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Evolution and human motivation: A fundamental motives framework

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Abstract

An evolutionary perspective on human motivation provides a means of identifying conceptually distinct motivational systems (including motives pertaining to self-protection, disease avoidance, affiliation, status, mate acquisition, mate retention, and parental care), each of which has unique implications for affect, cognition, and behavior. We provide an illustrative summary of some of these empirically documented implications—including those pertaining to individual differences in chronic motivational tendencies, as well as additional implications that follow from temporary activation of these motivational systems. We also summarize a variety of broader implications—both conceptual and practical—that follow from this framework.

1 | INTRODUCTION

What motivates human behavior? Models of human motivation come in two flavors, corresponding to Carver and Scheier's (2012) distinction between *the how* and *the what* of motivation. Models that focus on *how* questions are process-oriented, examining the mechanisms that govern how goal-directed behavior unfolds (e.g., Carver & Scheier, 1981, 2012; Higgins, 1998; Huang & Bargh, 2014). These models emphasize how psychological processes translate any motivational state into action, but are generally mute regarding the question of *what* motives actually define human nature. That question—the *what* question—must be addressed by a different conceptual approach, in which some principled means of conceptual analysis is used to identify motives that can be considered basic or primary or fundamental in some way (e.g., James, 1890; Maslow, 1943; McDougall, 1908; Murray, 1938; Ryan & Deci, 2008).

In this article, we summarize an evolutionary approach to the *what* of human motivation and highlight the generative utility of this approach. We begin by discussing what the concept of motivation means within an evolutionary framework. We then show how the conceptual tools of evolutionary biology can be used to identify which specific motivational systems are likely to have evolved in response to specific selection pressures operating on ancestral populations—and thus (in one sense of the word) can be considered to be “fundamental” motives. We then summarize research linking these motivational systems to phenomena within the realm of personality and social psychology.

2 | AN EVOLUTIONARY APPROACH TO HUMAN MOTIVATION

Evolutionary approaches to human psychology are predicated upon two basic principles of evolutionary and developmental biology: (a) The genes that define contemporary human populations are the product of a long history of evolution by natural selection, and (b) the human nervous system typically develops according to a recipe encoded in those genes (Neuberg & Schaller, 2014). It is with these foundational principles in mind that “human nature” can be characterized as comprising psychological mechanisms that exist because—over the course of our species’ long evolutionary history—they facilitated genetic reproduction.

Successful reproduction required our ancestors to successfully solve a wide range of distinct problems. Our ancestors needed to survive to reproductive age, which required that they acquire sufficient resources to sustain basic physiological functioning and that they defend themselves against predators and parasites. Because humans are a highly social species, our ancestors’ reproductive outcomes were contingent on the actions of others; consequently, they needed to live agreeably within social groups and to navigate social structures in such a way as to facilitate access to potential mates. They then needed to successfully produce offspring with those mates. And, because the mere production of offspring is a reproductive dead-end unless those offspring live long enough to produce their own viable offspring, our ancestors’ reproductive fitness also benefited from maintaining long-term mating relationships (which facilitates biparental care for offspring) and providing those offspring with protection and care.

The suites of psychological mechanisms that evolved to solve these problems were once known as instincts (e.g., James, 1890; McDougall, 1908). Within the contemporary psychological sciences, they are appropriately characterized as *motivational systems* that were designed—by evolutionary processes—to regulate functionally specific forms of behavior: “Exquisitely designed regulatory systems permeate the human body, producing functional outcomes by entraining processes at all levels of organization, from gene activation and protein synthesis to organ function to behavior. Motivational systems are simply one class of regulatory system” (Tooby, Cosmides, Sell, Lieberman, & Sznycer, 2008, p. 253–254). Whereas some regulatory systems (such as the immune system and the circulatory system) perform metabolic functions that typically operate outside the realm of psychological experience, motivational systems evolved to regulate behavioral interactions with other organisms and with the external environment more generally.

Integral to this evolutionary perspective on motivation is the principle of functional modularity (Barrett & Kurzban, 2006; Tooby et al., 2008): Through processes of natural selection, psychologically different motivational systems evolved in response to different selection pressures associated with different reproduction-relevant problems. For example, although different kinds of close relationships (e.g., relationships with coalitional allies, with sexual partners, and with offspring) may all have implications for reproductive fitness, these implications are predicated upon different kinds of behavioral responses (Kenrick, Neuberg, & White, 2013). Consequently, psychologically distinct motivational systems are likely to have evolved to regulate behavior within these different domains of interpersonal interaction. These psychologically distinct motivational systems may not be entirely anatomically distinct or encapsulated from one another (Barrett & Kurzban, 2006). Rather, they are “modular” in a functional sense: They are attuned to different kinds of cues in the environment, which inform different types of appraisals (regarding specific threats to be avoided or opportunities to be seized), which, in turn, trigger specific affective, cognitive, and behavioral responses.

By characterizing human motivation in terms of evolved behavior regulatory systems, this evolutionary perspective is conceptually distinct from—and complementary to—other perspectives that define human motivation primarily in terms of individuals’ goals or needs (e.g., Bargh, Gollwitzer, & Oettingen, 2010; Ryan & Deci, 2008; Sheldon, 2011). These regulatory systems evolved *not* because of their implications for individuals’ subjectively valued outcomes (such as happiness or health) but instead because of their implications for the reproduction of genes. This is not to suggest that these motivational systems do not have implications for subjectively valued outcomes; sometimes, they do. But, when employing the conceptual tools of evolutionary biology to address questions about *what* motivational systems are fundamental to human nature, these subjectively valued outcomes are not the primary logical focus. Rather than framing the *what* question in terms of individuals’ subjective outcomes (e.g., “What do people need in order to be happy or healthy?”), an evolutionary approach must instead frame that question in terms of evolutionary processes

operating over vast amounts of time: “What behavior regulatory systems are likely to have evolved in response to the fitness-relevant perils and prospects that characterized humans' ancestral ecologies?”

Once the conceptual tools of evolutionary biology have been employed to produce answers to that question, each of those answers then leads to follow-up questions. For example, “What implications does this particular evolved behavior regulatory system have for human affect, cognition, and behavior in contemporary human ecologies?” These follow-up questions can be answered with empirically testable theories, models, and hypotheses that specify relations between psychological constructs. Thus, the generative utility of an evolutionary framework lies not merely in the identification of evolved motivational systems that might be considered “fundamental” to human nature; arguably, its greatest utility lies in consequent empirical discoveries that elucidate the psychological implications associated with each of those fundamental motivational systems.

On the following pages, we illustrate the generative utility of this framework by summarizing conceptual and empirical insights that have emerged from it. First, we describe how this perspective has been employed to identify answers to the question of *what* motivational systems are fundamental to human nature. We then provide an illustrative overview of research documenting some of the unique implications that these particular motivational systems have for social cognition and social behavior—including those pertaining to individual differences in chronic motivational tendencies and additional implications that follow from their temporary activation.

3 | IDENTIFICATION OF EVOLUTIONARILY FUNDAMENTAL MOTIVATIONAL SYSTEMS

In recent years, the principles summarized above have been employed as a means to identify several different motivational systems that plausibly evolved in response to specific selection pressures operating on ancestral populations and that appear to be functionally discrete—attuned to different categories of stimuli that, when perceived, trigger different kinds of affective, cognitive, and behavioral responses (e.g., Aunger & Curtis, 2013; Bernard, 2012; Kenrick, Griskevicius, Neuberg, & Schaller, 2010).

For example, Kenrick et al. (2010) revisited Maslow's famous pyramid of needs and renovated it. Informed by evolutionary logic—and by Plutchik's (1980) “psychoevolutionary” perspective on human emotions—this renovated pyramid (a) depicts a set of conceptually distinct motivational systems that evolved in response to conceptually distinct reproduction-relevant problems and (b) organizes those “fundamental” motives within a hierarchical structure.

The renovated pyramid (depicted in Figure 1) identifies conceptually distinct domains of human motivation, but it does *not* depict each of the functionally unique motivational systems that exemplify these domains. This is the case especially for the lower levels of the pyramid. Multiple different regulatory systems govern the acquisition of different kinds of physiological needs (e.g., food, liquid, and warmth). Different motivational systems also evolved to solve different self-protection problems. One important distinction is that between large predators and tiny disease-causing parasites—a distinction with implications for the ways in which these different entities pose their threat and for the means through which these different threats might be mitigated. Consequently (and in contrast to models of motivation that identify an all-purpose “harm-avoidance” motive; e.g., Murray, 1938), an evolutionary cost-benefit analysis suggests that psychologically distinct motivational systems evolved as defenses against these different forms of threat (Schaller, 2016). Ample evidence attests to that conceptual distinction (Murray & Schaller, 2016).

More generally, abundant evidence is consistent with the various conceptual distinctions represented in this renovated pyramid. Much of this evidence pertains to the distinct emotional experiences associated with different “fundamental” motivational systems (Beall & Tracy, 2017). The functionally different forms of threat posed by predators and parasitic diseases tend to elicit different emotions—fear and disgust, respectively—that facilitate different kinds of behavioral responses (Neuberg, Kenrick, & Schaller, 2011). The different motivational systems that regulate behavior within different kinds of close relationships are also associated with functionally different emotional responses. The mate acquisition system is associated with sexual arousal, for instance, whereas the parental care-giving system

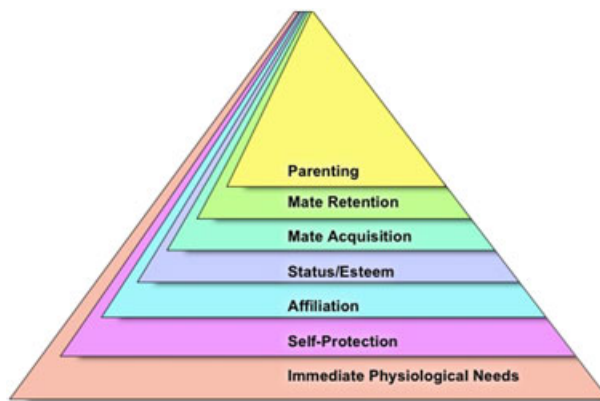


FIGURE 1 A hierarchy of fundamental human motives, informed by the logic of evolutionary psychology (image copyright: Douglas T. Kenrick, Vidas Griskevicius, Steven L. Neuberg, & Mark Schaller)

is associated with a tenderness response that facilitates the provision of protection and nurturance (Kalawski, 2010). Additional evidence comes from factor analyses of self-reported individual differences in motivational inclinations (Neel, Kenrick, White, & Neuberg, 2016). These factor analytic results corroborate the conceptual distinctions identified in Figure 1 and suggest several additional, more nuanced functional distinctions too.

In addition to identifying a logically deduced set of evolutionary fundamental motives, the renovated pyramid borrows from Maslow (1943) the assumption that some motives (those lower in the pyramid) manifest themselves earlier than others. In order to articulate the specific nature of that developmental prioritization, Kenrick et al. (2010) employed the logical principles of *life history theory*—a biological framework that describes how the allocation of bioenergetic resources is adaptively calibrated and thus differs depending upon organisms' ecological and developmental context (Del Giudice, Gangestad, & Kaplan, 2016; Stearns, 1992). Based on these principles, the behavior of newborn infants is presumed to be governed primarily by early-developing motivational systems that regulate the acquisition of resources (e.g., food, liquid, and warmth) required to satisfy basic physiological needs. As infants mature—and eventually become adults—additional reproductive problems must be solved and resources are likely to be re-prioritized accordingly. For instance, predators impose threats to very young children, whereas the functional utility of friendships arises somewhat later; consequently, children are likely to exhibit evidence of self-protection responses (e.g., fear of strangers) before they exhibit concerns with peer affiliation. And because social affiliation is a pre-requisite for the attainment of social status, affiliative responses are expected to manifest themselves prior to those that serve the function of status attainment.

In contrast to the lower parts of the pyramid, the upper half of Kenrick et al.'s (2010) pyramid differs substantially from Maslow's, and it does so because it is conceptually informed (and constrained) by the logic of reproductive fitness. Mating was essential to reproductive fitness, and beginning around puberty, mate acquisition is expected to become a paramount motivational concern. Successful mate acquisition introduces the problem of mate retention; thus, for people in mating relationships, mate retention is expected to become a more profound motivational concern. Similarly, among individuals who have mated and produced offspring, the motivational system that governs parental care-giving (and kin care more generally) would be expected to become more strongly activated, and more chronically engaged.

Two additional points are important to note. First, humans' normal development provides the physiological foundations of these motivational systems, and thus the underlying psychological architecture required for these motivational systems may exist even in those for whom the relevant "need" may not have yet arisen. (For example, although the parental care-giving motive may manifest itself especially strongly among actual parents, even non-parents exhibit caring responses to infants; Buckels et al., 2015). Second, although these motivational systems conform logically to a hierarchical structure, the hierarchy is psychologically fluid (represented by the visual overlapping of the motives in Figure 1). People do not "outgrow" motives as they mature; they add new ones. Because reproduction-relevant

threats and opportunities re-occur throughout individuals' lifetimes, even as later-developing motivational systems become psychologically paramount, other motivational systems (e.g., those closer to the pyramid's base) remain at the ready, prepared to respond whenever pertinent threats or opportunities are perceived to arise.

4 | INDIVIDUAL DIFFERENCES IN EVOLUTIONARILY FUNDAMENTAL MOTIVATIONAL SYSTEMS

These evolved motivational systems substantially define the nebulous concept of “human nature” and are part of the psychological architecture of all normally developing human beings. But this fact does not preclude individual differences (Neel et al., 2016). Life history theory (Del Giudice et al., 2016; Roff, 1992; Stearns, 1992) provides a logical basis for predicting and understanding the nature of many of these individual differences.

A foundational premise of life history theory is that time and energy resources are limited, with the implication that when resources are allocated to the development or deployment of any specific regulatory system, those resources are unavailable for allocation to other systems. Trade-offs are therefore inevitable. The manner in which these trade-offs are managed (i.e., the specific systems that are adaptively prioritized) varies predictably, depending upon reproduction-relevant demographic features such as individuals' sex and age.

We discuss sex differences at greater length below (within the specific context of mating motives); additional implications are associated with differences that correspond to “life stages” of specific kinds. For instance, among young adults who have reached reproductive age but have not yet reproduced, a substantial proportion of available resources are expected to be allocated to motivational systems that regulate mating behavior. By later adulthood, individuals are more likely to have produced offspring (who require protection and nurturance if they are themselves to eventually reproduce); consequently, resources that were once allocated to mating systems may be allocated to the parental care-giving system instead. The implication—supported by empirical evidence—is that activation of the mate-acquisition system peaks in early adulthood and drops off as adults mature and/or have children, whereas the parental care system is more readily activated among older adults and/or parents (Buckels et al., 2015; Neel et al., 2016).

Life history theory also yields predictions about motivational implications that arise from differences in early childhood ecologies. Different behavioral strategies may be adaptive under different ecological circumstances, and input from the environment influences the allocation of resources to the development of different regulatory systems—including motivational systems. For example, because unpredictable environments connote a relatively reduced life expectancy, individuals developing within such environments are more likely to demonstrate a speeded trajectory toward reproduction (i.e., a “fast” rather than “slow” life history strategy)—characterized by relatively greater focus on immediate rewards and increased allocation of resources to mate seeking (Belsky, 2012; Del Giudice, 2009; Ellis, 2004; Ellis, Figueredo, Brumbach, & Schlomer, 2009; Griskevicius, Delton, Robertson, & Tybur, 2011; Griskevicius, Tybur, Delton, & Robertson, 2011; Low, Hazel, Parker, & Welch, 2008; Nettle, 2010; Simpson, Griskevicius, Kuo, Sung, & Collins, 2012). Consistent with this general pattern of results, adults who grew up in less stable environments report stronger mate-acquisition motives (Neel et al., 2016).

Individual differences in fundamental motivational systems may result from other variables too (e.g., idiosyncratic differences in genetic make-up or learning histories). Regardless of their origins, these individual differences have wide-ranging consequences for social cognition and behavior. The following paragraphs provide illustrative examples pertaining to the motivational systems that evolved in the context of disease-avoidance, mating, and parental care-giving.

4.1 | Disease avoidance

Individuals differ in the extent to which they chronically perceive themselves to be vulnerable to diseases caused by parasite infection (Duncan, Schaller, & Park, 2009; Neel et al., 2016; Tybur, Lieberman, & Griskevicius, 2009). Even when controlling for other avoidant dispositions, individuals who are more highly motivated to avoid infection express

more powerful prejudices against categories of people who are tacitly perceived to pose an infection risk—including foreigners and individuals characterized by anomalous morphological features (e.g., being disfigured, disabled, or obese; Schaller & Neuberg, 2012). Additional implications follow from the fact that, historically, many cultural norms served as buffers against the spread of infectious diseases (Fabrega, 1997): More disease-avoidant individuals report more conformist attitudes, make harsher moral judgments when others fail to conform to conventional norms—especially norms that pertain to “purity”—and are more likely to express conservative sociopolitical attitudes (Brenner & Inbar, 2015; Horberg, Oveis, Keltner, & Cohen, 2009; Inbar, Pizarro, Iyer, & Haidt, 2012; Murray & Schaller, 2012; Terrizzi, Shook, & McDaniel, 2013).

4.2 | Mating

In the mating domain, some of the most profound motivational differences between individuals involve sex differences. These sex differences conform to the logical implications of evolutionary principles. Given that, historically, female and male reproductive potential was affected by different variables, the mate-acquisition motives of men and women evolved to be attuned to different characteristics of other individuals. Women are relatively more responsive to cues connoting social status, access to resources, and physical formidability; men are relatively more responsive to cues connoting youth and fertility (Kenrick & Keefe, 1992; Li, Bailey, Kenrick, & Linsenmeier, 2002; Singh, 1993). Additional implications follow from the fact that, compared to males, females are physiologically obliged to invest more resources toward production and care of offspring (e.g., in the form of gestation and lactation). Therefore—consistent with the evolutionary logic of *parental investment*—women tend to be more selective and cautious in their psychological responses to novel mating opportunities, whereas men are more inclined to avail themselves of those opportunities (e.g., Buss & Schmitt, 1993; Haselton & Buss, 2000; Kenrick, Groth, Trost, & Sadalla, 1993; Kenrick, Sadalla, Groth, & Trost, 1990).

Men and women differ more substantially in mate-acquisition motives than in mate-retention motives (Neel et al., 2016). Nevertheless, some manifestations of the mate retention motivational system do differ between the sexes. Research on jealousy offers one example, which follows from the different reproductive problems that partner infidelity posed for males and females. Males were more at risk of investing resources in a child who was not their actual offspring; females were more at risk of losing access to parental resources provided by mating partners. Hence, although men and women are similarly prone to jealousy, they differ in their sensitivities to sexual versus emotional infidelity (Sagarin, 2005).

There are within-sex individual differences too. Particularly notable is work on *sociosexual orientation*—individual differences in motivational inclinations toward restricted and unrestricted mating (Jackson & Kirkpatrick, 2007; Penke & Asendorpf, 2008). These individual differences have implications for visual attention (e.g., selective attention to attractive opposite-sex others; Duncan et al., 2007), mate preferences (e.g., the extent to which specific physical and dispositional traits are desired in a mate; Simpson & Gangestad, 1992), courtship behaviors (e.g., flirting; Penke & Asendorpf, 2008), and a wide range of other phenomena in the mating domain (for an overview, see Simpson, Wilson, & Winterheld, 2004). Sociosexual orientation influences not only responses to potential mates but also interactions with same-sex individuals who are tacitly perceived to be competitors for those potential mates. For instance, unrestricted men tend to be more directly competitive with other men (Simpson, Gangestad, Christensen, & Leck, 1999).

4.3 | Parental care

People—both parents and nonparents—differ in the extent to which the perception of young children arouses the protective and nurturant tendencies characteristic of the parental care motivational system (Buckels et al., 2015; Neel et al., 2016). People for whom this system is more readily activated respond more favorably not only to babies but also to baby-faced adults and express harsher judgments about others' norm violations (Buckels et al., 2015). Chronic activation of the parental care system is also associated with a stronger preference for mates who are kind, faithful,

responsible, and stable—traits that indicate a capacity to provide long-term biparental care to offspring (Buckels et al., 2015). Notably, the latter results show that individual differences in the parental care motive did *not* predict preferences regarding other characteristics that are generally desirable in a mate (e.g., physical attractiveness); the effect was specific to characteristics connoting a capacity for effective co-parenting of children.

5 | SITUATION-SPECIFIC ACTIVATION OF EVOLUTIONARILY FUNDAMENTAL MOTIVATIONAL SYSTEMS

Situations play a critical role in the activation of fundamental motive systems. Even when each system is *available* for use, its *actual* activation depends upon individuals' immediate context. Specific kinds of perceptual cues—and the appraisals that follow from those cues—activate specific motivational systems. Once activated, a motivational system governs responses to whatever stimuli triggered its activation, and as long as it remains activated, it influences how individuals respond to their environment more generally—with wide-ranging implications for social cognition and behavior. We summarize a few illustrative examples below, again pertaining to disease-avoidance, mating, and parental care motives.

5.1 | Disease avoidance

The disease-avoidance motivational system may be triggered by many different things—the sight of sores on someone's skin, a foul organic smell, or the mere awareness of an impending outbreak. Once triggered, the disease-avoidance motive has many downstream psychological consequences. For instance, compared to control conditions in which other kinds of threat are salient, when the threat of infectious disease is temporarily salient, people are more likely to exhibit strongly prejudicial attitudes toward people who appear morphologically unusual as well as more strongly xenophobic attitudes toward foreigners (Schaller & Neuberg, 2012). Activation of the disease-avoidance motive also has unique implications for conformist attitudes and conformity behavior: For example, compared to control conditions in which other kinds of threat are salient, when the threat of infectious disease is temporarily salient, people are more likely to endorse conformist attitudes, to like conformist individuals, and to engage in conformity behavior themselves (Murray & Schaller, 2012; Wu & Chang, 2012). There is now a large body of evidence documenting a wide range of unique cognitive and behavioral consequences that follow from temporary activation of the disease-avoidance motivational system (for a review, see Murray & Schaller, 2016).

5.2 | Mating

A mate-acquisition motive may be activated simply by the perception of a physically attractive potential mate or by a variety of other circumstances that make mating opportunities temporarily salient. Once activated, the motive has consequences for visual attention. Among heterosexual individuals—and primarily among those with an unrestricted sociosexual orientation—it selectively increases allocation of attention to attractive members of the opposite sex (Becker, Kenrick, Guerin, & Maner, 2005; Maner, Gailliot, Rouby, & Miller, 2007). It also leads to biases in social perception and social inference. For instance, activation of a mate-acquisition motive leads men to erroneously perceive sexual arousal in the faces of physically attractive women (Maner et al., 2005). And, among men specifically, the temporary activation of a mate-acquisition motive leads to increased incidence of many different kinds of behavioral outcomes indicative of an inclination to distinguish themselves from the many other men competing for access to choosy mates—including physical risk-taking, non-conformity, displays of creativity, and ostentatious acts of apparent altruism (Griskevicius, Cialdini, & Kenrick, 2006; Griskevicius, Goldstein, Mortensen, Cialdini, & Kenrick, 2006; Griskevicius et al., 2007; Ronay & von Hippel, 2010).

Rather, different outcomes follow from the temporary activation of a mate-retention (rather than mate-acquisition) motive. For instance, activation of a mate-retention motive actually leads to *decreased* (rather than increased)

visual attention to attractive opposite-sex others (Maner, Gailliot, & Miller, 2009; Maner, Rouby, & Gonzaga, 2008)—an attentional bias that may serve the function of relationship maintenance by reducing the likelihood of infidelity. Activation of a mate-retention motive can also increase attention to, and decrease trust of, same-sex individuals who may be rivals in the mating game (Krems, Neel, Neuberg, Puts, & Kenrick, 2016; Maner et al., 2007).

5.3 | Parental care

People are perceptually sensitive to cues diagnostic of individuals in need of protection and care (e.g., morphological features that constitute a “baby face,” such as small noses and big eyes). When these cues are perceived, they tend to arouse an emotional response—tenderness—characteristic of the parental care system (Kalawski, 2010). This, too, occurs among both parents and non-parents, and sometimes even if the bearer of these features is not actually a human infant but merely mimics the appearance of infancy (e.g., a kitten, a puppy, and a baby-faced adult; Sherman, Haidt, & Coan, 2009; Montepare & Zebrowitz, 1998).

Once activated, the parental-care motive influences individuals' attitudes and actions in a variety of ways likely to have had positive implications for offspring survival within ancestral ecologies. Not only do individuals exhibit *caring* responses, they also exhibit *careful* responses more generally—which shows up as cautious motor behavior and as risk-averse attitudes (Eibach & Mock, 2011; Sherman et al., 2009). Temporary activation of the parental care motive also amplifies individuals' inclinations to respond aversely to people believed to pose threats of various kinds—including strangers, members of potentially dangerous outgroups, and people who violate social norms (Eibach, Libby, & Ehrlinger, 2009; Eibach & Mock, 2011; Gilead & Lieberman, 2014).

6 | ADDITIONAL IMPLICATIONS

6.1 | Trade-offs and relations between motivational systems

Life history theory assumes that organisms' developmental trajectories and behavioral strategies are affected by trade-offs in the adaptive allocation of resources. One of the most fundamental trade-offs is between investment in mating effort versus parenting effort (Del Giudice et al., 2016). This suggests that there may be a mutually inhibitory relationship between motivational systems governing mate acquisition and parental care. This may occur on a developmental timescale, manifesting itself in a negative relation between dispositional inclinations toward short-term mating and toward parental care (Beall & Schaller, 2014). The inhibitory relationship may also show up on the briefer timescale of cognitive operations, such that activation of the mate acquisition system might temporarily inhibit activation of the parental care system, and vice versa.

Other cost/benefit trade-offs have other implications for relations between motivational systems. For example, reproduction required that ancestral humans engaged in sexual intercourse. One cost of sexual intercourse, however, is increased exposure to infectious diseases. One might thus expect that activation of the mate-acquisition motive would temporarily inhibit activation of the disease avoidance motive, and vice versa. Indeed, sexual arousal inhibits disgust (Stevenson, Case, & Oaten, 2011), and among women, the temporary salience of infection risk inhibits interest in short-term mating (Murray, Jones, & Schaller, 2013). Disease avoidance also trades-off with affiliation: People concerned with disease see themselves as less sociable (Mortensen, Becker, Ackerman, Neuberg, & Kenrick, 2010), and excluded people are less concerned with disease (Sacco, Young, & Hugenberg, 2014).

Along with inhibitory relations between some fundamental motivational systems, there exist facilitative relations between others. For instance, there are reproductive benefits associated with the acquisition of high-status mates, and historically, these benefits accrued especially to females. Consequently, women prioritize potential mates based, in part, on cues connoting social status. One implication is that, when mating motives are activated in men, motivational systems that govern status-seeking and status-displaying behavior are also likely to be activated—as indicated by the amplifying effect that mating motives have on men's tendencies to be competitively aggressive,

ostentatiously altruistic, and conspicuous in their purchase of status-connoting consumer products (Griskevicius, Tybur, et al., 2009; Griskevicius et al., 2007; Sundie et al., 2011).

6.2 | Variations across cultures and ecologies

The logical principles of evolutionary psychology have implications for different population-level outcomes under different ecological circumstances, some of which correspond to cross-cultural differences (Gangestad, Haselton, & Buss, 2006; Kenrick & Gómez Jacinto, 2014; Schaller & Murray, 2011). Because the fundamental motives framework is predicated on the principles of life history theory, the implication is that different populations of people may have different motivational profiles, depending upon ecological variables that have implications for organisms' life history strategies. Population density is one such variable, with high density being associated with slower life history strategies in humans, as it is in other species (Sng, Neuberg, Varnum, & Kenrick, 2017). In terms of fundamental motives, this slower life history strategy is likely to manifest itself as relatively lower investment in mate acquisition and relatively more investment in mate retention and parental care-giving. Other ecological variables also have motivational implications for humans. For instance, increased investment in self-protection and status motives is associated with relatively higher ratio of males to females in the local population and with higher degrees of income inequality (Daly, Wilson, & Vasdev, 2001; Gómez Jacinto, 2011; Kenrick & Gómez Jacinto, 2014).

6.3 | Relations between motivational systems and other evolved regulatory systems

An evolutionary perspective on human nature requires one to consider people's attributes and actions from the point of view of genes that design and build people to serve as vehicles for genetic reproduction (Dawkins, 1976). From this gene's eye view, there is no sharp categorical distinction between the different physiological systems that regulate different bodily functions (including, but not limited to, behavior)—and thus, no necessary conceptual partition between motivational systems (traditionally studied by psychologists) and other evolved regulatory systems of the sort studied by other biomedical scientists (Tooby et al., 2008). The implication is intriguing: Just as there may be functionally adaptive linkages between different motivational systems, there may also be functionally adaptive linkages between specific motivational systems and other regulatory systems that typically lie outside the realm of psychological analysis.

For instance, several lines of evidence indicate that the motivational psychology of disease avoidance has implications for actual immunological responses to infection, and vice versa (e.g., Fessler, Eng, & Navarrete, 2005; Miller & Maner, 2011; Schaller, Miller, Gervais, Yager, & Chen, 2010). Based upon these and other results, it has been suggested that the disease avoidance motivational system is not merely a functionally unique motivational system but also an integral part of the immune system that evolved to defend organisms' bodies against infection (Clark & Fessler, 2014; Gangestad & Grebe, 2014; Murray & Schaller, 2016). More broadly, an evolutionary perspective on human motivation offers a useful set of conceptual tools that may help integrate the study of human motivation with the study of bodily functioning more generally.

6.4 | A useful approach for characterizing both persons and situations

Dispositional differences between people are commonly characterized in terms of behavioral traits (extraversion, conscientiousness, etc.), but there is a conceptually complementary tradition of characterizing individual differences in terms of underlying motives (Winter, John, Stewart, Klohnen, & Duncan, 1998). The fundamental motives framework provides a conceptual structure for doing so in a way that is logically constrained but nonetheless broadly comprehensive—and that lends itself to efficient empirical measurement (Neel et al., 2016).

The fundamental motives framework also has useful implications for characterizing situations. The “power of the situation” is the defining theme of social psychology, yet social psychologists still know relatively little about what constitutes a meaningful situation, about which specific aspects of situations are most psychologically meaningful,

or about which types of situations are most psychologically important and to whom (Rauthmann et al., 2014; Reis, 2008). The fundamental motives framework offers one approach to answering these questions.

A meaningful situation can be thought of as a context that poses either threats or opportunities for the attainment of fundamental motives. This allows for a theory-driven taxonomy of situations (see Brown, Neel, & Sherman, 2015; Morse, Neel, Todd, & Funder, 2015). It follows, then, that the most psychologically salient elements of any situation will be those elements that connote the presence of goal-relevant threats and opportunities and that the salience of these elements may vary depending on the extent to which different fundamental motives are psychologically paramount. For example, when the disease-avoidance motive is acutely activated, people may be especially attentive to the crowdedness of a room and to the odors of the people in that crowd, but when the mate-acquisition system is acutely activated, they may instead be attentive to the relative ratio of men and women. Furthermore, people are likely to avoid situations that pose specific fitness-relevant threats (e.g., avoiding social gatherings when the disease-avoidance motive is active) and to approach situations that offer specific fitness-relevant opportunities (e.g., seeking out specific kinds of social gatherings, depending upon whether an affiliation or mate-acquisition motive is active). People are also likely to strategically modify situations so as to facilitate the satisfaction of specific fitness-relevant motives (Buss, 1987). In general, this perspective on the psychology of situations offers a generative approach to defining situations and understanding their psychological features (see Neel, Brown, & Sng, in press).

6.5 | Practical applications and implications

The regulatory mechanisms that define “fundamental motives” evolved because of the implications they had for genetic reproduction. In contemporary societies, these motivational systems have implications that matter for additional reasons, too (Griskevicius & Kenrick, 2013; Kenrick & Griskevicius, 2013). There are practical implications for consumer behavior: The activation of mating motives affects the specific kinds of products that people are inclined to purchase (Griskevicius et al., 2007; Sundie et al., 2011). More generally, the success or failure of specific persuasive appeals depends on the specific motives that are active (Griskevicius, Goldstein, et al., 2009). There are also implications for other forms of economic decision-making. For instance, activation of a mate-acquisition motive increases the tendency for men to focus on short-term (rather than long-term) economic outcomes and to be relatively less concerned about losses rather than gains (Li, Kenrick, Griskevicius, & Neuberg, 2012; Wilson & Daly, 2004). In contrast, among both men and women, activation of self-protective motives is associated with increased loss aversion (Li et al., 2012). Self-protective motives also have unique implications for intergroup relations, with different self-protective concerns (e.g., predator avoidance, and disease avoidance) facilitating different forms of prejudice—and thus also have unique applications for the design of prejudice-reduction interventions (Schaller & Neuberg, 2012). There are also implications for electoral politics. For instance, activation of the disease-avoidance system is associated with increased preferences for political candidates who are physically attractive and who are politically conservative (Beall, Hofer, & Schaller, 2016; White, Kenrick, & Neuberg, 2013).

Fundamental motives can also have implications for human health and well-being, although these implications are not always straightforward. For instance, activation of the disease-avoidance system facilitates behavioral responses (including conformity to existing cultural traditions) that generally had positive health consequences within ancestral ecologies, but in many modern ecologies—in which the ancient threat posed by parasites may be mitigated by novel medical and public health practices—these same behavioral responses can sometimes have *negative* health consequences instead (Schaller, Murray, & Bangertner, 2015).

Finally, although these evolved motivational systems are characterized as “fundamental” because of their evolutionary origins and not because of their consequences for subjectively valued psychological states, they may nonetheless guide individuals' pursuit of happiness and personal fulfillment. This is because reward mechanisms (e.g., neurochemical regulation of affective states) are integral to the suites of psychological adaptations that characterize these fundamental motives—with the consequence that many things that make people feel happy or fulfilled

correspond to the successful pursuit of fundamental motives (Buss, 2000; Krebs, Kenrick, & Neel, in press; Nesse & Ellsworth, 2009). That said, it is important to remember that an evolutionary perspective on human motivation is not defined by questions about what makes us healthy or happy; it focuses more fundamentally on what makes us human.

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