized

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humans' evolutionary history. I argue that such an approach can shed new light on myriad aspects of humans' mating psychology and that it (a) generates new predictions that are not easily derivable from adaptive reasoning alone and (b) has important implications for existing evolutionary psychological concepts.

This review is organized into three sections. In the first, I discuss the concept of evolutionary constraint, one of Steven J. Gould's many notable contributions to evolutionary biology (Gould, 1980, 1989a).[1] Evolutionary psychologists have not addressed constraint as comprehensively as they have Gould's other favored concepts, such as spandrel (Gould & Lewontin, 1979) and exaptation (Gould & Vrba, 1982), which have received extensive attention elsewhere (Andrews et al., 2002; Buss et al., 1998). Constraint is a broad topic in evolutionary biology, and there are a variety of different sources of evolutionary constraint, such as physical laws that keep large organisms earthbound and force their actions to have equal and opposite reactions (i.e., formal constraint; see Gould, 1989a). The present review focuses primarily on *historical* or *phylogenetic constraint*, defined as a restriction on, or source of, evolutionary change that exists because of prior selection pressures. Evolution manages historical constraint in a variety of ways, and one common solution that makes two noteworthy appearances during the evolution of human mating is the *adaptive workaround*. Adaptive workarounds emerge at the intersection of constraint and natural selection. The concept is defined as a new adaptation that functions, in part, to manage the maladaptive elements of an existing adaptation currently serving as a historical constraint. The adaptive workaround is a conceptual tool that can aid psychologists in integrating the array of motivations and behaviors that characterize modern human mating psychology.

To fully appreciate the role of constraint in the evolution of human mating, researchers must take a detailed look at the timeline of human evolution. Therefore, in the second section of this article, I proceed (a) to discuss seven features of the human mating psychology that a complete evolutionary psychology should strive to integrate and (b) to describe the timeline of the evolution of hominid mating with respect to these seven features, as is best suggested by the current state of the anthropological and archaeological record. This analysis includes a special emphasis on the way natural selection may have handled existing evolutionary constraints at two time points: once around the emergence of the genus Homo and once again around the emergence of modern Homo sapiens.

In reviewing the specific timeline of human evolution, I follow in the footsteps of other researchers who have used a detailed exploration of the fossil record to inform our understanding of the mind. As one example, Wynn (2002) used evidence provided by hominid tool construction to document two major evolutionary steps in the development of human spatial cognition, both occurring during the Pleistocene epoch (1.8 million to 10,000 years ago) and linked to unique selection pressures. As another example, Mithen (1996) used a variety of archaeological evidence to argue that humans' conceptions of their social, natural, and technological worlds became more integrated over time and ultimately fused in the mind of modern Homo sapiens. As a third example, Leary and Buttermore (2003) tracked the evolution of different aspects of the self in our hominid ancestors. Such analyses provide powerful protection against "just-so" stories (Deleporte, 2002) and offer the best route toward answering Tinbergen's (1963) phylogenetic

question with respect to human evolution.[2] Although evolutionary psychologists would agree in principle that human mating psychology was fashioned by many divergent selection pressures operating within and beyond the Pleistocene epoch, the specific timing of events is a critical component of evolutionary constraint and therefore is essential for reaching a complete understanding of the evolved human psyche.

Third, and finally, once the reader is equipped with the principle of constraint and the specific timeline of human evolution, I highlight new predictions generated by the phylogenetic framework and implications of this approach. Specifically, the constraint-based approach and the adaptive workaround concept suggest that newer elements of the human mating psychology should be designed, in part, to manage historical constraints, exhibiting the capacity to either mute or refocus the effects of earlier adaptations toward a new adaptive purpose. For example, adaptations for adult mating pair-bonds evolved less than 2 million years ago to promote intersexual cooperation in the lineage leading to Homo sapiens. Therefore, adaptations for pair-bonding should moderate the function of older adaptations that threatened intersexual cooperation (e.g., ovulatory cycle adaptations; Gangestad, Thornhill, & Garver-Apgar, 2005), and indeed, some recent data are consistent with this prediction (Eastwick & Finkel, 2009; Gray, Kahlenberg, Barrett, Lipson, & Ellison, 2002). I also discuss the implications of this approach for the short-term versus long-term mating distinction, the origin of sex differences in mating behavior, and other central topics within evolutionary psychology. As phylogenetic considerations become incorporated into the evolutionary psychological toolbox, researchers will be able to generate novel hypotheses and hone existing functional explanations for various aspects of human mating psychology.

Before proceeding, I offer a brief note about the methods used to conduct phylogenetic analyses: Evolutionary biologists frequently construct elaborate phylogenetic trees and track changes in evolved characters across a wide range of species (e.g., Moreau, Bell, Vila, Archibald, & Pierce, 2006). Recently, scholars have argued for the application of such comparative methods within evolutionary psychology, noting that phylogenetic data can complement and strengthen adaptationist hypotheses (Maestripieri & Roney, 2006; Roney & Maestripieri, 2002). One example relevant to the present report found that paternal investment in offspring consistently predicts the evolution of pair-bonding across both mammalian and primate phylogenetic trees (Fraley et al., 2005). Such phylogenetic analyses are common in evolutionary biology, and they frequently require specialized software (e.g., MacClade 4.08; Maddison & Maddison, 2008; APE; Paradis, Claude, & Strimmer, 2004) to handle the complex computations across large numbers of species. Phylogenetic analyses can be difficult with

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[1] Of course, Gould did not invent the concept of constraint; that credit would likely go to Darwin (1859), who drew attention to the "unity of type" across different species that share a phylogenetic history.

[2] The "just-so" story criticism is not of great concern to evolutionary psychologists because, as mentioned above, those scholars tend to focus on adaptive design, not evolution and phylogeny per se (e.g., Kurzban & Haselton, 2006). That being said, the most complete understanding of humans' evolved psychology undoubtedly will emerge as researchers endeavor to answer both of Tinbergen's (1963) ultimate questions.

ancestral humans because of the relative paucity of data; nevertheless, they can still be used to study human evolution, even when attempting to document the emergence of uniquely human traits. Indeed, scholars such as Wynn (2002); Mithen (1996); and Leary and Buttermore (2003) have previously examined small numbers of hominid and closely related pongid species and placed characters on the established hominid phylogenetic tree by hand using the principle of parsimony.[3] The present report uses this latter type of phylogenetic analysis; of course, all phylogenetic analyses are relevant to Tinbergen's (1963) evolutionary question and have the potential to strengthen evolutionary psychological hypotheses.

Evolutionary Constraint

> Evolution is best viewed as a history of organisms finding devious routes for getting around constraints. (Richard Lewontin, as cited in Maynard Smith et al., 1985, p. 282)

Natural selection has never had the benefit of foresight; it can only take current selection pressures into account as it fashions adaptations. The preferred metaphor for natural selection, then, is not that of architect or engineer, who has the benefit of starting with the ideal raw materials and working according to a preconceived plan drawn up to perfection. Rather, natural selection is a tinkerer, managing with some preexisting set of structures and ignorant of the final form of the untidy creature that will ultimately emerge (Jacob, 1977). Adaptations may be complex wonders to behold, but equally fascinating features of organisms lie just below the adaptive surface and betray some of the curious pathways that natural selection has chosen. For example, consider the respiratory system in terrestrial vertebrates, in which the respiratory pathway crosses the digestive pathway. This crossing is clearly suboptimal, yet it exists in humans and other terrestrial animals because of historical necessity. The respiratory system in fishes is integrated with the digestive system, and it was easier for natural selection to fashion lungs from fish air bladders and nostrils from fish nares than to design a completely independent respiratory system for terrestrial living (Futuyma, 1998).

This example illustrates the essence of historical constraint: Because evolution proceeds by tinkering, new adaptations must contend with the outcomes of prior selection pressures (Gould, 1989a). In other words, the presence of an ancestral state guides evolution down certain phylogenetic paths, and therefore only a subset of the entire universe of possible designs is likely to be realized in a given lineage. It is easy to overlook the power of constraint because designs that "might have been" are frequently unobservable, even difficult to imagine. Nevertheless, the fossil record offers important insights regarding constraint in evolution: Gould (1989b) noted the incredible disparity in the basic body plans of organisms that appear in the fossil record around the time of the Cambrian explosion roughly 530 million years ago. As a result of the mass extinction that soon followed, only a small subset of those body plans survived (including, thankfully, the phylum Chordata, which gave rise to humans), and no new animal phyla have evolved since. That is, once individual lineages had evolved a sufficient degree of complexity, it became impossible to evolve adaptations that substantially modified that body plan (see also Sterelny, 2001). The chordate body plan has constrained vertebrate evolution ever since, serving as a backdrop to the variety of naturally selected variants that followed.

Typically, constraints gently nudge evolution in one direction or another over time. They mark the limits of the evolutionary space, and the evolved variation that emerges within this space can then be subjected to natural selection pressures (see Maynard Smith et al., 1985, for a graphical illustration). In some cases, however, a new environment may cause natural selection to crash headfirst into existing historical constraints. Natural selection is a powerful force, to be sure, but constraints can also prove obstinate, especially when they are deeply embedded in the morphology of the organism. As the tinkering power of natural selection scaffolds additional adaptations on top of older features, those older features become more resistant to change, more "locked in" (Maynard Smith et al., 1985). Adaptive workarounds are born from the conflict between such entrenched constraints and natural selection.

In the typical course of natural selection, a novel environment exerts selection pressure on a species, thereby generating new adaptations that solve specific adaptive problems. In principle, any single feature is free to evolve as a function of natural selection, and if a feature becomes maladaptive in a new environment (e.g., a finch's beak is too small to break plentiful large seeds; Grant, 1999), natural selection may change the parameters of the adaptation (e.g., by increasing beak size). But in cases where a trait is sufficiently constrained by its own phylogenetic history, new selection pressures may be unable to produce an adaptive solution within the evolvable space by acting on the trait alone (e.g., if finches suddenly had to survive on meat, they would probably become extinct before evolving teeth and fangs). In such cases, a second element—the adaptive workaround—may evolve. Adaptive workarounds are new adaptations that function in part to manage features that have become maladaptive historical constraints; in other words, adaptive workarounds cleverly evade, but do not break, historical constraints. As quoted at the beginning of this section, Richard Lewontin finds that the history of evolution is teeming with evidence of these "devious routes." Adaptive workarounds are evident at every evolutionary level, from microscopic elements of proteins to broad morphological features; several illustrative examples follow.

Workaround Example 1—The Panda's Thumb

As described by Gould (1980), pandas feed mainly on bamboo, and they strip the bamboo shoots of leaves before consuming the shoots. This stripping activity requires great dexterity, and the panda accomplishes it with the help of a sixth digit: a "thumb" that is both opposable and flexible. Anatomically, however, the thumb is not really a thumb at all; it is part of the radial sesamoid, which in most animals is a small bone in the wrist (see also Davis, 1964). That is, natural selection shaped part of the panda's wrist into a sixth digit in order to solve the problem of manipulating and stripping bamboo. The constraint in this case was that the ancestor of the panda only had five digits originally, and just as in other carnivores, these digits were already adapted for clawing and

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[3] This exercise is like a problem to be solved by hand from an evolutionary biology textbook; it is smaller in scope than the traditional evolutionary biological phylogenetic analysis but it is no less valid.

scratching, not grasping and stripping.[4] Natural selection evaded this constraint by adapting part of the panda's wrist into a thumb. The constraint itself was not eliminated—the panda's remaining five digits still accomplish many useful clawing and scratching functions. Instead, the panda's thumb served as an adaptive workaround that accommodated natural selection pressures while dodging the constraint.

Workaround Example 2—Shell Construction in Shipworms

A second example is discussed by Maynard Smith et al. (1985) in a classic article on constraint. The ancestor of modern-day shipworms faced an adaptive problem: How could it extract nutrients from decaying wood and exploit it as a habitat? Shipworms are not worms but bivalves, and bivalves possess two shells that grow in logarithmic spirals and are mirror images of one another (picture the two halves of a clam shell). A hard, circular surface is needed to bore into wood and extract its nutrients, and though shells are sufficiently hard, there is unfortunately nothing circular about the logarithmic spirals of the typical bivalve shell. The common ancestor of shipworms solved this adaptive problem by evolving an unusual body orientation such that the shells do not cover the organism for protection but are instead positioned at one end of the organism like a drill. The constraint remains intact: Shipworms still possess two shells that grow in logarithmic spirals. However, their spiral shells come together such that, with the new body orientation, a nearly circular surface is created. Shipworms press this surface against the wood and bore into it using a circular motion, creating cylindrical burrows and doing great damage to the hulls of wooden ships. By selecting for an unusual body orientation, natural selection generated a feasible adaptive workaround in the shipworm.

Workaround Example 3–The Blind Spot

The vertebrate retina is inverted, which means that the photoreceptor cells lie at the back of the retina, and the incoming light must pass through layers of blood vessels and other cells before hitting the rods and cones. Given the presence of the inverted design, the common ancestor of vertebrates faced a problem as selection pressures favored greater eye complexity (probably during the Cambrian period; see Lamb, Collin, & Pugh, 2007). Specifically, the neuronal signal needed to be relayed to the brain, but the efferent neurons were placed on the wrong side of the photoreceptor cells. The workaround solution is the blind spot, where all the outgoing neurons come together to form the optic nerve and leave the eye through a single, small gap in the retina. In this gap, there is no room for photoreceptors, thus creating the vertebrate blind spot that inspires several classic optical illusions. The blind spot is an adaptive workaround that leaves the historical constraint (i.e., the "backwards" orientation of the photoreceptor cells) intact while permitting the neuronal signal to exit the eye through the retina at a single, central location.

Workaround Example 4—Extended Neoteny in Humans

This fourth example is explained in some detail, as it is of central importance to this review and relates directly to the repro-

ductive strategy of modern humans (see Fisher, 1987, 1989; Miller & Fishkin, 1997). The Australopithecines first appear in the fossil record approximately 4 million years ago; these early hominids were adapting from the arboreal lifestyle of our pongid ancestors to a more terrestrial lifestyle. Key to this transition was that their anatomy permitted upright walking, which would have had several advantages in terms of heat reduction and foraging efficiency (Wheeler, 1991). Over the next 2 million years, the cranial capacity of the Australopithecines gradually increased until the emergence of the genus Homo, at which point selection pressures favored a rapid increase in cranial capacity (see Figure 1; McHenry, 1994; McHenry & Coffing, 2000). The boost in cranial capacity during this time period reflected the increased importance of tool use, social intelligence, and a high-quality diet as early Homo began to exploit the rich resources of the African savannah (Aiello & Wheeler, 1995; Mithen, 1996).

However, selection pressures favoring increased cranial capacity encountered a major constraint at this juncture in hominid evolution. The Australopithecine transition to bipedalism had narrowed the hominid birth canal (Miller & Fishkin, 1997); the size and orientation of the upright female pelvis set an upper limit on adult cranial capacity at approximately 700 cc (as described in Lewin, 1982). This 700-cc limit is calculated using the following logic: Typical primate postnatal development involves an approximately twofold increase in brain size (Dienske, 1986), and modern human infants have a cranial capacity of approximately 350 cc. Assuming that there is an extraordinarily large cost of giving birth to a human infant with a cranial capacity larger than 350 cc (an assumption supported by the considerable mortality rates during childbirth, even in the modern era), a 700-cc adult cranial capacity should have been the largest possible size, given the constraint of the female pelvis. The cranial size of Homo habilis averages 601 cubic centimeters—just shy of the 700-cc limit. However, Homo ergaster cranial capacities ranged from 712 cc to as large as 1,035 cc (McHenry & Coffing, 2000), and Homo erectus cranial capacities ranged up to 1,250 cc (Mithen, 1996).

How did early Homo species overcome this "obstetric crisis" and evolve such large adult brains? A key element was the evolution of an extended period of infancy. If the infant's head remained 350 cc at birth, it stood a chance of passing through the birth canal safely, even if such a relatively small head would mean that the infant did not achieve the primate standard one half of adult size. In other words, any adult hominid with a cranium larger than 700 cc would likely have given birth to immature young relative to typical primates, as the reduced prenatal brain growth would have to be recouped during an extended period of infancy outside the womb (B. H. Smith & Tompkins, 1995). This shift to postnatal brain growth achieved the adaptive goal of increased brain size while working around the constraint imposed by the engineering of the pelvis. However, this tradeoff meant that early Homo infants were exceptionally altricial, requiring a level of care

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[4] There is an additional formal constraint that would have prevented the panda from evolving a true (i.e., independent) 6th digit: Put simply, the embryonic limb bud is not large enough to permit a 6th digit. The genes that regulate the development of digits carve the embryonic limb bud into 5 regions (Tabin, 1992), and any one region (depending on its size, see Alberch, 1985) may or may not generate a digit during development.
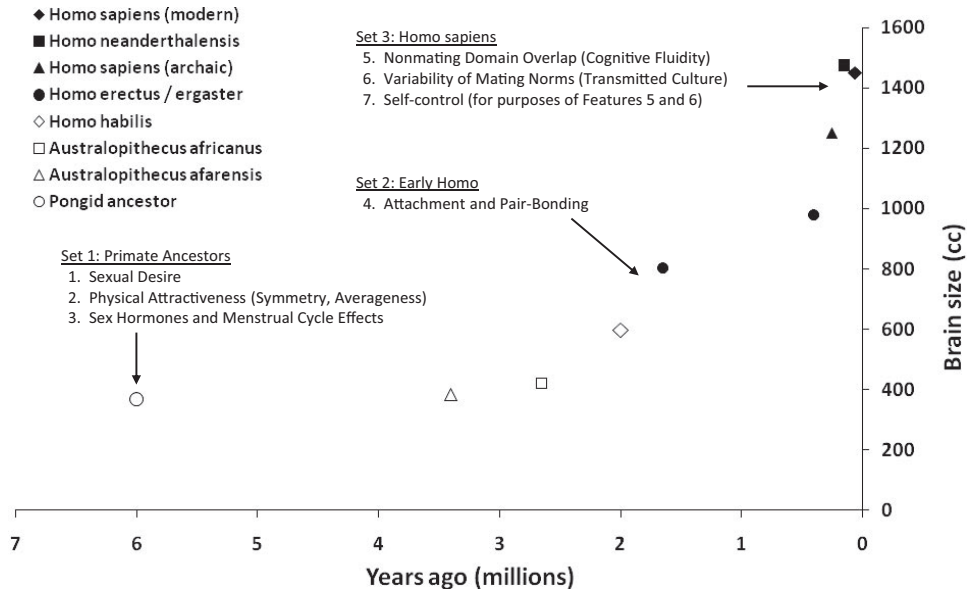
Figure 1. Cranial capacity (cubic centimeters) plotted against time (millions of years before present). Values are from McHenry (1994) and Mithen (1996); value for pongid ancestor is estimated from the average cranial capacity of extant bonobos and chimpanzees. Features of human mating (see Table 2) are organized according to the approximate time frame in which they evolved in the lineage leading to Homo sapiens.

far exceeding that of pongid infants, who can cling to their mother from birth. This new adaptive problem, extended human neoteny, was a major force in inspiring yet another workaround directly relevant to the hominid mating system to be discussed in detail later in this review.

Table 1 presents a summary of these four adaptive workaround examples. As the table illustrates, each example is characterized by (a) a historical constraint that has become maladaptive in a new environment, (b) a selection pressure favoring a new adaptation, and (c) a workaround solution that leaves the constraint intact but solves the adaptive problem. Although none of the four examples cited above dealt with mental adaptations per se, natural selection, of course, operates on the brain just as it operates on other features of organisms and is therefore a potentially rich source of adaptive

workarounds. In fact, the brain is literally layered such that newer structures (i.e., the neocortex) are scaffolded precariously on top of the old (i.e., the limbic system), a design that betrays the methods of its tinkering creator (Jacob, 1977). Table 1 also contains a summary of the two adaptive workarounds reviewed below that are central to the evolution of human mating.

There is one final point regarding the adaptive workaround that is worth noting: It is rarely true that the historically constrained trait will be rendered entirely maladaptive in the new environment. After all, the panda's digits are still extremely effective for scratching and clawing, and walking upright continued to provide many advantages for early hominids. Likewise, we would expect to find that any older mental adaptations that served as constraints during the evolution of human mating would con-

Table 1
Adaptive Workaround Examples

Example	Historical constraining element	Selection pressure	Adaptive workaround
Panda's thumb	Paws built for clawing	Capacity to grasp and strip bamboo	Wrist adapted for thumblike function
Shipworm	Shells grow in logarithmic spirals	Boring into wood requires a circular surface	Select unusual body orientation that allows shells to form a near-circular surface
Blind spot	Photoreceptor efferent neurons oriented "backwards"	With greater eye complexity, axons must pass through retina	Neuronal signal exits the eye at one central blind spot
Extended neoteny	Pelvis size limited by upright posture	Larger brains confer selective advantage	Brain develops longer outside the womb
Adaptation Set 2 (see Table 2)	Prior adaptations foster intersexual conflict	Raising of altricial infants requires intersexual cooperation	Attachment processes mute or refocus adaptations that foster conflict
Adaptation Set 3 (see Table 2)	Impulses incongruent with cultural norms, beliefs	Ability to override impulses, conform to culture	Self-control mutes or refocuses impulses in the service of beliefs and transmitted culture

tinue to remain adaptive under some, but not all circumstances in modern Homo sapiens.

Applying Phylogeny and Constraint to the Evolution of Human Mating

Traditionally, evolutionary psychologists have explored human mating by searching for evidence that particular mental adaptations are specially designed to address mating-relevant adaptive problems. Herein, I present a different, but equally evolutionary, two-step approach. First, I start not with particular adaptive problems but instead with a broad, descriptive approach. For this report, I have selected seven features of human mating (see Table 2), and in the section that follows, I argue for their importance in the mating lives of the majority, if not all, of Homo sapiens. Although research on some of these features (e.g., nonmating domain overlap, self-control in the mating domain) is just now beginning to emerge, I contend that a complete evolutionary psychology of human mating should strive to eventually explain the evolutionary origin of at least these seven features. Together, these features are likely to account for a healthy portion of humans' mating behavior, and they provide a useful starting framework that will subsequently allow for other important features to be incorporated.[5] Second, after identifying each of these seven features, I attempt to place each one within its evolved context by asking two complementary questions. First, did we inherit the feature from our primate ancestors? In other words, does the evidence suggest that the feature was already present and relevant to hominid mating when we diverged from our most recent common ancestor with the apes approximately 6 million years ago? If the answer is no, a second question becomes relevant: What selection pressures operated during the past 6 million years that fashioned mental adaptations relevant to the mating feature in question? To the extent that the archaeological record allows, I follow in the footsteps of Wynn (2002); Mithen (1996); and Leary and Buttermore (2003) and estimate the specific point during this 6 million year span at which a particular feature might have evolved. The phylogenetic picture of human mating that emerges from this analysis suggests that natural selection generated adaptive workarounds to deal with previously existing constraints at two different points during hominid evolution. The first of these adaptive workarounds appears toward the beginning of the Homo lineage, and the second appears at approximately the arrival of modern Homo sapiens. This approach allows for the evolution of human mating to be carved into three layers, or "sets," for conceptual purposes (see Table 2).

This constraint-based evolutionary approach generates new predictions, and I describe data that offer some initial empirical support for the approach in the final section of this article. In addition, the present analysis raises alternative explanations for some existing evolutionary psychological findings, providing fertile ground for new data to disentangle these explanations and produce an ever richer evolutionary psychology.

Seven Central Features of Human Mating

Feature 1: Sexual Desire

Sexual desire provides a useful starting point because of its obvious importance in motivating mating-relevant behavior. To-

day, a wide variety of independent motives are recognized and studied by psychologists (see Shah & Gardner, 2008), and sexual desire is included in this lot. But even during the heyday of behaviorism, when only a few broad motivations were thought to be sufficient to underlie all behavior, sexual desire was listed among them, alongside hunger, thirst, and pain (Hull, 1943). That is, even the behaviorists recognized that sex is frequently a reward in and of itself: The motivation to have sex does not need to be taught, although learning certainly plays an important role in shaping the intensity of the desire as well as sexual expression and behavior (e.g., Edward A. Smith & Udry, 1985). Typically, people experiencing sexual desire will be more likely to exhibit behaviors intended to increase the likelihood of sexual contact or, at a minimum, achieve some level of sexual gratification (e.g., masturbation). In addition, sexual desire is nearly universal: One recent study found that a mere 1% of respondents in a British representative sample identified themselves as asexual by agreeing with the item "I have never been sexually attracted to anyone at all" (Bogaert, 2004). Sexual desire is clearly an important motivator in humans, and because it inspires the reproductive act itself, its evolutionary significance is obvious.

The origin of sexual desire in humans. We cannot directly ask nonhuman animals whether they experience sexual desire. However, we can look for sensible correlates in animals, such as genital arousal or the inclination to pursue sex, and of course, sexually reproducing animals show precisely such tendencies. They, like humans, do not need to be taught to have sex; although also like humans, many animals (e.g., wolf spiders, Hebets, 2003; Japanese quail, White & Galef, 2000) show evidence that learning processes can direct sexual desire toward certain targets. The evolutionary origins and advantages of sexual (compared with asexual) reproduction constitute a vast and fascinating topic in its own right (Hurst & Peck, 1996), and a detailed review of that literature is not necessary here. Suffice it to say that sexual desire has deep evolutionary roots, perhaps as deep as sexual reproduction itself. Given that (a) our closest living ape relatives show evidence of sexual desire and (b) our common ancestor was certainly a sexually reproducing species, it is safe to conclude that we inherited this feature from our pongid ancestors. In other words, sexual desire was not an adaptation that arose during hominid evolution.

Feature 2: Physical Attractiveness (Symmetry, Averageness)

Humans tend to romantically desire physically attractive individuals. In studies that have examined live romantic interactions, there is an extremely large correlation ($r \approx .7$) between the extent to which a participant finds a potential romantic partner to be physically attractive and the participant's romantic desire for that partner (Walster, Aronson, Abrahams, & Rottmann, 1966; see meta-analysis by Feingold, 1990). Some aspects of physical attractiveness, such as thinness in women, have changed over the

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[5] In selecting these features, I did not assume a priori that they would be relevant solely to mating (i.e., that they are domain-specific). In fact, at least three features (nonmating domain overlap, variability of mating norms, and self-control) of the seven are partially domain general in that they extend to other aspects of mental life. (Physical attractiveness and attachment debatably could fit in the domain-general category as well.)

Table 2
Seven Features of Human Mating

Feature	Origin	Adaptation set
1. Sexual desire	Primate ancestors: >6 million years	1
2. Physical attractiveness (symmetry, averageness)	Primate ancestors: >6 million years	1
3. Sex hormones and menstrual cycle effects	Primate ancestors: >6 million years	1
4. Attachment and pair-bonding	Early Homo: 1.5 to 2 million years	2
5. Nonmating domain overlap (cognitive fluidity)	Homo sapiens: 40,000–50,000 years	3
6. Variability of mating norms (transmitted culture)	Homo sapiens: 40,000–50,000 years	3
7. Self-control (for purposes of Features 5 and 6)	Homo sapiens: 40,000–50,000 years	3

years (Pettijohn & Jungeberg, 2004) and differ across cultures (Anderson, Crawford, Nadeau, & Lindberg, 1992), but other aspects, such as the determinants of facial attractiveness, show substantial cross-cultural agreement (Langlois et al., 2000). Indeed, the importance of physical attractiveness does not appear to be limited to Western cultures (e.g., Gangestad & Buss, 1993).

Researchers have also uncovered several reasons why some people are considered to be more attractive than others. For example, physically attractive individuals tend to have symmetrical faces (Grammer & Thornhill, 1994), and their facial features tend to approximate the population average (Langlois & Roggman, 1990). A conceptually similar construct is fluctuating asymmetry, which refers to (often imperceptible) differences between an organism's bilateral features (e.g., hands, feet, ears). Humans with lower fluctuating asymmetry (i.e., more symmetrical individuals), especially men, tend to be more romantically desirable and have more attractive faces (Gangestad & Simpson, 2000). Given these associations between symmetry, averageness, and attractiveness, I have grouped them collectively as part of this second feature of human mating for the purposes of this review.

Why is physical attractiveness such a potent predictor of romantic attraction? This is a contentious question in evolutionary psychology, and there are at least three possible answers. The first is the "good genes" explanation, favored among many evolutionary psychologists. According to this explanation, physical attractiveness and associated constructs such as symmetry signal a robust developmental history (Thornhill & Gangestad, 1993, 1999). Some organisms possess genes that are more successful at fighting off illness and pathogens, and these healthier organisms develop to be more symmetrical. This symmetry serves as a signal of genetic fitness, and therefore organisms have evolved to prefer such symmetrical individuals as mating partners because the offspring of the symmetrical individual will likely inherit these genetic advantages.

A second possibility is that pronounced unattractiveness signals the presence of "bad genes." On the surface, this bad genes explanation seems indistinguishable from the good genes explanation described above. The novel element of the bad genes hypothesis as advocated by Zebrowitz, Fellous, Mignault, and Andreoletti (2003) is that there would only be an adaptive benefit to avoid mating with individuals in the lower portion of the physical attractiveness distribution. In other words, very unattractive faces signal genetic anomalies that could have negative consequences for an offspring's fitness, but extremely attractive individuals are no more genetically fit compared with individuals in the middle of the attractiveness range. This account is supported by

evidence that physical attractiveness correlates with health only in the lower half of the attractiveness distribution (e.g., Zebrowitz & Rhodes, 2004). The fact that physical attractiveness is still positively associated with romantic desirability and other positive qualities (e.g., intelligence) across the entire range of physical attractiveness is explained as an overgeneralization of the bad genes avoidance mechanism.

A third possibility is that physical attractiveness effects are due to the perceiver's feeling of fluency upon seeing a physically attractive individual. Fluency is experienced when a stimulus is processed easily, and processing ease is often marked with positive affect because it indicates that a stimulus is familiar (Zajonc, 1998) and is likely to be recognized and categorized quickly (for a review, see Reber, Schwarz, & Winkielman, 2004). Why should the perception of attractive individuals result in greater fluency compared with the perception of unattractive individuals? Symmetrical stimuli and average, prototypic stimuli are easier to process, and as noted above, these features are associated with physical attractiveness. Therefore, liking of physically attractive individuals may result from the experience of fluency that comes with processing a stimulus that is symmetrical or closely approximates a prototype. Given that processing fluency is associated with liking for a wide range of stimuli (Reber et al., 2004; Reber, Winkielman, & Schwarz, 1998), this third explanation for the association between physical attractiveness and attraction may not be specific to mating (i.e., it is domain general; see Halberstadt, 2006).

The origin of the desire for physically attractive partners in humans. Again, we cannot ask nonhuman animals whether they prefer physically attractive mating partners. In fact, it is not immediately obvious how one would assess whether an animal considers a conspecific to be physically attractive in the first place. However, we can examine evidence among nonhuman animals for the possible mechanisms underlying the physical attractiveness effects reviewed above. Whether one favors the good genes, the bad genes, or the fluency explanation for physical attractiveness effects in humans, supporting evidence for these mechanisms is found in nonhuman animals. For example, animals naturally avoid mating with sick or diseased individuals (e.g., Ehman & Scott, 2002), and evolutionary models of good genes sexual selection were originally developed on nonhuman animals and were only later extended to humans (Gangestad & Simpson, 2000). Fluctuating asymmetry in particular is associated with mating success across a wide variety of animal (see meta-analysis by Moller & Thornhill, 1998) and even plant (Moller, 1996) species. In addition, greater facial symmetry is associated with better health

among chimpanzees, our closest animal relatives (Sefcek & King, 2007). In support of the fluency explanation, animals also prefer symmetrical patterns (Rensch, 1957), and it is possible that this general tendency to mark symmetrical or average patterns with positive affect extends to the mating domain for animals as well. In short, whatever one's favored mechanism underlying humans' preference for physically attractive mating partners, the evidence suggests that those mechanisms have deep evolutionary roots within the human psyche and were inherited from our most recent common ancestor with other primates.

Feature 3: Sex Hormones and Menstrual Cycle Effects

Humans' sexual behavior is directly tied to several hormones. Some of these hormones, such as the androgens (e.g., testosterone), exist at greater levels in men compared with women, whereas others, such as the estrogens (e.g., estradiol), exist at greater levels in women compared with men. Nevertheless, both classes of sex hormones have important functions in both sexes. For example, testosterone is positively associated with sexual desire in both men and women, and low levels of testosterone can contribute to impotence in men. Indeed, testosterone supplements are often effective at both alleviating erectile dysfunction in men (Jain, Rademaker, & Mcvary, 2000) and increasing sexual desire in women (Simon et al., 2005).

Researchers have known for some time that sex hormones play essential roles in the reproductive lives of humans, including the fact that women's sexual behavior appears to change across the menstrual cycle (e.g., Udry & Morris, 1968). However, the psychological effects of sex hormones have received increased attention from researchers in recent years, and these findings offer vivid evidence that natural selection has shaped the sexes differently. For example, men evidence higher levels of testosterone after interacting with (and especially after trying to impress) an attractive woman (Roney, Mahler, & Maestripieri, 2003). In addition, an explosion of recent research has explored shifts in women's mating strategies across the menstrual cycle. This research has demonstrated that fertile (i.e., ovulating) women are more likely than women at the nonfertile stage of their menstrual cycle to prefer short-term mates that are symmetrical (Gangestad & Thornhill, 1998), socially dominant (Gangestad, Garver-Apgar, Simpson, & Cousins, 2007), masculine (Penton-Voak & Perrett, 2000), and creative (Haselton & Miller, 2006). In addition, when they are fertile, women dress to impress (Durante, Li, & Haselton, 2008; Haselton, Mortezaie, Pillsworth, Bleske-Rechek, & Frederick, 2007) and are more likely to want to go out to locations where they might meet desirable members of the opposite sex (Haselton & Gangestad, 2006). Furthermore, women who are dating romantic partners who are not desirable short-term partners are more likely to be attracted to other men when they are fertile relative to nonfertile (Haselton & Gangestad, 2006). Although these lines of research have not yet determined which hormones are mediating these effects, they clearly demonstrate that women's mating behavior changes in theoretically sensible ways across the menstrual cycle.

The origin of sex hormones and menstrual cycle effects in humans. Not surprisingly, the same hormones that regulate the human reproductive system have deep mammalian roots and play nearly identical roles in the reproductive lives of our close primate relatives. Although menstrual cycle length differs by a few days across the great apes, the pattern of follicle-stimulating hormone, estrogen, and progesterone seen in the human menstrual cycle is extremely similar to the pattern seen in chimpanzees, bonobos, gorillas, and orangutans (Shimizu et al., 2003). Natural selection seems to have left this critical reproductive mechanism more or less intact over the course of primate evolution. Our primate relatives also show psychological effects similar to those found in humans. Just as men's testosterone increases after interacting with an attractive woman, male chimpanzees evidence elevated levels of testosterone in the presence of desirable (i.e., parous) females (Muller & Wrangham, 2004). Like humans, female chimpanzees are sexually receptive throughout their menstrual cycle, but also like humans, female chimpanzees' mating behaviors change predictably during their cycle. For example, female chimpanzees are more selective (Stumpf & Boesch, 2005) and tend to prefer dominant males (Matsumoto-Oda, 1999) when they are fertile. This research investigating the hormonal influence on female mate choice in nonhuman primates is only recently starting to emerge, in step with the parallel research in humans. Nevertheless, the evidence to date suggests that natural selection honed the physiological and psychological functions of male and female sex hormones during the eons prior to the emergence of the Homo lineage. Although human females have not retained the obvious sexual swellings seen in chimpanzees (Pawlowski, 1999), in most other ways, humans do appear to have inherited the hormonal underpinnings of mating behavior from the most recent common ancestor with chimpanzees.

Feature 4: Attachment and Pair-Bonding

Bowlby developed attachment theory to explain several aspects of the infant–caregiver relationship (Bowlby, 1958, 1969). Human infants become attached to their caregivers around 6 to 8 months of age, approximately the time that infants start to become mobile. Infants begin to exhibit four distinct attachment behaviors at this time: proximity seeking (behaviors that bring the infant nearer to the attachment figure), separation distress (protest behaviors when the attachment figure is unavailable), safe haven (searching out the attachment figure for comfort), and secure base (using the attachment figure as a base for exploration). These behaviors serve the adaptive function of keeping the infant in close contact with the attachment figure for care and protection. Hazan and Shaver's (1987) ground-breaking insight was that attachment dynamics also have great theoretical utility for understanding adult romantic relationships. Romantic partners typically develop emotional bonds, and these bonds bear a striking resemblance to infant–caregiver bonds (Shaver, Hazan, & Bradshaw, 1988). For example, participants in firmly established relationships are more likely to report that they direct their proximity-seeking, separation distress, safe haven, and secure base behaviors toward their current partner compared with any other person (Hazan & Zeifman, 1994). Over the past 20 years, research on attachment theory and its implications for behavior in adulthood has exploded, and it is now one of the dominant theoretical perspectives on romantic relationships (Mikulincer & Shaver, 2007).

The vast majority of research on attachment theory derives from Ainsworth's classic studies (see Ainsworth, Blehar, Waters, & Wall, 1978) highlighting different ways that infants are attached to

their caregivers (e.g., secure, anxious, avoidant). The literature on individual differences in adult attachment style is enormous, and its theoretical coherence suggests that romantic relationships are attachment-relevant contexts. However, a small but growing body of research on normative attachment dynamics makes an even more powerful case that attachment is a central feature of human mating. This research has explored how the attachment system works adaptively in romantic relationships to form and maintain attachment bonds and how those bonds affect health and well-being. One flagship study on this topic studied romantic partners at an airport. Attachment theory predicts that separation should elicit attachment behaviors among bonded individuals, and indeed, partners who were facing an impending separation were more likely than participants who were not separating to engage in behaviors that had clear attachment connotations, such as contact seeking (e.g., remaining by the window after the plane has left) and caregiving (e.g., patting or soothing the partner; Fraley & Shaver, 1998). Furthermore, attached individuals' physiological states are often tightly coregulated, and therefore a separation or loss experience can precipitate a state of physiological withdrawal, disorganization, and even a full-blown stress (i.e., "fight or flight") response (Sbarra & Hazan, 2008; see also L. M. Diamond, Hicks, & Otter-Henderson, 2008). Social neuroscience has also started to make significant contributions to the attachment field, finding for example that holding the hand of one's spouse while anticipating an electric shock reduces the threat-related neural response (Coan, Schaefer, & Davidson, 2006). Finally, other recent evidence has suggested that attachment dynamics are relevant even during the initial stages of romantic relationships. Just as infants approach attachment figures when they experience anxiety, participants who experience attachment anxiety about a desired romantic partner are more likely to approach and initiate contact with the desired individual (Eastwick & Finkel, 2008).

Individual difference measures of adult attachment style have been validated across a variety of cultures worldwide (e.g., Schmitt et al., 2004a), but the normative adult attachment perspective has not received as much cross-cultural attention. However, attachment processes are implicated in the experience of passionate love, a topic that has been the subject of considerable cross-cultural research. For example, Jankowiak and Fischer (1992) documented the existence of romantic love in 88.5% of the cultures in Murdock and White's Standard Cross-Cultural Sample (Murdock & White, 1969), noting that only one ethnographer in this sample specifically denied the existence of romantic love. Passionate love has strong theoretical (L. M. Diamond, 2003; Hazan & Diamond, 2000) and empirical (Eastwick & Finkel, 2008) ties to the attachment-behavioral system; passion emerges when both the sexual and attachment systems are active and directed toward a particular romantic partner. Therefore, cross-cultural research on passionate love provides some support for the suggestion that normative attachment processes characterize human mating cross-culturally.

One final point is worth noting: In the anthropological and biological literatures, scholars often use the term *pair-bond,* like the term *attachment,* to refer to a relationship between two adult organisms that is characterized by affection, stability, reciprocity, and proximity seeking (Fuentes, 2002; Hinde, 1983; Krebs & Davies, 1997). Many anthropologists and evolutionary biologists are less than sanguine about the possibility that pair-bonds are broadly characteristic of Homo sapiens (e.g., Barash & Lipton, 2001; Fuentes, 1998). Perhaps the most consistently cited evidence against pair-bonding in humans is the fact that only a minority of cultures worldwide are strictly monogamous, with the majority allowing polygamous marriages (Murdock, 1967). However, attachment between adult romantic partners does not require a monogamous mating system; the human capacity to develop emotionally bonded romantic relationships is unlikely to be limited to any particular mating system (Fraley et al., 2005). Monogamy rates (or infidelity rates, see *Implications* section) do not address the psychological experience of attachment, and it is this psychological perspective that has made an enormous contribution to the science of human romantic relationships over the past two decades.

The origin of attachment and pair-bonding in humans. Dating the origin of Features 1–3 in humans was a relatively straightforward endeavor. It was parsimonious to suggest that those features evolved prior to the emergence of the Australopithecines and the Homo lineage that followed, mainly owing to the fact that those features also characterize modern great apes. As far as attachment is concerned, a huge variety of primates clearly possess well-developed attachment systems that operate during infancy. Some of the initial studies conducted in the wake of Bowlby's initial theoretical publications examined rhesus monkeys (Harlow & Zimmermann, 1959), and phylogenetic evidence suggests that the evolution of the infant–caregiver attachment system may approximately coincide with the emergence of the lineage ($\sim$35 million years ago; Schrago & Russo, 2003) that would eventually lead to the apes and Old World monkeys (Maestripieri, 2003; Maestripieri & Roney, 2006). However, there is no evidence for adult reproductive pair-bonds among orangutans, chimpanzees, bonobos, or gorillas. Adult gibbons do form pair-bonds, but our most recent common ancestor with the gibbons is older than our most recent common ancestor with the rest of the apes. Therefore, the parsimonious inference is that the evolution of adult attachment in humans is likely to be an event that took place sometime within the past 6 million years.

Before using the fossil record to estimate the point at which adult attachment evolved in the lineage leading to Homo sapiens, it is useful to first review the adaptive significance of this feature. Attachment theorists argue that the attachment-behavioral system, which already existed for the purpose of bonding in infancy, was modified by natural selection to bond adult mating partners to each other (Fraley & Shaver, 2000; Hazan & Diamond, 2000; Miller & Fishkin, 1997; Zeifman & Hazan, 2008). When bonded, two mating partners would be less likely to seek alternative mating partners and would be more invested in raising the offspring produced by this primary partnership. However, the attachment bond would not necessarily need to be permanent: At a minimum, the bond should be strong enough to carry a mating pair through gestation, childbirth, and the early stages of child rearing. Indeed, Fisher (1987, 1989) has demonstrated cross-culturally that if a pair bond does dissolve, it is most likely to dissolve at the 4-year mark, and Fisher drew a parallel between this divorce pattern and the average birth interval in nonindustrial societies. Among the Yanomamo, Australian Aborigines,!Kung San, and other hunting and gathering societies, 4 years is the typical period between successive births for women (Fisher, 1989; Lancaster & Lancaster, 1983). Therefore, a pair-bond would last long enough to reach the weaning stage for a single child at a minimum; these observations

led Fisher to declare that humans evolved to be a serial pair-bonding species.

What selection pressures led to the emergence of pair-bonding in humans? One important factor was increased importance of paternal investment in offspring (Fraley et al., 2005). As is evident in nonindustrial human cultures today, paternal investment offers substantial benefits for offspring, including a reduction in infant and child mortality (Geary, 2000). For example, an Ache child without a father is three times more likely to die from illness than if the child's father were present (Hurtado & Hill, 1992). If paternal investment became more important to the fitness of offspring at a particular point during human evolution, it makes sense that the attachment system would have been co-opted by natural selection to facilitate a shift in male mating strategy toward greater investment.

Yet pair-bonding is a rare adaptation in primates, and although many primate males do offer some care for offspring, they provide substantially less care than do females. According to parental investment theory (Trivers, 1972), males, as compared with females, can reproduce successfully by investing fewer resources in offspring. As a result of this conflict of interest, natural selection often shapes the sexes differently; as noted above, sex-differentiated effects of natural selection are revealed by the behavior of Homo sapiens (see Feature 3). Surely, sexual selection (i.e., pressures that foster intersexual or intrasexual conflict in the mating domain) was a prominent evolutionary force prior to the emergence of pair-bonding, as it has clearly impacted the rest of the great apes (e.g., body size dimorphism in gorillas, large testes in chimpanzees). However, with the evolution of pair-bonding, males would be substantially more likely to invest in their own offspring (Hazan & Diamond, 2000; Miller & Fishkin, 1997; Zeifman & Hazan, 2008). This event was the first of two adaptive workarounds in the evolution of human mating: Natural selection co-opted the attachment-behavioral system for use in adulthood in an effort to counteract other features that had been honed through eons of sexual selection. In other words, adult attachment was a jury-rigged evolutionary attempt to encourage intersexual cooperation and thwart intersexual conflict between mating partners, conflict that could potentially be maladaptive given the new selection pressures for greater care and provisioning of offspring. The assertion that pair-bonding evolved to manage the constraints imposed by earlier adaptive outcomes of sexual selection generates the novel prediction that attachment processes should function to either mute or refocus the effects of earlier adaptations that could have potentially threatened the pair-bond. These predictions, and the implications thereof, are discussed in the final section of this article.

Why would the benefits of paternal investment have started to weigh heavily against the costs of reduced mating opportunities for males (or females, for that matter) imposed by pair-bonding? One answer recalls an earlier example: extended neoteny. As discussed above, human infants are exceptionally altricial and require a great deal of care, even compared with other primates. This altriciality developed, in part, because the ever-expanding brain of Homo infants imposed escalating energetic demands (B. H. Smith & Tompkins, 1995), which could only be satisfied by consuming calorie- and nutrient-rich foods (Aiello & Wheeler, 1995). Fathers could have offered assistance in this endeavor (Quinlan & Quinlan, 2008), supplementing the subsistence provided by a mother's extended network of female kin (O'Connell, Hawkes, & Blurton Jones, 1999). As extended neoteny made child caretaking more burdensome and reduced women's foraging efficiency, the provision of meat and other calorie-rich sources of food by men (e.g., honey; see Marlowe, 2003a) could have become critical for the survival of childbearing women and their infants (Kaplan, Hill, Lancaster, & Hurtado, 2000; Lovejoy, 1981). A second possible explanation for the increased importance of male investment hinges not on their hunting abilities but rather on their ability to provide protection and, more specifically, to guard gathered calorie sources such as tubers (Wrangham, Jones, Laden, Pilbeam, & Conklin-Brittain, 1999). When humans started to control fire and use it to cook plant food sources, they would have unlocked more of the nutrients embedded in those foods. This development would have placed a premium on plant food collection and storage, and Wrangham et al. have argued that males would have formed a pair-bonded, protective relationship with a female to guard against the theft of her food stores. With this bond in place, fathers would presumably have been more invested in protecting infants from the threats imposed by the environment, predators, and fellow hominids as well. Yet a third possibility is that concealed ovulation evolved in human females to encourage males to have sex repeatedly within the context of a single relationship. This arrangement would have increased paternity certainty and facilitated bonding, though it remains unclear how fully concealed female ovulation is in humans (Haselton & Gangestad, 2006) or whether the loss of visible signs of ovulation should logically be associated with evolutionary changes in sexual behavior (Pawlowski, 1999). Almost certainly, the evolution of pair-bonding was a multiply determined event. It is worth noting, however, that all of the above explanations for pair-bonding are consistent with the parental investment logic. The present discussion highlights that the typical or average parental investment increased sharply for both sexes at some point in the lineage leading to Homo sapiens, and this increase was especially pronounced for men. The increase was significant enough that adult attachment evolved as a workaround solution to increase men's paternal investment.

So when did this evolutionary event take place? Although the anthropological and archaeological record cannot date the emergence of the pair-bond per se, it can offer evidence for several of the hypothesized antecedents of pair-bonding. As discussed earlier, extended human neoteny should have started to evolve as adult cranial capacity crossed the 700-cc threshold (Lewin, 1982; see also B. H. Smith & Tompkins, 1995, for a slightly higher estimate of 850 cc for this event). As shown in Figure 1, this would have corresponded to the beginning of the Homo lineage, around the emergence of Homo erectus/ergaster and the first explosive increase in cranial capacity approximately 1.5 to 2 million years ago (see also Fisher, 1989, for a similar date). In addition, greater paternal investment could have corresponded to the emergence of meat eating and coordinated hunting. These features evolved at approximately the start of the Homo lineage as well; although substantial debate exists regarding the hunting versus scavenging lifestyle of Homo habilis (e.g., Binford, 1981; Isaac, 1978), most scholars agree that systematic hunting was undertaken by Homo erectus (e.g., Surovell, Waguespack, & Brantingham, 2005). Finally, if the controlled use of fire was an important force in inspiring pair-bonding, as suggested by Wrangham et al. (1999), once again evidence points to the time of early Homo erectus as

the likely date for the emergence of this ability. Fires were first controlled by early Homo erectus in Africa approximately 1.6 million years ago (Rowlett, 2000), and the smaller teeth and gut size of these hominids (relative to Australopithecines) suggests that they were consuming higher quality food (Aiello & Wheeler, 1995). In total, the preponderance of the evidence suggests that pair-bonding likely evolved in humans sometime around the emergence of Homo erectus.

Two other characteristics of Homo erectus lend support to the idea that sexual selection pressures were shifting at this point in hominid evolution. For one, the fossil record reveals a precipitous drop in sexual dimorphism with the emergence of Homo (McHenry & Coffing, 2000): Males weighed approximately 35% to 40% more than females among the Australopithecines but only 18% to 20% more than females at the beginning of the Homo lineage. To be specific, female stature and mass increased considerably from the Austalopithecines through the early species of Homo; this change would be expected given continued brain expansion and the increasing quality of the diet. However male stature and mass increased only slightly during this time period, and thus sexual dimorphism decreased dramatically. Males may not have needed to maintain their large size if, indeed, sexual selection pressures had relaxed in lieu of selection pressures favoring adaptations, such as pair-bonding, that promoted intersexual and intrasexual cooperation (Wrangham et al., 1999). (The average size of males and females, and therefore the overall level of sexual dimorphism, has not changed appreciably since Homo erectus, although cranial capacity certainly has.)

Second, an intriguing trend is revealed by overall species-level amounts of fluctuating asymmetry (Frederick & Gallup, 2007). Recall that fluctuating asymmetry is an indicator of "good genes" because it indicates that an organism has had a robust developmental history. The overall level of fluctuating asymmetry increased during the course of human evolution, a trend that could indicate relaxed selection pressures for the presence of genes that promote robust development. Relatively asymmetrical individuals may have been able to successfully reproduce because early hominids began to use different strategies to attract mates and raise offspring, strategies that, in principle, could have included pair-bonding. Although the data on hominid sexual dimorphism and fluctuating asymmetry are far from conclusive, they add weight to the hypothesis that pair-bonding was selected in lieu of an emphasis on sexual selection and other older adaptations (such as good genes) around the emergence of Homo. If indeed adult attachment in early Homo served as a "devious route" around these preexisting mating-relevant adaptations, evidence for such a layered psychology may still be evident in modern humans today (see *Predictions* section below).

Feature 5: Nonmating Domain Overlap

In principle, mating-relevant cognitions and behaviors could function independently of the rest of the psyche. In humans, however, this is not the case: Mating behavior has implications for how humans obtain food and shelter, relevance for how humans pursue nonmating goals, and repercussions for social standing in general. This overlap between the mating and nonmating domains is due, in part, to humans' extraordinary cognitive fluidity, a term used by Mithen (1996) that refers to the ability to think flexibly or metaphorically across domains and to apply knowledge or concepts from different domains to one another. Mating behavior in humans is surely affected by psychological processes designed specifically for mating (e.g., ovulatory adaptations), but it is likewise influenced by other domain-general processes. In other words, courtesy of cognitive fluidity, our mating behaviors are tightly integrated with the rest of our psychology, both social and nonsocial.

For example, consider the abundance of research addressing how the self-concept, a broad and pervasive construct within social psychology, influences and is influenced by romantic relationships (Vohs & Finkel, 2006). On the one hand, people's self-concepts can be transformed by mating relationships. This process is exemplified by the Michelangelo phenomenon, which refers to the process by which individuals "sculpt" their romantic partners to become their ideal selves (Drigotas, Rusbult, Wieselquist, & Whitton, 1999). Findings have specifically revealed that, when individuals affirm that their romantic partner is the type of person he or she wishes to become, they help their partner grow toward that ideal and subsequently improve both partners' well-being. On the other hand, people's behavior within a mating relationship is affected by their self-concept, as demonstrated by Murray and Holmes's corpus of work on self-esteem and relationship functioning. Individuals with high self-esteem tend to pull closer to their partner when they feel rejected, but individuals with low self-esteem tend to pull away from their partner under these circumstances (e.g., Murray, Rose, Bellavia, Holmes, & Kusche, 2002). Presumably, the behavior of low self-esteem individuals serves a defensive, protective function, as low self-esteem individuals chronically doubt their partner's love and affection and therefore have difficulty facing the interpersonal risks inherent in close relationships (Murray, Holmes, & Griffin, 2000; Murray, Holmes, Griffin, Bellavia, & Rose, 2001). In short, human mating behavior and the self-concept have reciprocal effects on each other (see also Aron, Aron, Tudor, & Nelson, 1991); these findings suggest that the human mating psychology is not an independent entity but instead overlaps considerably with the sense of self—a broad, domain-general component of human psychology.

What other domains of human psychological life intersect with mating? Psychologists have developed a wide assortment of personality and attitude measures, and many of these measures were specifically designed to assess mating-relevant attitudes and behaviors (e.g., sociosexuality; Simpson & Gangestad, 1991). Pertinent to the present discussion are a variety of individual difference measures that are reliably associated with mating behavior but were not intended to assess mating behavior. For example, individuals who score high in Machiavellianism tend to be manipulative and self-serving, and not surprisingly, this general tendency emerges in the mating domain: Machiavellians are more willing to engage in selfish and deceptive acts, such as cheating, feigning love, inducing intoxication, and forcing others into sexual acts (McHoskey, 2001). In addition, men and women who report being "ethically inconsistent" are more likely to approve of and engage in casual sex, whereas men who exhibit dependability and a capacity to feel guilt are less likely to pursue casual sex (Reise & Wright, 1996; see also Hirsch & Paul, 1996; Paul & Hirsch, 1996). Many religions proscribe sexual activity outside of marriage, and thus religious individuals are less likely than nonreligious individuals to engage in premarital sex and other sexual behaviors (Lau-

mann, Gagnon, Michael, & Michaels, 1994; Mahoney, 1980). This association appears to be especially true for individuals who view religiosity as a worthy goal in and of itself (i.e., intrinsic religious orientation; see Rowatt & Schmitt, 2003). Finally, a well-established association exists among Whites between political conservatism and a lack of willingness to date interracially (Eastwick, Richeson, Son, & Finkel, in press; McClelland & Auster, 1990). In short, even though an individual difference measure may be a face-valid assessment of a construct that is far broader than mating per se, because human mating is integrated with the rest of our psychology, such measures often predict how people negotiate romantic relationships.

The previous examples focused on the association between mating behavior and socially relevant attitudes and values. Especially intriguing are two research programs illustrating that human mating may be integrated with not-necessarily social aspects of our psychology. First, people exhibit individual differences in regulatory focus, a construct that assesses a general inclination to pursue goals with either an eager (i.e., promotion) or a vigilant (i.e., prevention) orientation (Higgins, 1997). Items used to assess regulatory focus refer to broad tendencies (e.g., "I have often accomplished things that got me 'psyched' to work even harder"; Higgins et al., 2001) that stretch across social and nonsocial domains. Evidence suggests that regulatory focus as an individual difference is relevant to mating behavior: Individuals who possess a chronic promotion (relative to prevention) orientation are more likely to perceive that they possess romantic alternatives and that those alternatives are desirable (Finkel, Molden, Johnson, & Eastwick, in press). Second, people also naturally differ in the extent to which they think about future goals using a deliberative (i.e., weighing the pros and cons of pursuing the goal) or implemental (i.e., focusing on the methods of achieving the goal) mindset (Gollwitzer, 1990; Kruglanski et al., 2000). The effects of mindset also stretch into the mating domain: For example, individuals who were more deliberative about a major (nonromantic) life goal were more accurate than were implemental individuals at predicting the future length of their relationship (Gagné & Lydon, 2001). This overlap between mating and nonsocial psychological constructs demonstrates that humans can apply strategies and concepts across highly disparate domains—the essence of cognitive fluidity.

Finally, Eagly and colleagues have amassed data demonstrating that mating behavior is in part guided by people's beliefs about gender and their expectations about future occupational roles. For example, participants who hold traditional beliefs about men and women are more likely than nontraditional participants to desire sex-stereotypical qualities in a mate: that is, a younger partner with housekeeping skills for men, and an older partner with earning prospects for women (Eastwick et al., 2006; Johannesen-Schmidt & Eagly, 2002). In addition, participants exhibit this same sex-typing of mate preferences (a) in response to an experimental manipulation requiring them to imagine themselves in a future role that is sex-typical (i.e., a full-time job for men, a homemaker for women) versus sex-atypical and (b) to the extent that participants naturally expect to inhabit a sex-typical vs. a sex-atypical role (Eagly, Eastwick, & Johannesen-Schmidt, 2009). In other words, people's beliefs about gender roles and their personal expectations about future role activities influence their mating psychology in a predictable and theoretically sensible manner (see also Eagly & Wood, 1999; Wood & Eagly, 2002).

Humans can and often will use sex for a variety of nonmating goals: to gain social approval or a sense of belonging; to obtain resources; to give others pleasure; or even to cause pain, suffering, and humiliation (e.g., Cooper, Shapiro, & Powers, 1998). This feature of human mating, the overlap of the human mating and nonmating psychology, should not necessarily be construed as an attack on the principle of modularity. In fact, the current perspective is consistent with modern theories of modularity that do not require modules to be informationally encapsulated from one another (Barrett & Kurzban, 2006). By highlighting this feature, I am suggesting that much of the action in human mating is to be found at the overlap of different domains or modules. Mating-specific adaptations are undoubtedly important but cannot fully explain why or how humans engage in a variety of mating behaviors. To be sure, more research remains to be conducted in this area: For example, scholars could extend the research on religion to examine how people's personal values impact their mating behavior. The low-hanging fruit in this topic area is likely to entice many researchers in the coming years.

The origin of nonmating domain overlap in humans. Some animals do show evidence that mating behavior is integrated with other aspects of their social environment. For example, grooming serves a social function in many primates (Hemelrijk, 1994), and the fact that primates may also exchange grooming for sex (Gumert, 2007) suggests that their mating psychology overlaps to some extent with other aspects of their social psychology. However, there is a substantial difference in the magnitude of nonmating domain overlap when comparing humans to primates. It is difficult to imagine that even the most brilliant chimpanzee could develop the belief that an invisible authority figure encourages her to live by certain principles and that these principles include a prohibition against sexual activity in some contexts. To support this assertion that humans exhibit an unparalleled degree of cognitive fluidity, we again turn to archaeology and anthropology for evidence that (a) supports the existence of and (b) dates the origin of humans' exceptional ability to integrate information across domains.

Mithen (1996) consulted the fossil record to construct a detailed history of the cognitive development of the hominids that preceded modern humans, including Homo erectus (who lived between 1.8 million and 300,000 years ago) and the Neanderthals (who lived between 150,000 and 30,000 years ago). These hominids possessed extremely sophisticated knowledge structures that appear specially designed by natural selection to deal with different aspects of their environment. Mithen (1996) discussed, in particular, their natural history intelligence (e.g., understanding how to track animals across a varied landscape), social intelligence (e.g., communicating and coordinating with other group members), and technical intelligence (e.g., producing tools and other artifacts from mental templates) and noted how these hominids exhibited remarkable proficiency across these domains. For example, the Lavallois knapping technique used by the Neanderthals to create sharp stone points is technically demanding and difficult even for modern humans to master (Hayden, 1993), and the impressive geographical range of these hominids suggests that they could generate vast mental maps of their environment.

Curiously, there is virtually no evidence that the early hominid mind was able to process information simultaneously across different domains: Social information was processed separately from

information about the environment, which, in turn, was processed separately from information about technology. That is, hominid thought did not exhibit any evidence of analogy, metaphor, or symbolic representation. Mithen's (1996) evidence for this hypothesis comes from several different sources within the archaeological record. For one, despite the fact that these early hominids would have encountered a wide variety of different landscapes, climates, and predators as they spread throughout the Eastern hemisphere, they did not design specific tools to hunt or butcher specific animals, and their technology varied little across time and space. These features suggest the possibility that early hominids were not able to integrate their technical intelligence with their natural history intelligence. Similarly, early hominids did not imbue any artifacts with social significance; that is, they did not make beads, pendants, or paintings, which potentially implies that their social intelligence was not integrated with their technical intelligence. Finally, early hominids appeared to carry out various activities specific to each domain (e.g., butchering animals, creating tools) in spatially discrete locations across the landscape; this pattern suggests that, unlike modern hunter gatherers, early hominids appeared to engage in one activity (and perhaps one set of mental processes) at a time. Although early hominids surely possessed a measure of generalized intelligence that operated across domains (e.g., associative and operant learning mechanisms, as exhibited by all animals), this all-purpose intelligence may not have been sufficiently powerful to permit true analogical or metaphorical thinking.

Approximately 40,000 to 50,000 years ago, all of these features changed dramatically within the fossil record.[6] This moment is technically called the Middle/Upper Paleolithic transition, though scholars have also referred to it using more colorful terms such as "the cultural big bang" (Mithen, 1996), "the great leap forward" (J. Diamond, 1992), and "the dawn of human culture" (Klein & Edgar, 2002). The archaeological record points to the sudden emergence at this point in time of a number of distinctly human features. Our ancestors suddenly (at least on an evolutionary time-scale) started to create complex, multicomponent tools designed for specific purposes. For the first time, they turned animal products, such as ivory, antler, and bone, into useful technology. They created objects that had symbolic significance, such as statues and figurines. And they began to play musical instruments and paint the walls and ceilings of their habitats. According to Mithen (1996), this was a watershed moment in the evolution of hominid thought; from this point forward, Homo sapiens evidenced an unprecedented degree of cognitive fluidity. That is, humans could now think effortlessly across domains: Technological objects could have social significance (e.g., figurines and beads), animals could be viewed like people (e.g., totemism and anthropomorphism), and different tools could be designed for different purposes (e.g., specialized weapons for hunting certain types of game). Such cognitive fluidity seems so natural to modern Homo sapiens that it is difficult to imagine how one could think at all without the use of analogy, metaphor, or symbolism. Yet, for millions of years, our ancestors were unable to create anything approximating the lion-man statuette from Hohlenstein-Stadel (Marshack, 1990; see Figure 2) because they could not envision how an object could depict an animal, much less that the object-animal would possess any social significance.

So how does the cultural big bang relate to mating? The above evidence marshaled in support of Feature 5 (nonmating domain overlap) highlighted the effortless integration between Homo sapiens's mating psychology and other nonmating aspects of mental life. Consider again the regulatory focus evidence: Individual differences in regulatory focus predict both mating behavior (e.g., pursuit of romantic alternatives; Finkel, Molden, et al., in press) and performance on nonsocial, technical tasks (e.g., anagram completion for monetary rewards; Shah, Higgins, & Friedman, 1998). That is, a person who is motivated to achieve gains (rather than to avoid losses) behaves consistently with this chronic orientation in both mating and nonmating (even nonsocial) domains. This is precisely the kind of cognitive fluidity and analogical thinking that, according to prominent archaeologists, evolved only tens of thousands of years ago.

I am not the first psychologist to hypothesize about the implications of the cultural big bang for the evolution of the human psyche. Leary and Buttermore (2003) suggested that the cultural big bang coincided with the complete emergence of the modern conceptual self, which underlies Homo sapiens's ability to think symbolically and abstractly about their own traits, roles, and behavior. Humans could now "imagine themselves in the future in symbolic and abstract ways" (Leary & Buttermore, 2003, p. 387). Naturally, a conceptual self would be required for Homo sapiens to exhibit self-expansion effects (Aron et al., 1991) or the Michaelangelo phenomenon (Drigotas et al., 1999). But, in addition, it would be at this point in evolution that humans could alter their behaviors in accordance with abstract moral principles. As reviewed above, examples of such behavior abound in the mating domain: Individuals who refrain from engaging in deceitful acts in general will, to behave in accordance with this principle, eschew cheating and other Machiavellian mating behaviors (McHoskey, 2001). Once humans had evolved the ability to symbolically reflect on the self, mating behavior would have been subjected to a wide variety of abstract, intrapsychic forces.

Finally, Rossano (2003) argued that the cultural big bang also presaged the emergence of individual differences in acquired skills. In order to develop expertise at a particular skill, one must imagine the self at a future point in time possessing the skill, engage in deliberate practice to hone the skill, and organize actions sequentially and hierarchically (see Ambrose, 2001). With Homo sapiens's newfound conceptual self ability, skill acquisition could now serve a symbolic function, and Rossano (2003) argued that although expertise existed before this point in evolution, it required symbolic thought for acquired skills, such as those of toolmaker, artist, leader, and shaman, to take on social meaning. Therefore, the cultural big bang would have coincided with the evolution of occupational roles. These roles would have imposed structure on humans' daily activities and encouraged them to engage in behaviors congruent with their roles. This is not to imply that members

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[6] There has been (and no doubt will continue to be) considerable debate concerning whether anatomically modern Homo sapiens were engaging in symbolic behavior prior to 50,000 years ago (e.g., Klein & Edgar, 2002; Marean et al., 2007; McBrearty & Brooks, 2000). Regardless, most scholars are in agreement that symbolic reasoning and cross-domain thought are extremely recent evolutionary additions to the hominid repertoire, even though estimates for their emergence may differ by 100,000 years or so.

expectations about how men and women should behave in order to be successful. It is this symbolic content of social roles that has been shown to affect mating (e.g., men and women adjust their ideal romantic partner preferences according to expectations about their own future roles; Eagly et al., 2009).

Feature 6: Variability of Mating Norms

Just as some individual difference constructs vary within a population and predict mating behavior (e.g., religiosity), beliefs also vary between populations. In other words, different human populations share different norms, beliefs, and values as part of their culture, and these *cultural variants* (Richerson & Boyd, 2005) influence mating behaviors. Because there exists such a vast array of cultural variants relevant to mating throughout the world, mating in humans exhibits tremendous variability, far more than in any other animal.

The anthropological record reveals the variety of norms and beliefs relevant to mating. Although marriage exists in every human society, the type of marriage can take several different forms (e.g., monogamy, polygyny). Furthermore, even among societies that do permit polygyny, the percentage of polygynously married men varies widely; this variation can be predicted by factors such as the extent of male provisioning, with greater provisioning predicting decreases in polygyny (Marlowe, 2000, 2003b). Polyandrous mating systems have occasionally emerged throughout history as well (Levine & Silk, 1997). In a number of South American societies, a polyandrous-like system has developed from a shared belief in "partible paternity," that is, the belief that all men who have sex with a woman during her pregnancy share the biological fatherhood of the child (Beckerman et al., 1998). Other relevant data come from the work of Schmitt, who has assessed individuals from approximately 50 different nations as part of the International Sexual Description Project. These data have suggested that sex differences in sociosexuality become smaller as women gain economic power, political power, and reproductive freedom (Schmitt et al., 2005) and that women are more likely to make short-term mate poaching attempts as they achieve parity with men on indicators such as health and education (Schmitt et al., 2004b). There are innumerable ways that mating varies across cultures: Arranged versus love marriages, rules governing dating, sexual practices, how to become a desirable mate, typical age of marriage, and the prevalence of divorce constitute just a tiny fraction of the cultural norms relevant to mating that people must learn and negotiate.

One noteworthy mating-relevant cultural variant that has emerged several times throughout history and persists today in many populations is antisexuality or celibacy. Celibate individuals abstain from sex, and celibacy is required for Catholic, Hindu, or Buddhist individuals who wish to practice a monastic life (i.e., monks, nuns). Antisexuality is essentially the secular variant of celibacy; antisexuals avoid engaging in any type of sexual behavior because they believe that sex clouds judgment and leads to overpopulation, the deterioration of friendships, and other societal ills. Granted, celibacy and antisexuality will probably never be exceedingly popular, but the fact that some people would aspire to such a principle to facilitate a mating-irrelevant goal (e.g., piety) is

Figure 2. The lion-man statuette from Hohlenstein-Stadel, illustrating the human capacity to think flexibly across technological, natural, and social domains. The statue is approximately 30,000 years old. Photo from Wikimedia Commons, in the public domain.

of earlier hominid groups all performed identical tasks; after all, a division of labor by sex can be traced back to our primate ancestry (Galdikas & Teleki, 1981). However, it is only after the cultural big bang that humans' daily activities would have been driven by

nothing short of remarkable. It is difficult to imagine any other animal coming up with a norm not to have sex.

Wood and Eagly noted "how profoundly different the sexual practices of some nonindustrial societies are from those in . . . Western, industrialized societies" (Wood & Eagly, 2002, p. 716). They then proceed to describe the sexual practices of the Canela of Brazil, a nonindustrial culture that discourages sexual jealousy and encourages ritual group sex as well as extramarital sex. That people adapt to such a wide array of mating practices throughout the world is undoubtedly an important feature of mating psychology.

The origin of variability of mating norms in humans. The archaeological record unfortunately can tell us little about the variability of mating norms in hominids. However, we can draw preliminary conclusions by examining archaeologists' accounts of the variability of human societies in general. In fact, hominid societies were quite uniform in the fossil record until the cultural big bang, at which point the variability across human societies increased dramatically and suddenly. This event was due, in large part, to the evolution of a key component of Homo sapiens' psyche: the capacity for transmitted culture.

Transmitted culture refers to the tendency for humans to communicate different cultural variants, to adopt some cultural variants instead of others, and to accumulate improvements to existing cultural variants (Richerson & Boyd, 2005). Transmitted culture involves a number of different mental adaptations, such as humans' great skill at imitation and an assortment of biases in learning and communication. In addition, adaptations for transmitted culture are designed to function across domains (e.g., food preparation, hunting techniques, rituals) and allow humans to adapt quickly to rapidly changing environments. Perhaps the central feature of human transmitted culture is that it allows for the accumulation of adaptive cultural variants over successive human generations (Richerson & Boyd, 2005). The most impressive "artifacts" of human culture, such as the personal computer, the ability to produce steel, or Catholicism, could never have been invented by one person from scratch. Such examples of complex culture are built over vast stretches of time; Mozart may have been a prolific genius, but thankfully generations before him had already invented tonality, musical notation, and the violin. Successful cultural variants, whether tangible (e.g., the printing press) or intangible (e.g., courting rituals, democracy), are transmitted between individuals and through time. With additional improvements, some variants may be adopted by even more individuals, whereas other variants may become obsolete and disappear.

Many nonhuman animals exhibit at least modest amounts of cultural variation. Whiten et al. (1999) catalogued 39 different behaviors in chimpanzees that varied by site, including handclasp grooming and various techniques for obtaining food; moreover, this variability could not be explained by differing ecology between the sites. Social transmission of behavior has also been documented in animals. One famous example is the potato-washing behavior of Japanese macaques on the island of Koshima (Imanishi, 1952): A young female macaque discovered that potatoes could be cleaned by dropping them into the sea, and eventually this behavior was picked up by many other members of her group. Cetaceans (Rendell & Whitehead, 2001), parrots (Pepperberg, 1999), and elephants (McComb,

Moss, Durant, Baker, & Sayialel, 2001) also have impressive cultural repertoires.

However, examples of cultural accumulation in nonhuman animals are extraordinarily rare, if they exist at all (see Richerson & Boyd, 2005). In fact, there is little evidence of accumulated culture even among early hominids. The Levallois knapping technique of the Neanderthals required great skill and produced sharp stone points that were then fitted onto a shaft to create a spear (Shea, 1988). However, this technology is vastly simpler than the multicomponent tools that are vital to modern hunter-gatherers and were created through accumulated cultural change over generations. To take one example, whereas Neanderthal spears consisted of three components (i.e., the point, shaft, and binding material), Inuit hunter-gatherers created spears with up to 26 components, each serving a particular purpose in throwing and retrieving the spear (Oswalt, 1973). Such complex, multicomponent technology does not emerge in the archaeological record until after the cultural big bang approximately 40,000–50,000 years ago. As noted by Mithen (1996), it is at this point in hominid evolution that "we can see the processes of innovation and experimentation at work, resulting in a constant stream of new hunting weapons appropriate to the prevailing environmental conditions and building on the knowledge of previous generations" (p. 169). Thus, it is only within the past few tens of thousands of years that human transmitted culture evolved its current form.

Once equipped with the capacity for transmitted culture, human cultures advanced in a staggering variety of new directions. Before this event, stone technology was not specially designed to deal with particular elements of the local environment, such as the type of game; nearly all variation was due to the availability of local materials. However, variability became pronounced after the cultural big bang, as modern humans began to use animal products, complex "blade technology," and specialized tools to process plant material, trap animals, and tailor clothes (Mithen, 1996). These new developments contrast with earlier eons of relative cross-cultural monotony within the archaeological record. The considerable variability that is evident today across human cultures could not be created and maintained until the advent of transmitted culture.

As transmitted culture began to generate variability in nonmating domains, it is likely that the variability in mating norms, values, and customs across cultures also emerged at this time. Therefore, wide variability in mating norms among humans is probably a recent evolutionary development. To be sure, this suggestion requires additional evolutionary and archaeological research. For one, some mating behaviors that vary cross-culturally are plausibly due instead to evoked culture (Gangestad, Haselton, & Buss, 2006). *Evoked culture* refers to the outcomes of domain-specific mental adaptations that were designed by natural selection to respond to environmental conditions in a particular fashion. In other words, natural selection may have designed the human mind to be sensitive to environmental circumstances that occurred repeatedly in our ancestral past (e.g., the presence of pathogens) and to produce particular adaptive behaviors in response. Granting that evoked culture plays an important role in our mating psychology, it remains parsimonious at the present time to suggest that the great cross-cultural variability of mating norms is primarily due to transmitted culture, the same feature that generated cross-cultural variability in other nonmating contexts. Nevertheless, the relative

role of evoked versus transmitted culture in human mating and the precise timing of the evolution of independent pieces of evoked culture are important topics for future research.

Feature 7: Self-Control

As a result of people's idiosyncratic beliefs or the norms of a dominant culture, humans are not always able to act on their mating impulses. This conflict between immediate desires, on the one hand, and beliefs, norms, or other preexisting goals, on the other, can take a variety of forms. A prototypical example is the "off-limits" acquaintance of one's preferred sex, with whom no sexual contact can take place as a consequence of the loyalty one feels for a friend, current romantic partner, or perhaps God. Though often difficult, humans possess the ability to tear themselves away from such temptations in favor of a cold shower. In other cases, individuals might control their romantic impulses because they believe they are likely to be rejected, or because their impulses are directed toward an inappropriate target (e.g., a subordinate at work). People who are attracted to each other with no reason to suppress their attraction are often able to restrain themselves from having sex in public or other poorly chosen locations; even adolescents can contain themselves long enough to escape their parents' watchful eyes and reach the safety of the back seat of a Ford Escort. These observations should not minimize the fact that people do fall prey to their sexual desires when they should not and that the outcomes can be disastrous. However, people pursue abstract goals in lieu of sexual gratification with such regularity that these feats typically go unnoticed; the memorable cases are, of course, those in which people defy local norms and succumb to their sexual desires. The question posed here is: How do humans manage to thwart their sexual urges?

To answer this question, I appeal to a construct that is familiar to psychologists: self-control. Herein, I use the term *self-control* to refer to deliberate and conscious forms of self-regulation, and indeed the term is frequently used to refer to the intentional inhibition of impulses (Gailliot & Baumeister, 2007; Schmeichel & Baumeister, 2004). Classic feedback loop ("TOTE") models of self-regulation posit that people compare themselves to a desired end state (test), engage in behaviors intended to bring the self closer to the end state (operate), assess whether such behaviors were successful (test), and terminate the self-regulatory process when the desired end state is achieved (exit; Carver & Scheier, 1982). With regard to sexual restraint, the desired end state or goal will be influenced by beliefs and norms (e.g., the goal to not have sex with the former partner of a good friend), and self-control is a critical ingredient that can determine what behaviors are enacted or inhibited at the operate stage (e.g., not ordering the third drink). Although many forms of self-regulation can be executed outside of conscious awareness (Bargh, Gollwitzer, Lee-Chai, Barndollar, & Trötschel, 2001), to the extent that effortful self-control processes are required to achieve a goal, they draw on a limited, consumable resource (Muraven & Baumeister, 2000). In other words, acts of self-control are depleting, and consecutive acts of self-control become progressively more difficult to execute as greater quantities of the resource are consumed (Muraven, Tice, & Baumeister, 1998). Therefore, people should be likely to resist sexual temptations if they have not recently had to engage in other effortful tasks (e.g., managing negative affect or stress), but their attempts at self-control will likely become less effective after a hard day at work or a few disinhibiting alcoholic drinks.

Although the role of self-control in human mating is conceptually self-evident, empirical studies on this topic have started to emerge only recently. Somewhat relevant are data demonstrating that alcohol consumption predicts engaging in sexual behaviors and having multiple sexual partners (Graves, 1995; Santelli, Brener, Lowry, Bhatt, & Zabin, 1998), as alcohol reduces self-control and executive functioning. In one of the first social psychological analyses of self-control within romantic relationships, Finkel and Campbell (2001) found that participants responded to upsetting partner behavior (a) more destructively to the extent that they possessed less dispositional self-control and (b) less constructively after having their self-control depleted by an experimental manipulation. Self-control also appears to be an important predictor of intimate partner violence: Experimentally depleted participants and participants with low dispositional self-control are more likely to engage in violent behaviors toward their romantic partners (Finkel, 2007, 2008), and manipulations that increase participants' self-control strength over time successfully reduce their perpetration of violent acts (Finkel, DeWall, Oaten, Slotter, & Foshee, in press). Another relevant set of studies explored the role of self-control specifically within the sexual domain (Gailliot & Baumeister, 2007). Findings revealed (a) that participants who reported lower self-control in nonsexual domains also reported lower self-control in the sexual domain and (b) that depleted participants were more likely than nondepleted participants to express sexual thoughts. Furthermore, depletion caused sexually inexperienced participants to engage in more extensive sexual activity in the laboratory. These recent studies suggest that the intersection of self-control and human mating is promising underresearched territory.

The origin of self-control in humans. How old is the capacity for self-control? Many animals can enact behaviors that promote long-term over short-term gains. Typical studies of animal self-control require the animal to forgo a small but immediate reward in favor of a larger, but delayed reward, much like the classic marshmallow studies examining self-control in children (Mischel, 1974). The easiest type of animal self-control task requires the animal to make a discrete choice between receiving either a small reward now or a large reward later; a variety of different animals, even honeybees (Cheng, Pena, Porter, & Irwin, 2002), can learn to choose the delayed reward in this task. A slightly more difficult task requires the animal, while waiting for the larger reward, to resist making a response (e.g., pressing a bar or button) that brings the smaller reward instead of the larger reward. Even still, apes can succeed at this task (e.g., Beran, Savage-Rumbaugh, Pate, & Rumbaugh, 1999), as can pigeons (Grosch & Neuringer, 1981) and rats (Killeen, Smith, & Hanson, 1981). The most difficult variant of the self-control task requires the animal to refrain from taking the reward as valuable items are piled up one-by-one; instead, the animal must wait for all of the reward items to be presented before taking them. Thus far, apes appear to be the only nonhuman animals that can complete this task (Beran, 2002; see Evans & Beran, 2007). Overall, these studies suggest that there is a spectrum of self-control capacity across the animal kingdom; humans are not alone in their ability to inhibit impulses.

However, there are two ways that humans' capacity for self-control differs from that of other animals. The first is that humans

can use self-control to pursue a wide variety of symbolic or abstract goals. All of the animal experiments noted above required the animal to inhibit an impulse that would bring a small amount of food quickly so that they could consume a larger amount of food in the (near) future. But could an animal learn to forgo the larger amount of food in anticipation of a future motivational state that it was not currently experiencing? This is the essence of the Bischof-Kohler hypothesis, which suggests that animals have difficulty with precisely such tasks (Suddendorf & Corballis, 1997). Roberts (2002) illustrates the Bischof-Kohler hypothesis with an example involving laboratory-housed cebus monkeys: These monkeys would be fed to satiation once each day and would throw the extra food out of their cage instead of conserving it, despite that fact that they would reliably become hungry before the next meal time. Whether animals can anticipate their future motivational states is currently a hot topic, with some researchers suggesting that animals can accomplish this task within the motivational domains of hunger and thirst (e.g., Correia, Dickinson, & Clayton, 2007; Naqshbandi & Roberts, 2006) and others doubting that these findings conclusively demonstrate that animals can prepare for the future (Suddendorf & Corballis, 2007). Of course, humans can anticipate their future motivational states, and they can do so across different domains. For example, humans learn to inhibit their impulses to consume food in order to adhere to norms of politeness, to live up to religious or other moral (e.g., veganism) beliefs, or to improve their physical appearance and attract members of the opposite sex. Self-control appears to be a general tool that humans use to facilitate smooth and appropriate social interaction (von Hippel & Gonsalkorale, 2005). Thus, self-control may seem to be pronounced in humans compared with other animals because of an ability to exercise it across domains. In this sense, human self-control had not evolved its current form until humans began to think effortlessly across domains, which recalls the importance of cognitive fluidity, discussed as part of Feature 5.

The second way that humans' self-control differs from that of other animals is that humans can mentally project themselves far into the future, also called "extended-self" ability (Leary & Buttermore, 2003; Neisser, 1988). Most of the animal studies discussed above required acts of self-control that produced long-term rewards within minutes, but humans use self-control in pursuit of long-term rewards that do not arrive for months, years, or even until after death. The question of how far animals can extend themselves into the future is also hotly debated (Roberts, 2002); the fossil record provides some evidence on extended-self evolution in hominids. Leary and Buttermore (2003) suggested that the extended-self capability evolved gradually over time but was not clearly present until the Neanderthals, who were the first hominids to create any sort of permanent structures (e.g., hearths) that were designed for future use. In addition, even though the Neanderthals were the first hominids to bury their dead, these burials did not appear to have ritualistic significance, and therefore the extension of the self into an afterlife may not have evolved until Homo sapiens (Dickson, 1990). As hominids evolved the ability to imagine the self at distant points in the future, it is likely that self-control would have increased in importance as early hominids attempted to pursue various future goals.

Baumeister (2005) suggested that self-control became especially significant with the emergence of culture. He stated, "To enable human beings to participate in culture, evolution gave us the ability to override our initial responses, choose among different options, and let behavior be guided by meanings . . . evolution created us to be able to re-program ourselves" (Baumeister, 2005, p. 274). The importance of self-control makes adaptive sense considering the great toll that lapses in self-control can take on the lives of modern humans (Baumeister, Heatherton, & Tice, 1994) and that people tend not to function as well within their culture (e.g., they are less prosocial) to the extent that they believe that they cannot control their own actions (Baumeister, Masicampo, & DeWall, 2009). Furthermore, early hominid groups likely imposed strong sanctions against norm violators (Fehr & Fischbacher, 2004), especially in cases where the norm-violating act could have been controlled in principle (Dijker & Koomen, 2006). In other words, as the capacity for culture became a critical adaptation in and of itself, those early hominids who were able to successfully regulate themselves to conform to cultural norms (both relevant and irrelevant to mating) should have been more valued as group members and would therefore have had greater reproductive success. Metaphorically speaking, natural selection played a cruel joke on Homo sapiens: In a new environment that placed a premium on cultural norms and group cooperation and cohesion, it had become decidedly maladaptive in many cases to succumb to previously evolved impulses (Baumeister et al., 1994), and self-control provided an adaptive means by which to resist such impulses (e.g., McCullough & Willoughby, 2009).

Thus, the second of two adaptive workarounds in the evolution of human mating is located at the intersection of cognitive fluidity (Feature 5), variability of cultural norms (Feature 6), and self-control (Feature 7). Once early hominids had evolved (a) the ability to hold beliefs relevant to multiple domains and (b) the capacity for culture, natural selection recruited self-control as a mechanism for regulating behavior to conform to those beliefs and cultural norms. I previously suggested that Features 5 and 6 evolved with the cultural big bang approximately 40,000–50,000 years ago. Although self-control existed in a more or less rudimentary form throughout the Homo lineage, this feature also would not have been relevant to the regulation of beliefs and norms until this relatively recent time period. Thus, Features 5–7 constitute humans' most recent jury-rigged set of adaptations relevant to mating—newly minted and sitting precariously on top of our psyche.

By regulating themselves in the service of culture, humans have fundamentally transformed their environment (Baumeister, 2005; Richerson & Boyd, 2005). Yet beliefs and norms often come into conflict with impulses arising from older adaptations. Self-control is useful at overriding such impulses and reflects our evolution as "cultural animals," but self-control is not an infinite resource. Much like attachment in adulthood, the first mating adaptive workaround discussed above, additional testable predictions are generated when we consider that Features 5–7 may intersect to form a second adaptive workaround. These predictions are explored in the next section.

Predictions and Implications of the Phylogenetic Approach

The phylogenetic analysis used above highlights three *adaptation sets*, each consisting of different evolved features relevant to human mating. These sets are not sorted by the particular adaptive

problem they address, although such an approach would be sensible from an adaptationist perspective. Rather, consistent with the phylogenetic approach, the sets are organized according to the time periods in which they evolved in the lineage leading to modern Homo sapiens. The first set consists of extremely ancient adaptations: those that have been present in Homo sapiens's psyche for more than 6 million years and that we share with our pongid relatives. I have included sexual desire, the desire for physical attractiveness and symmetry in mating partners, and sex hormones among this set, and there are surely other features that belong here as well. The second set consists of adaptations relevant to adult attachment and pair bonding. This feature of human mating evolved around the emergence of the genus Homo approximately 1.5 to 2 million years ago and fostered male paternal investment in offspring and intersexual cooperation. The third set of adaptations arrived with the cultural big bang 40,000–50,000 years ago; once humans gained the ability to think flexibly across domains and acquired the capacity for transmitted culture, human mating practices became both highly variable and deeply integrated with other aspects of life. These two new developments required humans to use self-control in many cases to willfully regulate their own behavior to conform to cultural norms and beliefs.

In and of itself, the phylogenetic analysis is an interesting and worthwhile scholarly endeavor, but how exactly does it generate new predictions for evolutionary psychology or new explanations for previous findings? If all mating adaptations are psychologically equal—a milieu of forces competing for control over our behavior—then it presumably would not matter when a particular set of adaptations had evolved. However, because of the principle of evolutionary constraint, the timeline of evolutionary events typically has explanatory power when examining a given species' morphology and behavior. When selection pressures favor a new adaptation, older adaptations cannot be easily extracted and cast aside, even if they, at times, operate at cross-purposes with the new adaptation. Instead, natural selection will attempt to evade such constraints using the adaptive workaround, which means that the newer adaptation will be designed in part to contend with the outcomes of prior selection pressures. In other words, newer adaptations are often specifically designed to manage older adaptations. Given a situation where a newer adaptation is relevant or activated, it may possess the ability either (a) to mute the effects of older adaptations or (b) to refocus the functions of older adaptations toward a new purpose. In conjunction with the principle of constraint, a phylogenetic analysis is equipped to make powerful new predictions for evolutionary psychology.

Predictions

Set 1 versus Set 2: How might adaptations for attachment manage constraint? Humans are not always attached to their sexual partners. For example, if someone has never been distressed by a particular sexual partner's absence and has never sought support and comfort from him or her, this could indicate that normative attachment concerns are irrelevant to this particular relationship.[7] In these cases, attachment imposes no restrictions on the effects of earlier adaptations; it would make complete adaptive sense for unbonded women to be more interested in having extra-pair sex with desirable men at the fertile relative to the nonfertile stage of their menstrual cycle (e.g., Haselton & Gangestad, 2006).

But when attachment concerns are activated in the context of a sexual relationship, older adaptations may not exert their typical effects. Attachment evolved to promote pair-bonding and intersexual cooperation, and older adaptations that threatened this goal would have been counterproductive in the context of an attachment relationship. Therefore, we might expect to find that adaptations for attachment evolved to mute or refocus the effects of older adaptations.

Research on testosterone levels in men provides some support for this prediction. Men who are married or involved in a committed romantic relationship tend to have lower testosterone levels than uncommitted men (Burnham et al., 2003; Gray et al., 2004), and longitudinal work suggests that testosterone drops when entering a marriage and increases when divorcing (Mazur & Michalek, 1998). The rationale for these findings is that high levels of testosterone are costly to maintain, and once a male has secured a romantic partner and does not have to compete for a mate, the advantages of high testosterone (e.g., sexual assertiveness, muscle mass) are no longer worth the costs. Another cost could be that the extra-pair mating effort inspired by testosterone could lead to behaviors that disrupt a man's primary attachment relationship. Thus, the moderation of testosterone levels by relationship status is consistent with the idea that adaptations for attachment evolved to mute the effects of older adaptations—in this case, suppressing levels of an ancient sex hormone. However, relationship status alone is a poor indicator of attachment status, as people enter and remain in romantic relationships for a variety of reasons without necessarily establishing an attachment bond. Especially intriguing are data from Gray et al. (2002) demonstrating that men have lower levels of testosterone to the extent that they invest in and spend time with their spouse (these two constructs are more similar to attachment bondedness than is relationship status). These negative correlations were large: between $r = -.50$ and $-.65$. Within the context of an attachment bond, high levels of testosterone are unnecessary and potentially counterproductive, and attachment adaptations may be designed to reduce the influence of the hormone.

Two studies that were directly inspired by the present constraint-based approach have also garnered support for the prediction that adaptations for attachment were designed by natural selection to manage the effects of older adaptations (Eastwick & Finkel, 2009). These studies assessed the strength of women's attachment bonds to their dating partners with items from the Attachment Features and Functions Scale (Tancredy & Fraley, 2006), a scale used by attachment researchers to assess proximity-seeking, separation distress, safe haven, and secure base behaviors. One study revealed a significant Attachment Bond Strength × Fertility Status interaction predicting the likelihood that women would be interested in going home with a desirable member of the opposite sex whom she had just met that evening. To the extent that women were more bonded to their romantic partner, greater fertility was associated with a decreased desire to go home with another man. In fact, women who were one standard deviation

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[7] According to life history theory, stressful rearing environments may lead some individuals to be reluctant to attach to romantic partners in general, instead favoring a low-investment mating strategy (Belsky, Steinberg, & Draper, 1991).

above the mean on bondedness showed a significant negative relationship, such that they were less likely to want to have such an extra-pair liaison on high-fertility relative to low-fertility days. In other words, when the attachment system was activated for these women, fertility actually made them less likely to seek out a desirable alternative partner.

So what are bonded women doing if they are not out meeting desirable alternative partners when fertile? We hypothesized that fertility would lead bonded women to want to strengthen their current attachment bonds. Indeed, a second study derived support for this hypothesis. Over a 4-month period, women periodically completed an online questionnaire about their romantic lives. Every time the women engaged in sexual contact, they reported the extent to which they engaged in the sexual contact to "foster an emotional connection" with their partner. Again, a significant Attachment Bond Strength × Fertility Status interaction emerged: To the extent that women were bonded to their sexual partners, greater fertility was associated with an increased tendency to engage in physical contact to foster an emotional bond. Specifically, bonded women were significantly more likely to foster an emotional connection on high-fertility relative to low-fertility days.

Together, these two studies suggest that when the attachment system is activated for women, adaptations linked to fertility and the menstrual cycle are rechanneled toward the new adaptive purpose of protecting and strengthening the pair-bond. These findings make sense given the phylogenetic perspective: When the attachment system evolved to promote bonding between adult romantic partners, like other adaptive workarounds, it had to manage the constraints imposed by adaptations that were already in place. As it would have been prohibitively costly for natural selection to completely redesign the menstrual cycle, it instead found a way to adapt menstrual cycle effects toward a new goal: avoiding risks associated with extra-pair copulations and further cementing the attachment bond. Surely, a great deal more research is needed on the links between attachment and other mating adaptations, and the phylogenetic perspective should nicely complement the adaptationist perspective in that endeavor.

Sets 1 and 2 versus Set 3.   How might uniquely human adaptations manage constraint? Impulses can be counterproductive in human societies, in part because humans establish rules and norms that proscribe certain impulses in certain situations. Natural selection led to the emergence of cognitive fluidity and transmitted culture in Homo sapiens, and it expanded upon our ancestors' self-control abilities to aid humans in regulating their behavior to conform to beliefs and norms and become valued, well-functioning participants in a culture. But once again, natural selection would be unlikely to erase earlier adaptations; instead, just like other adaptive workarounds, the features associated with Set 3 should have evolved the ability to manage older adaptations when called for by the situation.

Some mating-relevant studies were reviewed in the Feature 7: Self-Control section. For example, depleted (relative to nondepleted) participants who were sexually inexperienced were more likely to act on their sexual urges in a psychology laboratory (Gailliot & Baumeister, 2007). Because it is not normative to engage in sexual contact in such a setting, a plausible explanation for this effect is that depleted participants had less of a consumable self-control resource to draw upon to resist their sexual impulses

(Muraven & Baumeister, 2000). Other data that address the intersection of Set 3 adaptations and older adaptations were collected as part of the two studies reviewed above examining attachment processes and fertility status (Eastwick & Finkel, 2009). In the first study, to the extent that normally cycling women possessed more trait self-control (e.g., "I am good at resisting temptation"), they reported that they would be less likely to go home with a desirable man as fertility increased. This same interaction pattern emerged among women in a second study reporting on their sexual partners over a 4-month period. To the extent that these women possessed more relative to less trait self-control, they were less likely to report that the romantic physical contact in which they had engaged was a "bad idea" as fertility increased. Future studies using Muraven et al.'s (1998) two-task depletion paradigm could examine whether experimentally depleted women show similar effects.

Recent adaptations for culture and self-control may also moderate adaptations relevant to attachment, though the evidence for this hypothesis is sketchy and anecdotal at present. In the United States and other Western countries, it is culturally normative for romantic partners to form attachment bonds with one another and to base their marital decisions accordingly. However, individuals living in cultures with arranged marriages do not typically have the same ability to marry someone to whom they are already bonded. Of course, such cultures have existed for hundreds, if not thousands, of years, so it is safe to suggest that arranged marriage has some utility as a cultural variant (Xiaohe & Whyte, 1990). Therefore, to the extent that individuals living in such cultures ascribe to the norm of arranged marriage, they should be likely to suppress any passionate love and attachment they feel for alternative partners and instead follow the arranged marriage norm (see Burbank, 1995). Even within Western societies, a wide variety of predictions could be explored at the intersection of Set 2 and Set 3 adaptations. For example, beliefs and norms could moderate how and when romantic partners turn to one another for support and advice, and self-control could affect how successfully individuals regulate their behavior in this regard.

The present approach also highlights new predictions for researchers who study animal behavior. I have suggested that humans' use of self-control in the service of abstract, long-term rewards and cultural norms in the mating domain is a recently evolved feature of our psychology. But are humans the only animals who use self-control at all in the domain of mating, regardless of the type of goal? As noted earlier, animals do possess some measure of self-control, so it is possible that animals use it to adjust certain aspects of their mating behavior (cf. Bjorklund & Kipp, 1996). After all, many primates have dominance hierarchies that determine who is allowed to mate with whom, and lower ranking individuals will frequently restrain themselves to avoid retaliation or eviction (Johnstone & Cant, 1999; Saltzman, Digby, & Abbott, 2009). When primates conform to a dominance hierarchy by inhibiting their impulses to mate with an off-limits partner, do these inhibitory behaviors require a consumable resource? If nonhuman primates are less successful at such tasks to the extent that their self-control has been depleted by engaging in effortful tasks in other domains, this would suggest that they do indeed use self-control in the service of mating. Alternatively, primate compliance with dominance hierarchies could be under close genetic control and driven by domain-specific calculations; a general, all-purpose capacity for self-control may not be required to per-

form such behaviors. In fact, when primate researchers discuss restraint models of dominance hierarchy maintenance, they typically refer not to a general, consumable resource as evidenced by humans but instead to specialized (e.g., hormonal) mechanisms (e.g., Saltzman et al., 2009). Nevertheless, tests of nonhuman animals' self-control ability in the mating domain have not yet been conducted, so it remains unclear whether (a) the use of self-control at all in the mating domain is a recent, uniquely human adaptation or (b) the use of self-control in the service of cultural norms and abstract goals in the mating domain is a recent, uniquely human adaptation.

Implications

Short-term versus long-term mating. A key component of evolutionary psychological theorizing is the distinction between short-term mating and long-term mating. As Buss and Schmitt (1993) originally noted, a mating relationship can last anywhere from minutes to decades, and human mating behavior may differ depending on the duration of the relationship (see also Gangestad & Simpson, 2000). Over the past 15 years, the short-term versus long-term dimension has become a core construct within evolutionary psychology. For example, people's ideal partner preferences differ depending on whether researchers ask them to imagine a short-term partner versus a long-term partner (Li & Kenrick, 2006), and the qualities that women find attractive when evaluating someone as a short-term (but not a long-term) mate shift over the course of the menstrual cycle (Gangestad et al., 2007). Evolutionary psychologists have suggested that selection pressures favored a "mixed" mating strategy in humans' evolutionary past, generating some adaptations for short-term mating and some adaptations for long-term mating.

The present analysis can impose conceptual structure on the short-term versus long-term mating distinction that cannot be achieved with generic appeals to selection pressures operating in the Pleistocene. Consider Set 1 and Set 2 processes alone. Given that our common ancestor with chimpanzees and bonobos likely did not form mating bonds, Set 1 adaptations would have been primarily relevant to short-term, low-investment mating. Set 2 attachment adaptations, on the other hand, would have been oriented toward long-term, high-investment mating. Therefore, one evolutionarily and theoretically grounded way to assess whether a relationship is "long-term" would be to assess the relevance of normative attachment processes, such as the extent to which a participant desires a close emotional bond with a sexual partner. In other words, the phylogenetic analysis encourages researchers to explore processes related to specific selection pressures in lieu of assessing desired relationship length, and thus it should do a better job of cleaving human mating psychology at its natural joints.

This approach will add a greater level of nuance and specificity to our understanding of humans' evolved mating psychology. Consider the following example: A woman has a 5-day affair with an attractive, desirable man while on a vacation with friends. A contemporary evolutionary psychological explanation for this behavior would appeal to short-term mating strategies, such as the woman's desire to obtain developmentally robust genes for her offspring or the man's desire to have low-cost sex with a fertile woman. However, despite the fact that 5 days is clearly a short-term relationship, it is also plausible that the two were motivated

by feelings of emotional attachment typically characteristic of long-term relationships and perhaps even exhibited attachment behaviors (e.g., distress or physiological dysregulation when separated, using one another for comfort and advice). Although it takes approximately 2 years on average for attachment bonds to fully form between romantic partners (Fraley & Davis, 1997; Hazan & Zeifman, 1994), recent evidence reveals that the attachment behavioral system may be activated in the early stages of a romantic relationship, before it is even "official" (Eastwick & Finkel, 2008). As a result, fledgling relationships or even brief affairs may feel long-term, even though they realistically may be very limited in duration.[8] How commonly people exhibit attachment-like behaviors under such conditions and whether those behaviors unambiguously indicate the activation of the attachment behavioral system requires additional research, but it is possible that researchers will discover that many brief affairs are psychologically similar to long-term mating when viewed through the lens of attachment theory.

The above example exposes the conceptual ambiguity of the short-term versus long-term distinction. After all, the true construct of interest is almost never the length of the relationship per se: Purely sexual relationships can persist on and off for years, whereas deeply significant emotional relationships can last mere days. Rather, researchers are typically interested in the psychological processes that are activated by particular relationships and what those processes reveal about our evolutionary heritage. The short-term versus long-term dimension by itself may not be an explanatory construct in humans but rather an epiphenomenon or symptom of the true process of interest. Undoubtedly, evolutionary psychologists will continue to find it useful to question why people feel compelled to invest, emotionally or otherwise, in some relationships and not others. The phylogenetic analysis is a promising conceptual tool in this endeavor because it can both (a) perform the explanatory duties of the short-term/long-term distinction while (b) highlighting specific selection pressures in our ancestral past and the order in which various mating-relevant adaptations evolved.

What is adaptive? Phylogenetic explanations should typically complement, not antagonize, those derived from the adaptationist approach. However, there will be cases in which a combined phylogenetic and adaptationist approach generates an explanation for a particular behavior that differs from one derived from adaptationism alone. For example, one adaptationist explanation for human menstrual cycle effects is that women achieved the greatest reproductive success by (a) mating with symmetrical or dominant men and extracting genetic benefits when fertile while (b) cuckolding their bonded partner and continuing to extract his resources (Gangestad et al., 2005). Phylogenetic considerations change the adaptive story: Early Homo females achieved the greatest reproductive success by establishing a pair-bond, but older features remained adaptive at times when women did not possess a strong pair-bond. That is, older features were managed, but not eliminated, by newer adaptations for pair-bonding.

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[8] Given that an attachment bond is typically a "long-enduring tie" (Ainsworth, 1989), attachment behaviors in such contexts would not necessarily indicate the presence of an attachment bond but could indicate the activation of adaptations relevant to the attachment behavioral system.

Because of conflicting explanations like this one, scholars should be wary of concluding that the persistence of ancient adaptations in modern humans means that those adaptations had fitness-enhancing consequences for humans. For example, sexual desire certainly remains adaptive in humans in a huge variety of circumstances, especially when there are no symbolic goals (Set 3) that would cause humans to inhibit their desire. But once humans had evolved the ability to resist a sexual advance for any of a number of symbolic reasons, was it ever adaptive on average for humans to fail to inhibit sexual impulses when symbolic goals dictated otherwise? That is, was it adaptive for men and women to engage in a forbidden sex act (e.g., extrapair copulation in a culture that discourages it) after their self-control efforts had failed? To answer "yes" is to suggest that, in certain situations that occurred repeatedly during our (probably recent) evolutionary past, self-control failures enhanced reproductive fitness. For researchers familiar with the adaptive benefits of self-control (Baumeister et al. 1994; Bogg & Roberts, 2004), this is a counterintuitive hypothesis, but it certainly could be tested empirically. Pure adaptationism might predict self-control to be less effective at inhibiting men's or women's sexual desire in some situations (e.g., when the female partner is fertile) relative to others (e.g., when the female partner is nonfertile), controlling for the strength of the sexual impulse.[9] If this or similar hypotheses were not supported, however, it would be consistent with the principle of constraint: Self-control does its "adaptive best" as a limited resource to manage older adaptations, given that natural selection could not endow humans with an alternative, infinite resource (Baumeister, 2005).

Another way of distinguishing conflicting explanations of mating behavior would involve the application of methods employed by human behavioral ecologists (Eric. A. Smith, Borgerhoff Mulder, & Hill, 2001). Human behavioral ecologists use formal models to estimate the fitness costs and benefits of particular behaviors, and they attempt to validate and adjust such models using actual reproductive data from nonindustrial cultures. On the one hand, if self-control failures were adaptive under some circumstances, researchers could formally model these circumstances and validate the model with actual data on reproductive success. On the other hand, the same data could instead confirm that self-control failures are accompanied by heavy social and reproductive costs that outweigh the adaptive benefits that might occur under some circumstances in the sexual domain. Similar analyses could be conducted for pair-bonding: Does the cost of engaging in an act that would threaten a strong pair-bond outweigh any adaptive benefits of the act in some cases? Of course, as such models would be validated by data on humans, they are primarily useful in explaining what may or may not still be adaptive for humans in particular, rather than what was adaptive for early Homo or primate ancestors. Nevertheless, the application of phylogenetic analyses to human mating highlights the utility of human behavioral ecological methods in determining what may or may not be adaptive human behavior.

Where are all the sex differences?   The seven features that I have emphasized do not constitute a comprehensive account of human mating. Rather, they provide a sampling of important yet broad features of the human mating psychology that can be dated with some degree of confidence using the phylogenetic approach. As a result, this article has reviewed only a small fraction of the entire corpus of evolutionary psychological research. Readers fa-

miliar with this literature might wonder, why, aside from sex hormones (Feature 3), I have spent little time describing the sex differences that constitute some of evolutionary psychology's most highly publicized findings. For example, I have not attempted to date the origin of sex differences in mate preferences (Buss, 1989) or the sex difference in the desire for casual sex (Buss & Schmitt, 1993; Schmitt et al., 2005). Indeed, these are some of evolutionary psychology's most contentious findings, sparking significant scholarly debate about their nature and origin (e.g., Buller, 2005; Eagly & Wood, 1999).

The phylogenetic perspective can add clarity to these disagreements. Consider women's greater (relative to men's) stated preference for mates with good earning prospects. One explanation for this sex difference derives from parental investment theory (Trivers, 1972) and suggests that women evolved this domain-specific preference because a male's increased investment through provisioning would have improved her offspring's likelihood of survival (Buss, 1989). An alternative biosocial explanation for this sex difference is that it emerges because (a) social roles that generated wealth could be performed with greater proficiency by men (e.g., productive labor) and, therefore, (b) women have tended to occupy social roles that offer poorer earning prospects (e.g., child caretaking, domestic labor) compared with men (Wood & Eagly, 2002). Both of these explanations are equally evolutionary, but they propose different underlying psychological mechanisms, which, in this case, can be linked to different time points in the hominid lineage. The parental investment perspective would likely predict that women evolved the specific preference for earning prospects around the time of early Homo, when investment in young offspring became critically important. Alternatively, the biosocial perspective emphasizes the expectations that people have about their roles as providers or caretakers, in which case the mechanism underlying the sex difference would have emerged when symbolic social roles evolved with the cultural big bang.[10] With these competing explanations on a common phylogenetic playing field, new evolutionary predictions emerge. For example, the parental investment perspective might predict that the mechanism underlying the sex difference in earning prospects is linked to attachment processes, which were also evolving at the time of early Homo (e.g., does a partner's earning potential better foster an attachment bond for women than for men?). Alternatively, the biosocial perspective might predict that the mechanism underlying the sex difference would be linked to self-regulation processes required for participation in human culture. Disagreements about timing could underlie other scholarly debates about sex differences: Is men's (relative to women's) greater interest in casual sex (Buss & Schmitt, 1993) grounded in ancient parental investment sex differences (Set 1) or a function of expectations regarding

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[9] Unambiguously distinguishing between the effects of impelling (e.g., sexual desire) and inhibiting (e.g., self-control) forces is a difficult task, although new methods in social cognition (e.g., the quad model; Sherman et al., 2008) hold great promise in this regard.

[10] According to Wood and Eagly's (2002) biosocial theory, the sex difference itself would not have emerged until the advent of agriculture, when men's size and strength enabled them to perform productive activities with greater efficiency than women and gave men access to the profits of agricultural economies (Harris, 1993).

reproductive activities as well as norms that have come to be sex-differentiated in modern industrial societies (Set 3)? The phylogenetic approach presents a useful organizational framework that will help researchers to better understand (and generate new predictions regarding) sex differences in human mating.

Conclusion

Humans possess a complex mating psychology, as a wide assortment of mental adaptations are relevant to the way that we pursue mates, retain mates, and integrate our mating behavior with other aspects of symbolic culture. Like other analyses that have used the anthropological and archaeological record to inform psychological research (Leary & Buttermore, 2003; Mithen, 1996; Wynn, 2002), the present report asserts that adaptations relevant to mating evolved in a particular order in the lineage leading to modern Homo sapiens. Our ancestors were subjected to shifting and often conflicting selective forces before and during the Pleistocene epoch; by tracing these selective pressures over time to the best that the fossil record allows, we can better understand how we are connected to our primate ancestors and what, if anything, makes us unique members of the animal kingdom.

Critical to this analysis is the concept of the adaptive workaround—that new adaptations are designed in part to manage the outcomes of prior selection pressures. This is the tinkering process of natural selection: The ancestral state of an organism constrains it to evolve with the materials at hand and with certain structures already in place (Jacob, 1977). Of course, older adaptations in humans would still serve adaptive functions in many circumstances. After all, what would have become of Homo sapiens if we never felt the impulses to eat, sleep, or have sex? But in other circumstances, such as when attachment bonds were activated or self-control was required, some older mating-relevant adaptations may not have generated their original fitness-enhancing consequences. Newer adaptations were thus scaffolded on top of the old: first pair-bonding and attachment approximately 1.5 to 2 million years ago, followed by cognitive fluidity, transmitted culture, and improved self-control ability only tens of thousands of years ago. Drawing from the principle of constraint, I have suggested that these newer adaptation sets may function in part by muting or refocusing the effects of older adaptations, and indeed some of the evidence reviewed above is consistent with this possibility. This depiction of human mating psychology is, in a sense, "mixed"—our repertoire is diverse as evolutionary psychologists have noted—although more apt terms might be "layered" or "hierarchical." The phylogenetic analysis thus offers a new way of thinking about our evolved psychology: Not only did natural selection shape our most deep-seated instincts, it also gave us additional adaptive tools that permit us to attach to romantic partners under the right conditions, to express or inhibit our impulses when appropriate, and to fashion cultural structures that give symbolic meaning to all of our mating-relevant emotions and behaviors.

Finally, the phylogenetic analysis is likely to be useful in exploring aspects of human psychology that stretch beyond mating. Recently, Williams and colleagues have argued that abstract goals and concepts are scaffolded on our basic sensory experiences with the world (Williams, Huang, & Bargh, in press). In one vivid illustration, participants were more likely to perceive a target individual to be interpersonally warm after holding a cup of hot versus iced coffee (Williams & Bargh, 2008). Evolutionarily old goal structures, such as the motive to be clean and free of contaminants or to remain warm and safe, may have served as a foundation for the later emergence of the abstract counterparts of these goals (e.g., the goal of being morally pure and to interact with warm, friendly people, respectively). And, of course, other features of our psychology perhaps can be reliably dated to a particular era in our evolutionary past (e.g., ingroup love, outgroup hate; see Brewer, 2007), and psychologists could use this information to generate new hypotheses as well. Courtesy of evolutionary psychology, researchers now routinely use functional reasoning to explain data or generate hypotheses. Armed with the phylogenetic analysis (Maestripieri & Roney, 2006) and the lessons of archaeology and anthropology, evolutionary psychologists stand to make novel contributions to a variety of different areas within psychology by considering Tinbergen's (1963) other evolutionary question.

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Call for Nominations

The Publications and Communications (P&C) Board of the American Psychological Association has opened nominations for the editorships of **Experimental and Clinical Psychopharmacology, Journal of Abnormal Psychology, Journal of Comparative Psychology, Journal of Counseling Psychology, Journal of Experimental Psychology: Human Perception and Performance, Journal of Personality and Social Psychology: Attitudes and Social Cognition, PsycCRITIQUES, and Rehabilitation Psychology** for the years 2012–2017. Nancy K. Mello, PhD, David Watson, PhD, Gordon M. Burghardt, PhD, Brent S. Mallinckrodt, PhD, Glyn W. Humphreys, PhD, Charles M. Judd, PhD, Danny Wedding, PhD, and Timothy R. Elliott, PhD, respectively, are the incumbent editors.

Candidates should be members of APA and should be available to start receiving manuscripts in early 2011 to prepare for issues published in 2012. Please note that the P&C Board encourages participation by members of underrepresented groups in the publication process and would particularly welcome such nominees. Self-nominations are also encouraged.

Search chairs have been appointed as follows:

- **Experimental and Clinical Psychopharmacology,** William Howell, PhD
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- **Journal of Comparative Psychology,** John Disterhoft, PhD
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- **Journal of Experimental Psychology: Human Perception and Performance,** Leah Light, PhD
- **Journal of Personality and Social Psychology: Attitudes and Social Cognition,** Jennifer Crocker, PhD
- **PsycCRITIQUES,** Valerie Reyna, PhD
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Prepared statements of one page or less in support of a nominee can also be submitted by e-mail to Emnet Tesfaye, P&C Board Search Liaison, at emnet@apa.org.

Deadline for accepting nominations is January 10, 2010, when reviews will begin.