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Abstract

Maslow's pyramid of human needs, proposed in 1943, has been one of the most cognitively contagious ideas in the behavioral sciences. Anticipating later evolutionary views of human motivation and cognition, Maslow viewed human motives as based in innate and universal predispositions. We revisit the idea of a motivational hierarchy in light of theoretical developments at the interface of evolutionary biology, anthropology, and psychology. After considering motives at three different levels of analysis, we argue that the basic foundational structure of the pyramid is worth preserving, but that it should be buttressed with a few architectural extensions. By adding a contemporary design feature, connections between fundamental motives and immediate situational threats and opportunities should be highlighted. By incorporating a classical element, these connections can be strengthened by anchoring the hierarchy of human motives more firmly in the bedrock of modern evolutionary theory. We propose a renovated hierarchy of fundamental motives that serves as both an integrative framework and a generative foundation for future empirical research.

Keywords

motivation, evolutionary psychology, development, life-history theory, humanistic psychology, positive psychology

Almost 70 years have passed since Abraham Maslow's classic 1943 *Psychological Review* paper proposing a hierarchical approach to human motivation. Maslow's model had an immense influence on the field of psychology, including the subfields of personality, social psychology, psychopathology, developmental psychology, and organizational behavior, and it continues to be cited widely in textbooks (e.g., Kreitner & Kinicki, 2008; Myers, 2009; Nairne, 2003). Indeed, the powerful visual image of a pyramid of needs (see Fig. 1) has been one of the most cognitively contagious ideas in the behavioral sciences.

Unfortunately, many behavioral scientists view Maslow's pyramid as a quaint visual artifact without much contemporary theoretical importance. We suggest, on the contrary, that the idea can take on a new significance when combined with later theoretical developments. In this article, we revisit the idea of a hierarchical approach to human motivation, suggesting some renovations to Maslow's approach. This revised model not only provides useful connections to current innovations in

psychology (e.g., evolutionary and positive psychology) but also raises a number of broader empirical questions for future research.

We propose an updated and revised hierarchy of human motives, building on theoretical and empirical developments at the interface of evolutionary biology, anthropology, and psychology (e.g., Cosmides & Tooby, 1992; Crawford & Krebs, 2008; Dunbar & Barrett, 2007; Gangestad & Simpson, 2000; Haselton & Buss, 2000; Kaplan & Gangestad, 2005; Kenrick, Li, & Butner, 2003). This revision retains a number of Maslow's critical insights, including the hierarchical structure and several original needs such as physiological, safety (self-protection), and esteem (status). However, we update the model

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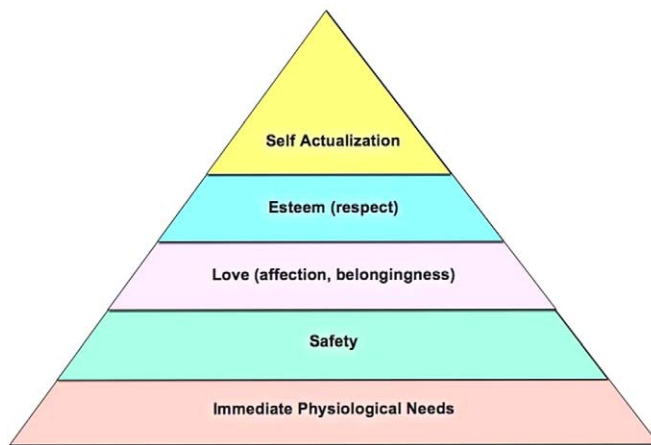


Fig. 1. Maslow's classic hierarchy of needs.

in several important ways. Most important, we believe it useful to examine basic human motives at three different levels of analysis often conflated in Maslow's work: (a) their ultimate evolutionary function, (b) their developmental sequencing, and (c) their cognitive priority as triggered by proximate inputs.

The implications of this three-level analysis are significant. Among other things, considerations at the functional level of analysis suggest that, although self-actualization may be of considerable psychological importance, it is unlikely to be a functionally distinct human need. Consequently, we have removed self-actualization from its privileged place atop the pyramid and suggest that it is largely subsumed within status (esteem) and mating-related motives in the new framework. Consideration of the developmental level of analysis led us to draw on the biological framework of life-history theory. Following this perspective, the top of the pyramid includes three types of reproductive goals: mate acquisition, mate retention, and parenting. And consideration of a proximate level of analysis along with life-history theory led us to change the way in which the goals are depicted in the pyramid: Rather than depicting the goals as stacked on top of one another, we instead depict them as overlapping (see Fig. 2). This change explicitly reflects the assumption that early developing motives are unlikely to be fully replaced by later goals but instead continue to be important throughout life, depending on individual differences and proximate ecological cues.

We end by discussing some of the broader questions raised by these renovations and their implications for the humanistic elements underlying Maslow's approach to human motivation. Modern evolutionary theory and research provides a new perspective on two key features of the traditional humanistic approach. First, it is now clear that human beings indeed have an array of diverse motivational systems not well represented by invoking only a few general motives shared with laboratory rats. Second, evolutionary logic is perfectly compatible with a humanistic emphasis on positive psychology. Indeed, a fuller understanding of evolved motivational systems—and their dynamic connection to environmental opportunities—can be used to enhance human creativity, productivity, kindness, and happiness.

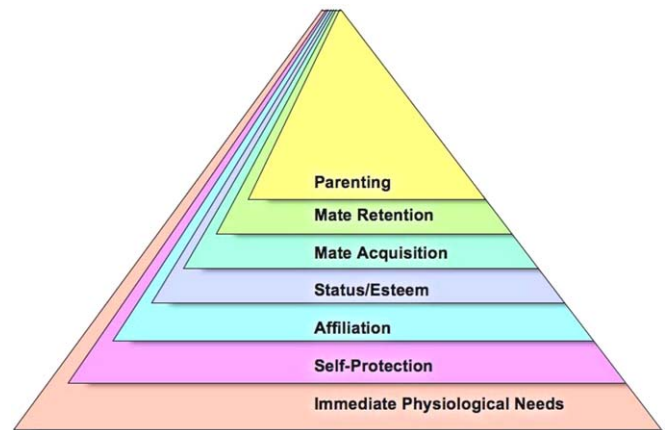


Fig. 2. An updated hierarchy of fundamental human motives. This figure integrates ideas from life-history development with Maslow's classic hierarchy. This scheme adds reproductive goals, in the order they are likely to first appear developmentally. The model also depicts the later developing goal systems as overlapping with, rather than completely replacing, earlier developing systems. Once a goal system has developed, its activation will be triggered whenever relevant environmental cues are salient.

Maslow's Motivational Pyramid

At the core of Maslow's theory of motivation are two important ideas: (a) there are multiple and independent fundamental motivational systems and (b) these motives form a hierarchy in which some motives have priority over others.

Multiple Fundamental Motivational Systems

Maslow's proposal of multiple and independent motivational systems was advanced partially as an alternative to the influential behaviorist view championed by Watson, Skinner, and Dollard and Miller. In the middle of the 20th century, the accepted view was that there were only a handful of "primary drives," such as hunger and thirst. These few primary drives were presumed to be present early in life and to provide the foundation for later "secondary drives" that are learned via simple conditioning principles. For example, a child's mother is always present during nursing, and she continues to provide intermittent food rewards even after weaning. Because of the repeated association between food and social contact, the child learns to desire contact with other people.

In contrast to the prevailing behaviorist view, Maslow (1943, 1970) proposed several independent sets of basic human needs. He presumed a universal set of distinct motives related to physiology, safety, affection, esteem, and self-actualization. Maslow's ideas about independent motives built upon the research of his graduate advisor, Harry Harlow, who found that rhesus monkeys raised in isolation came to prefer contact with a soft, cuddly surrogate mother, even when they were fed exclusively at a nearby wire surrogate (e.g., Harlow & Zimmerman, 1959). Harlow's work demonstrated that the motivation to obtain contact comfort was independent of conditioning experiences with hunger satisfaction. These findings undergirded

Maslow's conclusion that "... we could never understand fully the need for love no matter how much we might know about the hunger drive" (Maslow, 1970, p. 21). Research since that time has lent support to the notion of multiple motivational and learning systems, showing that systems controlling human food preferences, food aversions, fears, and other motivations operate using different rules and that they are sometimes controlled by architecturally distinct areas of the brain (e.g., Barrett & Kurzban, 2006; Cosmides & Tooby, 1992; Garcia & Koelling, 1966; Öhman & Mineka, 2001; Pinker, 1994; Sherry & Schacter, 1987; Wilcoxon, Dragoin, & Kral, 1971).

Hierarchical Organization of Motives

Probably the most enduring aspect of Maslow's theory is his idea of organizing fundamental motives into a hierarchy. The hierarchical arrangement suggested that some motives take precedence over others, which in turn take precedence over others. If a person is starving, for example, the desire to obtain food will trump all other goals and dominate the person's thought processes. This idea of *cognitive priority* is represented in the classic hierarchy shown in Figure 1.

In addition to suggesting that some motives take cognitive priority over others, Maslow's scheme also assumed that an individual's priorities shifted from lower to higher in the hierarchy as the person matured. That is, Maslow's hierarchy also reflected *developmental priority*. For example, infants are only concerned with physiological needs, such as hunger and thirst, and concerns about affection presumably emerge later in development. After a person accomplishes the goal of winning affection, he or she focuses increasingly on gaining esteem, and concerns about affection are presumed to fade into the background.

Maslow also proposed that the goal at the top of the hierarchy is self-actualization—fulfilling one's creative potential. Self-actualization might mean different things to different people (e.g., a musician would pursue music, an artist would pursue painting, a researcher would pursue knowledge in a specific area). According to Maslow's hierarchical approach, self-actualization only becomes a priority after all other needs are satisfied. Maslow's focus on self-actualization combines two recurring themes in his approach: the emphasis on positive aspects of human psychology over negative aspects and the belief that some human motivations are not directly linked to physiological needs of the homeostatic variety, implying that they are therefore not well understood by studying hungry rats.

Motivational Hierarchies at Multiple Levels of Analysis

In Maslow's theory, the ideas of cognitive priority and developmental priority were sometimes blurred together on the presumption that the two types of priorities move in synchrony with one another. But cognitive and developmental priorities may not, in fact, overlap perfectly. For example, physiological needs were placed at the bottom of the hierarchy and are

therefore presumed to arise early in development. This certainly is true of needs such as hunger and thirst, but other physiological needs, such as the hormonally driven desire for sexual satisfaction, do not become active developmentally until adolescence. At the same time, sexual desire, as well as other physiological needs such as hunger, can be suppressed by social concerns (e.g., esteem) even when those physiological needs are salient. Hence, the developmental hierarchy need not correspond precisely to the cognitive hierarchy. Moreover, the cognitive hierarchy might change dynamically with context at any point in an individual's life. For example, although a successful artist is normally motivationally focused on higher concerns and can ignore physiological needs that would monopolize an infant's attention, most artists focus on food if they are truly starving. Thus, the order of the development of fundamental motives, and a person's currently conscious priorities, are two separable issues.

Maslow acknowledged that there was an imperfect correspondence between the developmental order and the current prioritization of needs, though he frequently treated the discrepancies as noise in an otherwise orderly system. We will argue that it is worthwhile to explicitly separate these issues and to add at least one more level of analysis within which to consider motivational hierarchies. In what follows, we will consider motivational hierarchies at three levels of analysis: evolutionary function, developmental sequencing, and current cognitive priority (the proximate level).

In behavioral biology, historical controversies have been fueled by failures to distinguish between different levels of causation, with some theorists mistakenly suggesting developmental or immediate cognitive triggers as "alternatives" to functional accounts. As a consequence, there has been extensive discussion of the importance of distinguishing evolutionary function, ontogenetic development, and proximate determinants of any given behavior (e.g., Sherman, 1988; Simpson & Gangestad, 2001; Tinbergen, 1963). As an example, consider the question of why mammalian mothers nurse their offspring. This question can be answered correctly at three different levels of analysis. First, functional or evolutionary explanations are concerned with the ultimate adaptive purposes of behavior. An explanation in terms of evolved function might suggest that mothers nurse offspring because this behavior increases offspring survival rates.¹ Second, developmental explanations are concerned with life-span-specific inputs that sensitize the organism to particular cues. A developmental explanation might suggest that mothers nurse offspring because pregnancy and childbirth trigger puberty-dependent shifts in hormones and milk production in mammalian females. Finally, proximate explanations focus on the immediate triggers for a given behavior. A proximate explanation might suggest that nursing occurs because an infant has begun suckling on the female's nipple, which leads to immediate hormonal changes that stimulate milk release.

Sometimes there is an obvious connection between all three levels of analysis. In the case of nursing, for instance, the developmental changes in lactation capacity accompany the

other changes during pregnancy, and the infant, who receives obvious functional benefits from the nursing, triggers the immediate proximate release of milk. But connections between the three levels of analysis are not always clear. Consider the question of why birds migrate each year. A proximate explanation is that birds migrate because days are getting shorter—the immediate cue that triggers migration. The ultimate reason for such migration, however, is survival and reproduction; the distribution of desirable food and mating sites varies seasonally. Yet birds do not likely have any awareness of the indirect connections between day length and survival. There are two key implications here: (a) animals, including humans, need not be consciously aware of the ultimate function of their behavior, and (b) the connection between long-term goals and immediate goals is often indirect.

In what follows, we consider the notion of motivational hierarchies at each of these three levels of analysis. Considered at the level of evolutionary function, there is a natural hierarchical relationship between survival and reproductive goals, with survival goals undergirding reproductive goals. There is also evidence suggesting independent motivational systems designed to deal with different functional threats and opportunities, thus supporting Maslow's distinctions between central motives, albeit in a slightly reframed and expanded fashion. At the developmental level of analysis, Maslow's distinctions can be integrated with those offered by biological life-history models, which focus on how organisms confront different goals at different phases of the life span. This integration can expand both approaches in theoretically productive ways. At the proximate level of analysis, this integrative approach emphasizes that there is a continual dynamic interplay between motivational systems, cognitive appraisals, and environmental threats and opportunities.

Functional Level of Analysis

At the broadest level, an evolutionary approach implies that all behavior is goal-oriented, resulting from psychological adaptations that were designed by natural selection to deal with recurrent threats and opportunities. A considerable body of comparative and neuropsychological evidence now supports the assumption of multiple motivational and cognitive systems. There is also reason to presume some degree of hierarchical relationship between functional motivational systems. We elaborate on these points of agreement with Maslow's general approach below, and we also propose a reframing of Maslow's ideas in light of subsequent theory and evidence. Such a reframing suggests some important additions to and expansions of Maslow's model of fundamental human motivational systems.

At the simplest level, modern evolutionary theorists presume that if one observes a recurrent pattern of behavior in an animal species, it is likely to reflect the operation of mechanisms that were selected because they increased our ancestors' reproductive success. In more technical terms,

evolutionary biologists presume that all living organisms have been selected to promote their *inclusive fitness*, which means their relative success at passing genes into future generations via either direct reproduction or helping kin reproduce. Inclusive fitness is presumed to underlie all evolved mechanisms, including any innate systems that contribute to an animal's survival and ultimate reproductive success. Evolutionary analyses of behavior sometimes directly consider the influence of inclusive fitness on behavior, as in studies of selective investment of resources in grandchildren (Laham, Gonsalkorale, & von Hippel, 2005). Other analyses focus on reproductive behavior, as in studies of criteria for mating partners (e.g., Durante, Li, & Haselton, 2008; Garver-Apgar, Gangestad, & Thornhill, 2008; Li & Kenrick, 2006; Schmitt, 2003). However, promoting the ultimate goal of inclusive fitness also requires the pursuit of many other goals that contribute indirectly to survival and reproductive success.

Domain-Specificity of Motivational Mechanisms

Successful reproduction involves a great deal more than accomplishing a goal of sexual satisfaction. In the service of reproduction, an animal must accomplish many subsidiary goals. Any social animal—such as a prairie chicken, a chimpanzee, or a human being—must negotiate a set of complex interactions with other members of its species, establish and maintain a network of alliances, and attract a mate, which may require first gaining status or acquiring territory. Evolutionary analyses of behavior tend to consider behavioral mechanisms in terms of the specific problems they are designed to solve. Such analyses focus on the domain-specific mechanisms that solve specific adaptive problems. Different problems often require different, and often incompatible, solutions, which can often be better solved by independent motivational and cognitive systems.

Following Harlow's early work, later research has revealed the presence of distinct learning systems tuned to specific adaptive pressures faced by particular animal species. For example, Wilcoxon et al. (1971) found that both rats and quail condition aversions to foods that are followed by nausea. Whereas rats condition aversion to gustatory rather than visual cues associated with the novel foods, quail do the reverse, conditioning aversion more readily to visual cues rather than gustatory cues. These learning biases make adaptive sense because rats search for food in the dark using smell and taste as cues, whereas quail use vision to search for food during the day and eat many foods that do not contain strong scent cues, such as seeds. Many other findings support the notion that different kinds of information are acquired and stored very differently, albeit in ways that make adaptive sense (Rozin & Kalat, 1971; Sherry & Schacter, 1987). For example, birds use very different and often incompatible rules, sometimes controlled by different brain areas, to store information about food location, species song, and foods that made them sick (Sherry & Schacter, 1987). Findings from

human cognitive neuroscience have converged with findings from comparative biology to suggest that human beings, like other animals, have distinct neurological and motivational systems for dealing with different problems, such as learning about physical safety threats, detecting cheaters, and finding mates (e.g., Barrett & Kurzban, 2006; Cosmides & Tooby, 1992; Kurzban & Aktipis, 2007; Öhman & Mineka, 2001; Sherry & Schacter, 1987).

Fundamental Needs in Functional Perspective

Maslow believed that the motives in his hierarchy were probably universal features of human nature. In Maslow's time, however, psychologists interested in human nature did not tend to think in terms of functional adaptations. Modern evolutionary analyses begin by considering how a particular motivation might be linked to a recurrent adaptive problem, the solution of which would tend to serve survival or reproductive goals. Maslow's taxonomy of important human motivations is consistent with later functional analyses (e.g., Bugental, 2000; Kenrick et al., 2003). These analyses are consistent with his suggestion that there are different domain-specific motivational systems for physiological needs, safety (self-protection) needs, esteem (status) needs, and belongingness (affiliation) needs. As we discuss below, however, a functional analysis suggests that Maslow sometimes lumped together functionally (and psychologically) distinct needs into single, overly broad categories. Furthermore, a functional analysis suggests that self-actualization is not a functionally distinct need at all.

Physiological motives The adaptive function of what Maslow called physiological needs is fairly straightforward; he included here homeostatic needs such as hunger and thirst, which are obviously essential for survival. Logically, the satisfaction of such physiological needs is foundational to other motives. Maslow also considered sexual desire in the same category, although he acknowledged that the satisfaction of sexual desire was likely linked to other social motives as well. In what follows, we suggest that sexual motivation should be treated distinctly from basic survival needs such as hunger and moved to a different position in the hierarchy. Maslow also noted emerging research on "specific hungers," which indicated that even a motive as apparently simple as hunger might be more complex than it appeared. That research suggested that people and other animals might come to crave foods rich in particular nutrients that had been lacking in their diets (e.g., Hughes & Dewar, 1971; Hughes & Wood-Grush, 1971; Rozin & Kalat, 1971). Conversely, pregnancy sickness seems to involve the avoidance of foods that could damage the developing fetus, occurring most frequently during the period of fetal organ development and most likely to be elicited by vegetables containing toxins and meats that carry bacterial infections (Fessler, Eng, & Navarrete, 2005; Profet, 1992). The bottom line of these findings is that physiological cravings are designed to be adaptive and involve specific environmental tuning, but they are unlikely to have been learned according

to simple processes such as classical conditioning or to be the product of conscious computation.

Self-protection and safety motives Once people meet their basic physiological needs, Maslow reasoned that safety needs become the next priority. Later research supports the suggestion that human beings have unique motivational systems for dealing with threats. These systems include rapid learning of associations for stimuli that would likely have threatened our ancestors, as well as attentional systems attuned to angry expressions, particularly on the faces of unfamiliar males, who would have posed an especially great threat (Ackerman et al., 2006; Becker, Kenrick, Neuberg, Blackwell, & Smith, 2007; Öhman & Mineka, 2001).

A key feature of modern evolutionary analyses is the consideration of trade-offs (e.g., Gangestad & Simpson, 2000; Kaplan & Gangestad, 2005; Stearns, Allal, & Mace, 2008). No behavioral inclination is likely to operate without costs, and fear reactions are a good example. On the one hand, fearful avoidance is necessary when confronted with predatory or poisonous animals or when outnumbered by hostile strangers. On the other hand, fear can lead to the avoidance of risky situations that, if confronted, could yield payoffs (e.g., public speaking anxiety or other forms of social anxiety). Hence, a central part of a functional analysis of any behavioral proclivity is an assessment of the perils and prospects associated with performing different behaviors within any particular ecological context. When the risk of physical damage is highly costly, threat-avoidance systems are likely to be set like smoke alarms, favoring false positive alarms rather than false negative complacency (Haselton & Nettle, 2006; Nesse, 2005; Rozin & Royzman, 2001); it is better to unnecessarily flee a misperceived potential threat than to mistakenly remain in a dangerous situation.

Affiliation and belongingness motives Maslow treated the needs for love, affection, and belongingness as a single category. These social motivations differ from physiological and safety needs in that they are not absolutely necessary for personal survival. Indeed, many other animals live more or less solitary lives outside the mating season. However, human beings are exquisitely sensitive to cues of social rejection, and they respond to such cues using some of the same neural circuits used to register physical pain (Eisenberger, Lieberman, & Williams, 2003; MacDonald & Leary, 2005). The adaptive functions of social affiliation have been extensively reviewed (Baumeister & Leary, 1995; Boyd & Richerson, 1985; Sedikides & Skowronski, 1997; Stevens & Fiske, 1995; Wisman & Koole, 2003), and there appear to be some general oxytocin-based neurophysiological systems associated with social attachment (Brown & Brown, 2006; Carter, 1992; Hazan & Zeifman, 1999; Taylor et al., 2000).

Modern humans' hunter-gatherer ancestors lived in groups, as did most of the primates from which they evolved (Lancaster, 1976). In terms of trade-offs, a solitary life avoids costs such as competition over local resources, socially transmitted diseases, and exploitation by fellow group members. However, there are also great benefits to social life, and human

groups involve extensive sharing of resources, knowledge, and parenting chores with other group members (e.g., Henrich & Boyd, 1998). Anthropological analyses of hunter-gatherer societies indicate that food sharing within such groups provides an essential insurance policy for survival through spotty times (K. Hill & Hurtado, 1989).

Although social affiliation appears to be a fundamental motive, as Maslow proposed, it is worth considering some important differences among the various forms of affiliation. There are functional and neurological differences between systems involved in romantic love, affiliation with family members, and affiliation with other group members—all of which Maslow lumped into one motivational category. For instance, relationships between romantic partners, friends, and family members tend to be governed by distinct affective states and cognitive decision biases (e.g., Ackerman, Kenrick, & Schaller, 2007; Diamond, 2004; Fiske, 1992; Kenrick, 2006). Sexual arousal and sexual jealousy are distinctly designed to deal with opportunities and threats arising in romantic relationships, but not in family relationships. Grossly uneven distributions of benefits and costs, taken for granted between parents and children, can trigger emotional reactions associated with injustice if occurring between friends and could be grounds for terminating the friendship. Because romantic love, friendship, and familial bonds are also likely to be associated with different developmental periods, we argue that it is worth clearly distinguishing them in a hierarchy of motives.

Status and esteem motives Maslow classified esteem needs into two related sets—one consisting of desires for strength, achievement, and mastery (which contributed to one's self-esteem) and the other consisting of desires for reputation, status, dominance, and glory (or the esteem of others).

Henrich and Gil-White (2001) note that status in humans can arise from physical dominance and threat in the same way that it typically does in other animals. They distinguish this from prestige, which is freely conferred deference toward individuals who possess special skills and information. Even among hunter-gatherers, many human activities depend on highly technical information (e.g., fishing, hunting, food preparation, building canoes or huts, and so on). It is much more efficient to learn by modeling the behaviors of successful others than by using trial and error (Boyd & Richerson, 1985; Henrich & Boyd, 1998), so people are willing to defer to, and perform favors for, others who have acquired skills. Unlike physical dominance, which leads subordinate individuals to avoid those with the potential to harm them, prestige leads subordinates to actively try to get close to higher status individuals.

As in other animals, higher status results in benefits for both men and women because it often translates into others performing favors for them. Status also has an additional benefit for human males in increasing their access to mates (Betzig, 1992; J. Hill, 1984; Li & Kenrick, 2006; Sadalla, Kenrick, & Vershure, 1987; Turke & Betzig, 1985). This helps explain why males are often more willing to take social and physical risks to attain status, a proclivity that is enhanced when mating motives are salient (Griskevicius, Goldstein, Mortensen,

Cialdini, & Kenrick, 2006; Griskevicius, Tybur, et al., 2009; Wilson & Daly, 1985). A functional analysis also addresses why people are motivated not only to attain status, but also to defer to others who are high in status. If those others are physically dominant, deference reduces the odds of physical conflict; if they have information-based prestige, deference increases the odds of learning from them (Henrich & Gil-White, 2001).

Related to the goal of status is the notion of mastery, which Maslow viewed as contributing to self-esteem and which also contributes to self-confidence and to prestige-generating skills. A motive to solve or master novel problems is likely to facilitate the attainment of status and others' esteem, with consequent implications for reproductive fitness. It is possible that mastery may have additional adaptive consequences that are not specific to status or esteem. Deci and Ryan (2000) posited a domain-general need to "to engage optimal challenges and experience mastery or effectance in the physical and social worlds" (p. 252). These authors link this need to curiosity and play, which they suggest can generate various adaptive consequences. They suggest that a general inclination to seek novel information and explore alternative solutions would be useful for solving problems across domains, including the satisfaction of physiological needs such as hunger and thirst, as well as problems involving safety and affiliation. To the extent that this is true, a general inclination to master problems would likely arise very early in development and should be clearly distinguished from status motivation, as well as from each of the other problem focused motives. Considerations of domain specificity and of the costs involved in acquiring skills caution that such a motivation will not be completely general, but will be directed to solving particular problems, and the problems deemed most worthy of mastery should vary depending on one's current opportunities and threats in interaction with current developmental phase.

Self-actualization In defining self-actualization, Maslow most commonly offered examples involving creative displays: "A musician must make music, an artist must paint, a poet must write, if he is to be ultimately at peace with himself" (Maslow, 1943, p. 382). Maslow believed that the desire to fulfill one's own unique potential was disconnected from biological needs. Although such higher needs may be separated from simple physiological imbalances, no human need can be meaningfully separated from biology. A modern functional analysis demands that one ask what adaptive (i.e., fitness-relevant) payoffs might be associated with a motive for self-actualization or, alternatively, whether the capacity to strive for self-actualization might be a nonadaptive consequence of other adaptive mechanisms.

That possibility that self-actualization is a by-product of other mechanisms is worth considering first. Many higher order human phenomena exist not because they serve specific fitness-relevant functions, but because they emerged as by-products or nonadaptive effects of psychological mechanisms that evolved for somewhat different reasons altogether (Park, 2007). Researchers have applied this perspective to understand

the origins of complex psychological phenomena such as religion and morality (e.g., Atran & Norenzayan, 2004; Boyer, 2003; Krebs, 2008). For example, the belief in supernatural beings may confer no functional benefits whatsoever. Instead, these beliefs emerge naturally as nonadaptive consequences of specific kinds of cognitive abilities (e.g., abilities to detect agency in other beings, to ascribe intentions to those beings, and to construct cognitive representations of things that aren't immediately perceptible). Those cognitive abilities might have evolved in response to fitness pressures that have nothing whatsoever to do with supernatural beliefs. It is possible that, just as transcendent religious beliefs serve no adaptive function, the transcendent strivings associated with self-actualization may also be essentially functionless—natural consequences, perhaps, of a basic capacity for goal construction coupled with the uniquely human capacities for self-reflection and the imagination of possible selves.

On the other hand, there may be specific fitness-relevant consequences associated with the striving for self-actualization. But these consequences may not be specific to self-actualization. The functional benefits associated with self-actualization may be no different from those associated with esteem/status or mating-related needs.

Although creative expression may often seem like mere self-entertainment, human displays of creative and intellectual capacities are directly linked to reproductive success. Talented artists, musicians, or writers frequently show off their creative outputs to others and may receive very high levels of fame, resources, and romantic interest as a result. Pablo Picasso, Diego Rivera, Duke Ellington, John Lennon, and Pablo Neruda all converted their considerably actualized talents with paintbrushes, musical notes, and words into fame, fortune, and reproductive opportunities. Miller (2000) reviews an extensive body of literature to make a case that creative displays in humans follow many of the same rules of sexually selected displays in other animals, such as peacocks' tails. For example, males are more likely to publicly draw attention to their creativity than are females, and females are likely to choose creative men as mates. As in competitions for status, males are more likely to display their creative talents when mating motives are activated (Griskevicius, Cialdini, & Kenrick, 2006).

From a modern perspective on functional adaptations, an explanation is not complete until a goal is connected to an external outcome. For instance, although feeling a sense of accomplishment, self-satisfaction, or philosophical insight is often a sign that progress has been made toward an adaptive goal, the good feeling is not a sufficient explanation in itself. One must ask what adaptive outcomes would have tended to follow from feeling good in one way as compared with another. For example, Maslow viewed esteem mostly in terms of self-evaluation, putting "opinions of others" at the end of a list of terms like self-esteem. This contrasts with the emphasis of more recent functional views—informed by evolutionary theorizing and supported by empirical research—that explicitly contemplate the relationship between self-esteem and external outcomes, such as one's standing in a social group (e.g.,

Kirkpatrick, Waugh, Valencia, & Webster, 2002; Leary, Tambor, Terdal, & Downs, 1995). This distinction is important from a functional perspective because any self-inflating tendencies that were not calibrated to others' respect could have maladaptive consequences for success in social groups (Kurzban & Aktipis, 2007). In a related vein, Maslow viewed self-actualization in very individualist terms, presuming that once one has attained the respect of others, one could move to a "higher" level by pursuing one's idiosyncratic goals. We suggest that, although the pursuit of one's unique talents may be experienced as distinct from the pursuit of esteem, these phenomenologically distinct pursuits are rooted in a common motivational system and produce functionally identical outcomes. Self-actualization, in this light, can provide an alternative pathway to esteem and to social status and, consequently, has indirect implications for successful mating and reproductive fitness.

This does not, of course, imply that whenever an individual strives to master a musical instrument or a mathematical proof, that individual does so with some conscious desire for status or mates. Nor does it imply that striving for a transcendent state of self-actualization involves any conscious desire to transform transcendence into tangible resources. The motives that govern behavioral strivings often lie outside of conscious awareness, as do the functional implications of those strivings. By removing self-actualization from our renovated pyramid of needs (Fig. 2), we in no way diminish the phenomenological or psychological importance of self-actualization itself. But neither phenomenological nor psychological importance is sufficient argument to accord self-actualization the status of a functionally distinct motive or need. By removing self-actualization from the pyramid, we simply recognize that its privileged position cannot be compelled nor justified by the functional logic of human evolutionary biology.

Summary of Functional Level of Analysis

A functional analysis of fundamental human motives suggests good support for many of Maslow's ideas, including the idea that humans have different motivation systems for physiological needs, safety (self-protection) needs, belongingness (affiliation) needs, and esteem (status) needs. However, a functional analysis also suggests several revisions to Maslow's model. First, whereas Maslow paid little attention to mating and included sexual motivation as a subset of physiological needs, mating needs are more sensibly identified as a separate category (as we discuss more fully in the next section). Second, what Maslow called belongingness is comprised of the different needs of romantic love, affiliation, and familial care, which ought to be considered separately. As we discuss below, a consideration of biological theories of life-history development suggests the addition of differentiated goal systems linked to mating, parenting, and kin care. Third, a functional analysis suggests that self-actualization cannot be considered a unique human need itself, but that it instead might sensibly be

subsumed within the broader sets of needs pertaining to status and mating.

Developmental Level of Analysis

Maslow's hierarchical theory of needs assumed that an individual's priorities shifted from lower to higher in the hierarchy as a person matured. In this section, we examine the notion of developmental priority in light of life-history theory. Several important points arise from this consideration: (a) there is broad biological support for the idea that motivational priorities change with development; (b) in species like humans, early developing life-history goals continue to operate alongside those that develop later in life; (c) life-history priorities involve necessary trade-offs in the allocation of effort to survival, growth, and reproduction; and (d) reproduction is the ultimate goal of such trade-offs, but successful reproduction involves multiple goals. These considerations suggest the addition of three sets of later-developing goals to the traditional hierarchy: mate acquisition, mate retention, and parental care. Life-history theory also suggests that there are likely to be important individual differences in motivational priorities—some linked to gender and others linked to within-sex variations in strategies emerging from interactions with the developmental environment.

Life-History Theory

Biological theorists have developed a powerful set of ideas called *life-history theory* that have profound implications for the developmental sequencing of human motivation (e.g., Kaplan & Gangestad, 2005; Kenrick & Keefe, 1992; Kenrick & Luce, 2000; Stearns et al., 2008). The field of life-history evolution explores how each animal's life cycle—from conception to death—is shaped by natural selection to facilitate reproductive success (Stearns et al., 2008). A life history is a genetically organized developmental plan—a set of general strategies and specific tactics by which an organism allocates energy to survival, growth, and reproduction (Crawford & Anderson, 1989; Partridge & Harvey, 1988; Stearns, 1976).

Life-history researchers ask questions such as “Why do some organisms have longer or shorter periods of bodily development preceding reproduction?”, “Once mature, does an organism devote all its resources to one short reproductive burst, or does it spread its reproductive efforts over several episodes spanning months or years?”, and “Does the organism allocate resources to caring for its offspring after they are born, and if so, how much care should be invested before leaving the offspring to fend for themselves?” Life-history models assume that resources are always limited and that development involves trade-offs in when and how to allocate those scarce resources. What constitutes a favorable or unfavorable trade-off depends on a dynamic interaction of environmental pressures (current threats and opportunities), inherited predispositions (useful traits and constraining traits the animal inherited), and the animal's current stage of development.

Life histories are commonly divided into two broad categories: *somatic effort* and *reproductive effort* (Alexander, 1987). Somatic effort is the energy expended to build the body. It is analogous to making investments to build a larger bank account. Reproductive effort is analogous to spending that bank account in ways that will replicate the individual's genes. Reproductive effort can be further divided into mating, parental care, and investment in other relatives (Alexander, 1987). Investment in other relatives is considered reproductive effort because grandchildren, siblings, nieces, nephews, or cousins share common genes.

The Life-History Developmental Hierarchy

The key life-history tasks can be arranged into a simple developmental hierarchy. Somatic efforts form the necessary developmental base required before mating efforts can unfold, and parenting efforts build on the base of earlier somatic and mating efforts. In any species reproducing more than once, these goal systems do not replace one another. For example, adult mammals divide current resources between somatic effort (eating, drinking, and protecting themselves), attracting and keeping mates, and caring for offspring. Given that resources are inherently finite, time and energy invested in one activity must be taken from others. For example, more mating effort means fewer resources available for parenting.

Animals show an amazing array of life-history patterns. One species of tenrec (a small mammal found in Madagascar) reaches sexual maturity 40 days after birth. Elephants, on the other hand, take 100 times that long to reach sexual maturity. Why don't all animals start reproducing as soon as possible and have as many offspring as possible? The answer is that the goal is the successful production of viable offspring, which may not follow from the production of as many offspring as possible as quickly as possible. The optimal investment of reproductive effort depends on the features of a particular species and the particular ecological constraints faced by that species. For large mammals like elephants, females are not physically able to produce and nurture offspring until they are several years old. And for elephants, as for any species providing parental care, having too many offspring too soon decreases the chances that any will survive (Lack, Gibb, & Owen, 1957).

Humans are closer to elephants than to tenrecs in our developmental life histories. Humans do not sexually mature for over a decade, during which individuals not only develop physically but also learn social skills that enable them to form networks of friends and establish social positions within those networks. After a variable period of mating effort, humans typically dedicate a great deal of energy to parenting, caring for slow-maturing large-brained offspring that in ancestral times did not thrive well without resources from both mothers and fathers (Geary, 1998). While human offspring mature, they, like elephants, often continue to receive care and resources from grandparents and other relatives (Laham et al., 2005; Sear, Steele, McGregor, & Mace, 2002). These life-history considerations are depicted by the addition of three separate

motivational systems to Maslow's hierarchy: mate acquisition, mate retention, and parenting (Fig. 2). Survival and social goals, on this view, provide the foundation for acquiring mates. Acquiring mates provides a foundation for forming a long-term bond, which in turn undergirds the goal of producing and successfully raising offspring.

Life History and Individual Differences

Biologists have noted three key sources of motivationally relevant individual differences across a wide range of animal species. First, across many species, it is common for males and females to differ in how they allocate resources to somatic development and reproductive effort. Second, not all members of one sex adopt the same strategy; there are often systematic individual differences within a sex linked to different mating strategies. Third, those differences in mating strategies are often systematically linked to ecological factors, and many of the same ecological factors (e.g., sex ratio, mortality levels, distribution of resources) are important across species.

Between-sex variations Many sex differences are linked to the general biological principle of *differential parental investment*. Both within and between species, animals that invest more in their offspring tend to be more selective about choosing mates. Within mammals, there is a natural division in parental investment because females gestate the young within their bodies (for almost 2 years in the case of elephants, for the better part of a year in the case of humans), and then nurse them afterwards (often for several years). Thus, females have a higher minimal obligatory parental investment than do males. Males could, in theory, contribute little more than sperm to the offspring, which is the typical pattern for more than 90% of mammalian species. This difference in parental investment is linked in turn to differences in sexual selection, with female mammals tending to be more selective in choosing mates, generally picking males who have established their superiority by dominating other males or who exhibit traits suggesting relatively greater health and development.

Male investment varies across species. To the extent that male investment in offspring increases, the degree of sexual dimorphism is reduced (as in many bird species, in which both parents devote effort to nest-building and offspring care). In rare cases, a male actually invests more resources in the offspring than does the female, as in the case of bird species such as phalaropes—a type of sandpiper in which the female leaves the male to tend the eggs while she searches for another mating opportunity. Sex differences in morphology and behavior tend to reverse for such species, as would be expected, given the tenets of parental investment theory.

Because all the usual mammalian constraints on gestation and nursing apply to humans, several broad sex differences—regarding greater female mating selectivity and greater male intrasexual competition—apply to humans as to other mammals (e.g., Clark & Hatfield, 1989; Kenrick, Groth, Trost, & Sadalla, 1993; Wilson & Daly, 1985, 2004). One indirect

consequence of greater female selectivity is slower maturity for males (Geary, 1998). The reason for the maturational delay among males in dimorphic species is that it takes longer for males to reach a size when they are likely to successfully compete for females. In line with this general rule, human males typically reach sexual maturity much later than females and attain a somewhat larger size.

Similar differences in size and maturity rates are found in other species in which females exercise selection pressure by choosing more dominant males (Geary, 1998). Human males across societies are also more likely to engage in intrasexual competition in the form of male-to-male assaults and homicides as well as other risky behaviors (Daly & Wilson, 1988; Griskevicius, Tybur, et al., 2009; Wilson & Daly, 1985). The general mammalian pattern is somewhat (but not completely) qualified because human males frequently do contribute resources directly to the offspring (Geary, 1998; Kenrick et al., 1993; Kenrick, Sadalla, Groth, & Trust, 1990).

Within-sex variations Not all members of one sex within a species adopt the same mating strategy. Among several fish species, for example, there are different male mating strategies with different developmental trajectories. One common type of male grows very large and colorful and defends a territory to which he attracts females. Another type looks and acts more like a female but actually sneaks in to release sperm when a true female releases her eggs in response to the large male's courtship efforts (Gross, 1984; Warner, 1984). There are also within-sex variations in human mating strategies, with both men and women varying in their courtship strategies and degree of parental effort in ways that are linked to different developmental trajectories (Belsky, Steinberg, & Draper, 1991; Gangestad & Simpson, 2000). Men who adopt an unrestricted (nonmonogamous) mating strategy, for example, are larger, more physically attractive, and more competitive than those who adopt a restricted strategy characterized by high investment and greater monogamy.

Mating strategies are linked to attachment styles, suggesting that attachment takes different forms for males and females. Beginning at about 8 years old, females with insecure attachment styles move to an anxious/ambivalent style, whereas insecure males become avoidant. Del Giudice (2009) connects this developmental divergence to different life-history trade-offs between mating and parental effort for men and women (see also Kirkpatrick, 1998). Ecological and cultural factors also influence tendencies toward restricted or unrestricted mating, but men are universally more inclined toward unrestrictedness (Schmitt, 2006). This has implications for motivation and social cognition. For instance, an unrestricted mating orientation is associated with greater attention to attractive opposite-sex faces but, predictably, this effect is specific to male perceivers (e.g., Duncan et al., 2007).

As indicated by these findings on attentional differences, variations within and between sexes have implications for motivational priorities in responding to proximate environmental cues, an issue to which we will return.

Implications of Life-History Theory for a Revised Motivational Hierarchy

Life-history models have generally been developed from work with nonhuman animal species, but they have clear applicability to human beings (Del Giudice, 2009; Geary, 1998; Kaplan & Gangestad, 2005; Kenrick & Keefe, 1992; Kenrick & Luce, 2000). Many of these implications remain unexplored. As noted above, life-history theory includes an implicit assumption of a hierarchy of goals that can be broadly applied across the animal kingdom, with somatic effort at the base, reproductive effort in the middle, and parenting effort at the top. That simple hierarchy does capture some of human development, but it falls short in at least two important ways. First, although it encompasses broad goals that all animals must accomplish, the simple hierarchy is insufficiently specific to capture the separate problems involved in human survival and reproduction. Second, that simple hierarchy does not develop connections with the phenomenology of human goal-seeking, which is often concerned with more specific intermediate goals that contribute to reproductive success in important, but often indirect, ways. An integration of Maslow's approach to development with the biological life-history approach could provide a fuller understanding of the developmental psychology of human motives.

Do later developmental goals replace earlier ones? Do later developmental goals replace earlier ones, or do they simply add to one another? Maslow hedged a bit on this issue. On the one hand, he observed that starvation or social rejection later in life could certainly redirect attention from the so-called higher goals. On the other hand, he also argued that the relative emphasis shifted from the lower to the higher goals. If all was going very well, he presumed further that most of a person's effort could be directed toward higher goals, to the point that a person could ignore hunger and even the need for social contact (as in the case of Isaac Newton, who spent long periods in isolation and ate very little when he was working on scientific problems).

Some amount of developmental sequencing in human goals makes logical sense. Infants are concerned with getting food and liquids and unconcerned with making friends until they are beyond the toddler stage. Similarly, concerns about one's esteem in the eyes of others only make sense after there is a network of associates to impress. A life-history perspective on development certainly supports the basic idea that organisms must change the order of goal priorities as they develop: Some amount of somatic effort necessarily precedes mating effort, which necessarily precedes parenting effort. Our revised hierarchy adds the three reproductive goals following this developmental line of reasoning: Young children do not seek mates at all and, after puberty, maintaining a mating relationship or caring for offspring do not become issues until one has first attracted a mate.

A comparative life-history perspective adds another dimension to this issue, because animals vary in the extent to which mating effort replaces somatic effort. Biologists who have

studied the diverse life-history strategies in other living organisms sometimes make a distinction between two major patterns: *semelparity* and *iteroparity*. Semelparous animals mate only once, expending all their somatic energy in one burst, and then typically die (as in the case of salmon). For these single-burst reproducers, reproductive effort completely replaces somatic effort. Iteroparous animals, however, mate repeatedly over the life span. Those animals do not spend their whole bank account of resources in one effort, but conserve some for later mating efforts. Humans are clearly an iteroparous species, producing offspring over a period of up to three decades for females and potentially longer for males. Furthermore, unlike salmon, all mammals, including humans, must maintain their own bodies in order to nurture and care for their offspring. Hence, humans need to continue contributing to their personal bank account of physical and social resources even after they have begun mating. For a species like ours, physiological needs never disappear. Adults continue to require food and water, to avoid freezing and overheating, and so on.

On the one hand, it seems reasonable to assume that needs such as hunger might recede into the background among people living in modern industrialized societies. Even if this were the case, however, it is likely that, rather than disappearing, the satisfaction of those needs goes the route of well-learned motor skills, which become increasingly automatic (therefore requiring less central cognitive processing; e.g., Schneider & Shiffrin, 1977). Even so, physiological drives may not ever become completely automatic. Consider hunger: Human beings the world over dedicate a great deal of attention, conscious thought, and conversation to the selection, preparation, and presentation of food, and there is a great deal of cultural elaboration of these processes (Rozin, 2007a, 2007b). Indeed, the description of a culinary experience as pleasant or unpleasant may not be totally arbitrary, but linked to human's ability to detect subtle nutritive properties of foods (Katz, Hediger, & Valleroy, 1974). Recent evidence suggests that even "cultural" variations in food preference, such as the relative preference for spicy food in Central America versus Scandinavia, is actually linked to differential value of foods to people living in places with varying numbers of food-borne parasites (Sherman & Hash, 2001). Furthermore, there are interesting coevolutionary processes involved in food preparation. For example, corn is deficient in several nutrients, but it can be made much more valuable if prepared with alkali. Native American tribes whose corn preparation involves alkali eat substantially more corn than the other groups, although they are unaware of the underlying biochemistry—they simply regard corn prepared with alkali as better tasting (Katz et al., 1974). Finally, the hunger drive can be interlinked with other physiological developments in later life, most notably pregnancy (Flaxman & Sherman, 2008). Pregnant women's particular food preferences and aversions occur during the period when the fetus is developing its major organ systems and is highly sensitive to the influence of extrinsic toxins and infection. Women during this period are most likely to avoid foods that contain high levels of toxins (e.g., bitter vegetables) or which are likely to carry dangerous

bacteria (e.g., fish and meats). Rather than being a pathology, pregnancy illness is associated with better fetal health and lower rates of spontaneous abortion (Fessler et al., 2005; Profet, 1992).

This reasoning applies not only to hunger, but also to other simple physiological needs, including the desire to remain dry and warm. Mark Twain famously wondered why people bother talking so much about the weather but nobody does anything about it. But Twain's quip, however clever, may have been only half right. If our neighbors express some consensus about the upcoming weather, often we can do something about it—carrying an umbrella if we are told it is going to rain, or a coat if we are told it's cold outside—so that communication with others is potentially quite useful rather than idle chit-chat. In short, basic physiological needs probably never disappear from the motivational landscape, whether consciously or unconsciously.

Similar reasoning applies to later developing needs. Adults, even attractive and well-connected college students, remain exquisitely sensitive to social acceptance and social rejection, and they experience the latter using some of the same physiological mechanisms used to register pain (MacDonald & Leary, 2005). Indeed, individuals who are inattentive to affiliative goals as adults may be manifesting more pathology than self-realization. It thus seems that research since Maslow's time better supports a view that later developed motivations build upon earlier motivations rather than replace them (see also Krebs & Van Hesteren, 1994). Although earlier developed needs must necessarily share time with those that come later, and although their satisfaction may occur more automatically, they do not disappear in healthy, well-functioning adults but instead remain available to respond as relevant threats and opportunities arise. Thus, the overlapping triangles in Figure 2 are meant to explicitly reflect the assertion that later developmental needs and goals add to, rather than replace, existing ones.²

Summary of Developmental Level of Analysis

A developmental level of analysis and consideration of life-history theory suggest several important revisions to Maslow's original hierarchy. First, the revised hierarchy contains three later-developing reproduction-focused goals of mate acquisition, mate retention, and parental care. Second, this analysis suggests that the different motives in the hierarchy continue to operate alongside those that develop later in life—a point reflected visually by the overlapping triangles in the hierarchy. Third, this analysis suggests important individual differences in motivational priorities that result from interactions between development and current environment, which we discuss further below.

The Proximate Level of Analysis

Our review thus far suggests that adult humans always have multiple motivational systems at the ready and that (depending

on life-history considerations) some of these motives may be more ready than others. But potential activation does not equate to actual activation. At a proximate level of analysis, the key question is this: What determines which of the many potential motivational systems is actually active at any specific moment in time?

This question is not likely to be effectively addressed by a hierarchy of needs that is rigid or inflexible. A particular individual may, in general, prioritize affiliation goals over mating goals, but that prioritization may temporarily reverse when presented with a particularly salient mating opportunity. Indeed, one of the most potent conclusions to emerge from the enormous psychological literature on goal activation is that goal activation is highly sensitive to immediate contextual cues (e.g., Aarts & Hassin, 2005; Bargh & Morsella, 2008). To be applicable to a proximate level of analysis, a renovated pyramid of needs must incorporate this insight.

Motivational Priorities Vary With Immediate Ecological Context

The functional perspective offered by evolutionary theorizing in general, and life-history theory in particular, suggests that the motivation system active at any given time is likely to depend on some implicit evaluation of the trade-offs inherent in the ecological context. If you are having lunch with your boss, and you discover a scorpion crawling up your leg, self-protection goals are likely to trump whatever food- or status-related goals were salient a moment earlier. But if it is merely an ant on your leg, and your boss has just asked you to consider a promotion, the self-protection goal is not likely to be foremost in mind. In general, cues in the current situation are expected to dynamically interact with a person's developmental phase and recent deprivation or satisfaction of different needs, as well as the individual's cognitive, affective, or morphological traits that might make any particular threat or opportunity more threatening or potentially beneficial (Neuberg, Kenrick, & Schaller, 2010).

Although Maslow noted the dynamic interaction between a person's motives and his current environment, his general aversion to "situationism" led him to give short shrift to the proximate level of analysis: "It remains to caution the theorizer against too great a preoccupation with the exterior, with the culture, the environment, or the situation. Our central object of study here is, after all, the organism or the character structure" (Maslow, 1970, p. 28). Maslow justified this deemphasis of the situation by suggesting that fundamental needs are "relatively constant and more independent of the particular situation in which the organism finds itself," in part because a psychological need "organizes and even creates the external reality" (Maslow, 1970, p. 29). In contrast, an evolutionary perspective on human psychology implies that internal needs—and the extent to which those needs precipitate actual affective, cognitive, and behavioral responses—must be calibrated to specific threats and opportunities in the immediate ecological context.

Just as an evolutionary approach to human development (i.e., life-history theory) requires an assessment of fitness-relevant trade-offs, an evolutionary approach to behavior at the proximate level of analysis also requires an assessment of trade-offs. The activation of a particular motivational system may produce specific kinds of benefits (e.g., activation of a self-protective goal is likely to precipitate the strategic avoidance of potentially dangerous people), but it also may entail specific potential fitness costs as well (e.g., halting consumption of caloric resources, temporary cessation of behavior promoting reproduction). Consequently, these motivational systems are likely to have evolved in such a way as to be responsive to perceptual cues that indicate—even if imperfectly—the extent to which fitness-relevant benefits outweigh costs. When contextual cues indicate an unfavorable cost–benefit ratio associated with a particular motivational system, that motivational system is unlikely to be activated. But when contextual cues indicate a relatively favorable cost–benefit ratio, then that motivational system will be temporarily prioritized and is likely to exert substantial consequences on cognition and behavior (cf., Ackerman & Kenrick, 2008).

The temporary prioritization of any motivational system can be inferred from the observation of specific behaviors that are functionally predicted by that system. For instance, the acoustic startle reflex—the tendency for sudden loud noises to elicit a surprise response—indicates the temporary activation of a self-protective goal. In the realm of social cognition, specific kinds of stereotypical inferences also indicate the activation of a self-protective goal (e.g., the perception of male ethnic outgroup members as angry or aggressive; Ackerman et al., 2006; Maner et al., 2005). If implicit cost–benefit analyses set the priorities for momentary changes in motivational systems, then responses such as these should occur under conditions in which contextual cues imply that the benefits of a fearful, self-protective response are especially likely to outweigh the costs of such a response. If these cues imply that perceivers are especially vulnerable to harm, for instance, then those perceivers may show especially strong startle responses and may be especially likely to ascribe stereotypically dangerous traits to ethnic outgroups. Consider the psychological effects of ambient darkness. Humans depend substantially on visual perception to maneuver safely through the environment. When temporarily deprived of visual cues—when in the dark—we feel especially vulnerable to harm. Consequently, self-protective motives are prioritized. When people are in the dark, their acoustic startle responses are exaggerated (Grillon, Pellowski, Merikangas, & Davis, 1997). Similarly, people in the dark are especially likely to perceive ethnic outgroups as stereotypically aggressive and untrustworthy (Schaller, Park, & Faulkner, 2003).

Temporary activation of a single specific motive may influence a wide variety of cognitions and behaviors that, although superficially different, are linked in functionally relevant ways. Self-protection is frequently served not simply by fight or flight, but also by affiliative behavior, given that humans experience safety in numbers (Geary & Flinn, 2002; Kenrick & Johnson, 1979; Taylor et al., 2000). Consistently,

activation of a self-protective goal enhances conformity behavior among both men and women (Griskevicius, Goldstein, et al., 2006; Griskevicius, Goldstein, et al., 2009). In contrast, activation of a mating goal enhances conformity among women but actually leads to a reduction in conformity among men, who seek to stand out under these conditions. Mating goals also increase behaviors linked to the attainment of status, but they do so for males more than for females (Griskevicius, Cialdini, & Kenrick, 2006; Griskevicius, Goldstein, et al., 2006; Griskevicius et al., 2007). The nature of these sex differences fits with considerations derived from life-history theory discussed earlier, involving differential parental investment and sexual selection.

These and other lines of research (e.g., Ackerman et al., 2009; Neuberg, Kenrick, Maner, & Schaller, 2004; Van Vugt, De Cremer, & Janssen, 2007; Van Vugt & Spisak, 2008) support the general assumption that there is a continual interplay between motivational systems and the perception of affordances (fitness-relevant threats and opportunities) in the immediate environment. One important implication is that motivational systems include not just feelings, but also functionally specific cognitive problem-solving tools designed to facilitate the ongoing analysis of trade-offs involved in pursuing one goal as opposed to another (Kenrick, Li, & Butner, 2003). Table 1 provides a rough outline of the kinds of triggers likely to be functionally connected to each motivational system (for additional elaboration, see Kenrick, Maner, & Li, 2005; Kenrick & Shiota, 2008; Neuberg et al., 2010; Schaller, Park, & Kenrick, 2007). Many specific questions regarding the particular links between motives, threats, and opportunities—and the particular ways they are prioritized—remain to be empirically investigated.

Individual Differences Linked to Processing of Motivation-Relevant Cues

Motivational priorities may be extraordinarily sensitive to immediate contextual cues. This does not obviate the fact that different people may vary in the extent to which different motives are chronically prioritized (Funder, 2006). Both genetic and epigenetic (i.e., developmental) factors influence the extent to which an individual is chronically anxious, for instance, and therefore places a chronically high priority on self-protective goals. Similarly, the chronic activation of mating motives also varies considerably, not just between sexes but between individuals of any particular sex.

Regardless of the exact origins of these individual differences, they have important implications for cue-based activation of motivational systems. Generally speaking, we would expect that individual differences are likely to interact with situational inputs in functionally adaptive ways. Contextual cues connoting vulnerability to danger are likely to trigger self-protective motives most strongly among individuals who chronically perceive themselves to be vulnerable, but they are less likely to do so among individuals who, for whatever reason, perceive themselves to be invulnerable to harm. Empirical

evidence suggests that this is the case (Park & Buunk, in press). The impact of ambient darkness on prejudicial perceptions of ethnic outgroups occurs primarily among individuals who are chronically worried about interpersonal threats, not among individuals who feel chronically safe and secure (Schaller, Park, & Mueller, 2003). In a similar manner, cues connoting potential social exclusion appear to activate belongingness goals (as indicated by attempts to establish new social connections) among individuals who generally perceive social interactions in a optimistic way; but among those who suffer from social anxiety, on the other hand, the threat of social exclusion seems to more strongly activate a self-protective motivational system instead (Maner, DeWall, Baumeister, & Schaller, 2007).

Sex differences (and sex similarities) also have implications for processing motivation-relevant cues. The sex difference in intrasexual competition suggests that developmental issues surrounding esteem motivation are likely to differ somewhat for males and females. Women are more likely than men to regard social status as a necessity in a mate (Li, Bailey, Kenrick, & Linsenmeier, 2002). Hence, men are expected to be motivated by esteem needs to a somewhat greater degree than women and to have their sense of self-esteem more strongly linked to intrasexual competitive success. Indeed, when mating motives are activated, males are especially likely to show off in various ways—to become more creative, to conspicuously consume expensive goods, to desire higher paying jobs, and to opt for money now rather than later (e.g., Griskevicius, Goldstein, et al., 2006; Griskevicius et al., 2007; Roney, 2003; Wilson & Daly, 2004). Activating either mating or status motives leads men to report more inclination toward direct aggression in response to an insult in ways that seem tailored to impress other men and maintain their position in the social dominance hierarchy (Griskevicius, Tybur, et al., 2009).

Men are also selective about the characteristics they desire in long-term mates (in whom they will make potentially high investments), but men don't tend to select mates based on their mate's relative competitive success. Instead, men prefer mates who show physical cues associated with youth and fertility and who demonstrate traits (such as kindness and warmth) indicative of successful parenting ability (e.g., Griskevicius et al., 2007; Li & Kenrick, 2006; Singh, 1993; Zaadstra et al., 1993). Consistently, female esteem is more likely to be linked to physical appearance and to cues suggesting that they are cooperative and likeable (Ben-Hamida, Mineka, & Bailey, 1998; Gutierrez, Kenrick, & Partch, 1999).

Consistent with the sex difference in offspring care across societies and with the relatively lower advantages that females gain from acquiring multiple mates, women are generally expected to devote less time and energy to mating effort and more time and energy to parenting effort. Women are generally less interested in casual mating opportunities, whereas men generally have a lower threshold for initiating sexual interest (e.g., Buss & Schmitt, 1993; Clark & Hatfield, 1989; Haselton & Buss, 2000; Kenrick et al., 1990, 1993; Schmitt, 2003, 2006). And, as noted earlier, an enhanced mating motive leads men to

mistakenly perceive sexual arousal in the faces of attractive women, but no such reciprocal effect emerges among women (Maner et al., 2005).

The links between individual differences and proximate motivational cues is an area ripe for additional empirical exploration. Existing findings suggest the potential utility of thinking about goal-linked individual differences in a functional light (e.g., Tybur, Lieberman, & Griskevicius, 2009). However, much additional research is required to determine the specific ways in which individual differences link up with differential sensitivities to functionally relevant goal systems.

Different Motivational Priorities Depend on Developmental Sensitization to Ecological Features

Many motivational systems require developmental inputs to be fully activated (Lieberman, Tooby, & Cosmides, 2003). Mating motivation is unlikely to be triggered in a prepubescent child, for example. Sexual jealousy mechanisms are less strongly activated in young people who have not yet had a serious romantic relationship (Buss, Larsen, Westen, & Semmelroth, 1992). The motive to protect children is more strongly activated once a person becomes a parent, and women with children are acutely sensitive to the specific cries of their own children (Soltis, 2005). Parenting behavior itself seems to result from a cascade of hormonal and neurobiological responses to early experience with offspring, in interaction with the parents' own earlier experiences (Mayes, Swain, & Leckman, 2005).

This is another area where life-history theory can help put human motivational systems in broader comparative perspective. For instance, research with other animal species has indicated that mating strategies and correlated developmental changes are keyed to ecological inputs. In some species, the presence of local dominant males can suppress sexual maturation in nearby younger males (signaling that the metabolic costs of mating effort would not be worthwhile; e.g., Davis & Fernald, 1990; Sapolsky, 2005). As another example, in normally monogamous species, the availability of resource-rich territories may precipitate more polygynous arrangements (as females become more predisposed to share a single male mate who defends an especially rich territory; Orians, 1969).

These issues of developmental sensitization may also have implications for regional or cultural differences in motivational priorities. Some cultural variations seem to represent an interaction between a flexible evolved mechanism and particular triggers in the social or physical environment (Gangestad, Haselton, & Buss, 2006; Kenrick, Nieuweboer, & Buunk, 2010; Tooby & Cosmides, 1992). Specific motivational systems may be prioritized to a greater or lesser degree, depending on ecological variables that affect the functional implications of those systems. Ecological variables such as sex ratio and infant mortality predict worldwide variations in mating strategies (Schmitt, 2006). Ecological variations in the prevalence of disease-causing pathogens have been linked to

Table 1. How Different Motivational Systems Are Triggered by Proximate Cues and Individual Differences Linked to Fundamentally Important Threats and Opportunities

Motivational system	Proximate triggers	Moderating individual differences
Immediate physiological needs		
Opportunities: Nutrients, liquids, etc.	External incentives associated with past reductions of physiological needs (e.g., smell of food cooking)	Genetic variations in metabolic processes
Threats: Starvation, dehydration, overheating, etc.	Internal physiological imbalances	Developmental experiences with different cues for reinforcement (e.g., local cuisine)
Self-protection		
Opportunities: Safety provided by others	Presence of familiar, similar others; being in familiar surroundings	High dispositional trust in others; being large or male
Threats: Violence from other people; contagious diseases	Presence of unfamiliar, dissimilar, angry males; being in unfamiliar surroundings; darkness; unfamiliar smells; presence of others with morphological abnormalities	Past experience of being physically harmed; being of small stature or female; chronic belief in a dangerous world; chronic high disease concern.
Affiliation		
Opportunities: Share resources, receive material support, enhanced self-protection, access to mates	Familiarity; past acts of reciprocity, trustworthiness; others' adherence to group norms; facial characteristics signaling trustworthiness	Coalitional identity or investment; gender; "collectivistic" cultural context and proximity to kin networks; dispositional trust in others; need for belongingness and/or social approval
Threats: Exposure to disease, cheating/free-riding, incompetence, excessive demands	Subjective "foreignness" of others; unfamiliarity of other; other's acts of cheating or norm violation	Own inclinations to cheat; personal vulnerability to disease; location (central vs. peripheral) within group network
Esteem/status		
Opportunities: Status enhancing alliances, access to resources and (for males) mating opportunities	Nonverbal status-conferring displays (e.g., eye-contact, bodily orientation, etc.) by others; shifts in exchange rules; others willingness to invest in oneself	Current status level; presence of potential familial coalitional partners; presence of desirable (female) mates
Threats: Loss of status, social regard, status-linked resources and mates	Nonverbal dominance displays by others; shifts in exchange rules; lack of apparent respect from others	Current status level; public versus private nature of interactional context; optimism and self-efficacy
Mate acquisition		
Opportunities: Availability of desirable, opposite-sex others	Opposite-sex others' age, attractiveness, status, bodily symmetry, morphological abnormalities, scent, nonverbal flirting behaviors	Relative mate value and age; restricted or unrestricted sexual strategies; current ovulatory status or testosterone level; histocompatibility
Threats: Presence of desirable, same-sex others	Same-sex others' age, status, symmetry, masculinity/femininity, flirting behaviors	Relative mate value; male-female ratio of available mates; status-linked distribution of resources; unpredictability of resource availability
Mate retention		
Opportunities: Long-term parental alliances	Others' expressions of love, intimacy, commitment; others' and own age (i.e., postmenopausal females).	Shared children; own mate value; own resources; availability of desirable alternative mates
Threats: Sexual infidelity, mate poaching	Partner flirtation behaviors; presence of nearby, high mate-value, opposite-sex individuals	Relative mate value; own resources; availability of desirable alternative mates; ovulatory status
Parenting		
Opportunities: Enhanced reproductive fitness	Proximity of one's own children; nonverbal cues eliciting care (e.g., smiles)	Oxytocin levels; gender; number of other children of one's own, siblings, or nieces/nephews; age of child; availability of tangible resources
Threats: Especially high costs imposed by children, cuckoldry (for males)	Signs of distress in own children; apparent physical (dis)similarity of child	Degree of paternal uncertainty; step-parenthood; age of child; number of other children of one's own, siblings, or nieces/nephews

cross-cultural differences in behavioral traits (e.g., introversion vs. extraversion) and values systems (individualism vs. collectivism) that have functional implications for disease transmission (Fincher, Thornhill, Murray, & Schaller, 2008; Schaller & Murray, 2008). It seems likely that these and other cross-cultural differences may result, in part, from differences in the extent to which distinct motivational systems are sensitized to input from the environment within which individuals develop. Again, one sees many interesting empirical implications of this line of thinking.

Further Implications

We have reconsidered the idea of a hierarchy of fundamental motives in light of empirical and theoretical developments at the interface of evolutionary biology, anthropology, and psychology. We considered motivational hierarchies at three levels of analysis often used by behavioral biologists. Many—but not all—of Maslow's motives make sense at a functional evolutionary level. It is clear that behavioral systems involved in seeking safety, affiliation, and esteem serve adaptive goals. In contrast, however, goals relevant to self-actualization are perhaps more sensibly subsumed within other, more functionally defensible motivational categories.

At a developmental level, we considered the human motivational hierarchy in light of the broader biological theory of life-history strategies, which has revealed some general patterns in the energy trade-offs made by organisms as they develop. Both the life-history and functional levels of analysis suggest that Maslow's original hierarchy missed the importance of the ultimate goal of successful reproduction (represented by the specific fundamental motives of mate acquisition, mate retention, and parenting in the revised pyramid). The life-history perspective also suggests that later developing motivational systems are not likely to replace those that developed earlier. The continuing accessibility of earlier developing systems is represented in the revised pyramid by overlapping systems rather than stacked systems.

Finally, at a proximate level of analysis, we suggested that many interesting questions involve the ways in which motivational systems are triggered by events in the current environment in interaction with individual differences. Some individual differences in response to the environment depend upon developmental sensitization experiences. A key point of this revised perspective is the focus on the ongoing dynamic interaction between internal motives and their functional links to immediate environmental threats and opportunities.

There is some empirical support for the perspective we have presented here. And there appears to be considerable theoretical value in placing the motivational hierarchy in light of a broad interdisciplinary framework provided by evolutionary biology. However, much of what we have suggested remains in the realm of speculation. This perspective raises several important questions but is not presented as a final set of answers. In fact, we believe the utility of this reconsideration is that it generates a number of interesting, but as yet

unanswered, empirical questions. This perspective implies important individual differences in motivational hierarchies, linked to ecological factors, gender, mating strategy, and life-history phase. But exactly which ones remain to be determined. Does the pyramid look different for men than for women? How exactly do motivational priorities link up with particular ecological factors (such as sex ratios of available mates, conspecific density, mortality level, and resource scarcity)? How exactly does the order of priorities change as one becomes a parent or grandparent? Given that adults often have multiple motivational systems at the ready, what exactly are the situational triggers for the different systems, and which ones are likely to trump the others? How might life-history considerations, and the ecological variables bearing on them, be linked to specific cross-cultural differences in motivational systems? To the extent that these kinds of questions generate theories, hypotheses, and empirical discoveries, the fundamental motives framework outlined here can be extraordinarily generative.

Given the already broad aims of this article, we cannot review the immense research literature on motivation or the various theoretical views advanced in the decades since Maslow proposed his influential theory. We believe that the broad, integrative perspective suggested here has numerous implications for other theories and empirical findings on motivation, but developing those connections would go well beyond the scope of this article. We do, however, briefly consider three broad sets of issues: (a) the relationship between physiological needs, goals, and motivational systems; (b) the links between conscious and unconscious motivation; and (c) the links between evolutionary and humanistic approaches to psychology. Each of these issues also inspires a corresponding set of empirical questions.

Needs, Goals, and Motivational Systems

Throughout this article, we have used the terms *needs*, *motives*, and *goals* somewhat loosely. Our view of motivational systems follows that of evolutionary theorists such as Plutchik (1980) and Scott (1980), with connections to the views of the original evolutionary psychologists such as William James (1890) and McDougall (1908) and to Carver and Scheier's (1998) cybernetic view. On that view, any motivational system includes (a) a template for recognizing a particular class of relevant environmental threats or opportunities, (b) inner motivational/physiological states designed to mobilize relevant resources, (c) cognitive decision rules designed to analyze trade-offs inherent in various prepotent responses, and (d) a set of responses designed to respond to threats or opportunities represented by the environmental inputs (i.e., to achieve adaptive goals). Consider, for example, the self-protection management system. As noted in Table 1, this motivational system is triggered by various threats, such as the presence of unfamiliar, dissimilar angry males encountered in unfamiliar surroundings or the dark. The motivational states most likely to be activated by such stimuli are those linked to anxiety or fear, and the likely responses include flight, freezing, or fight (depending

on analysis of various trade-offs inherent in the particular threat and one's own characteristics and current surroundings).

Physiological needs and psychological deprivations As reviewed by Deci and Ryan (2000), the term "need" has been used in various ways, but it is most closely associated with physiological deficits such as low blood sugar, which triggers hunger, or high blood salt, which triggers thirst. Deci and Ryan argue that certain human needs may not be based in physiological deficits, including those for affiliation, mastery, and autonomy. Our perspective agrees with the view that there are innate biological underpinnings to motivational states other than physiological deficits such as hunger. If you do not drink when you are thirsty, you get thirstier and eventually die; if you do not have sex when you are feeling strong attraction, you will not die. Nonetheless, although higher or psychological needs are not typically deficit driven, they are likely to have important and revealing physiological correlates. For example, oxytocin, testosterone, progesterone, and estrogen have been linked to affiliation, parental care, status seeking, and mate choice in various ways (e.g., Brown & Brown, 2006; Durante et al., 2008; Gangestad, Garver-Apgar, Simpson, & Cousins, 2007; McIntyre et al., 2006). And although deprivation of such needs is not fatal, it can certainly become relevant to activation. For example, being in an environment where a particular motivational system is regularly triggered but the motivation is not satisfied may lead to a sense of deprivation, as when an individual lacking respect, affection, or romantic love is exposed to people high in status, with many warm friendships, or with attractive mates. There are a number of empirical questions remaining to be answered about exactly how higher needs are linked to physiological states and about the role of deprivation in triggering those states.

How many different motives are there? The answer to this question no doubt depends on whether one is asking about cognitively separable goals (in which case, there are lots of them) or motivational systems (in which case, there are fewer). In discussing the various physiological deficits, Maslow noted that there are many atomistic needs but that they could be arranged in a "hierarchy of specificity":

The true picture is not one of a great many sticks lying side by side, but rather of a nest of boxes in which one box contains three others, and in which each of these three contains ten others, and in which each of these ten contains fifty others, and so on. (Maslow, 1970, p. 25)

As a minimum, we have noted that each motivational system is connected to a set of different threats and opportunities. Moreover, the behaviors, feelings, and decision rules involved in making one's mate happy are different than those involved in defending against infidelity and those involved in making friends are different from those involved in catching cheaters on social contracts. Thus, it is perhaps more appropriate to think of motivational systems as somewhat akin to Martindale's (1980) notion of "subelves"—as sets of subprograms for dealing with general categories of adaptive problems, linked in

associative networks (Kenrick, 2006; Kenrick & Shiota, 2008; Kurzban & Aktipis, 2007). For example, seeing an attractive member of the opposite sex can prime a network of thoughts and feelings involving one's own partner and one's own mate value, activate strategies designed to increase or decrease commitment to the relationship, and so on (e.g., Gutierrez et al., 1999; Maner, Rouby, & Gonzaga, 2008; Roney, 2003).

This issue is linked to a set of interesting questions about the extent to which different psychological mechanisms are shared between different cognitive modules. On a strict modular view, mental mechanisms or systems (such as the motivational systems we have been discussing) are completely encapsulated and even physically distinct from one another. However, very few modern evolutionary theorists believe that these criteria apply to most psychological systems, instead preferring a view of functional modularity (Barrett & Kurzban, 2006; Kenrick, Sadalla, & Keefe, 1998). Thus, the demonstrations of domain-specific mechanisms do not obviate the possibility of various domain-general mechanisms as well. We suspect that different motivational systems can share access to information and to submechanisms useful in solving common problems (for example, contrast mechanisms operate in several different judgmental contexts). Even though there may be some degree of sharing of general mechanisms, the specifics of how they operate may change in important ways in different motivational systems governing the solution of different problems. The extent to which particular motivational systems invoke domain-general, domain-specific, and partly shared mechanisms raises a host of empirical questions.

Which motives come to the fore? We have argued that adults have a full range of motivational systems at the ready. What determines which motives come to the fore? Obviously, various particular threats and opportunities available in the immediate environment will be critical, as discussed in the section on the proximate level of analysis. We noted that whether a person is or is not sensitive to a particular stimulus may also depend on developmental sensitization experiences. It is also likely that individual learning experiences during development play an important role, with people stressing different goals as a function of past reinforcement history as well as local ecological factors (e.g., the availability of mates as well as one's own physical attributes alters whether one adopts a restricted or unrestricted mating strategy; Gangestad & Simpson, 2000). Socially shared experiences that result from one's particular culture will also be important (e.g., Japanese and Americans respond differently to opportunities to interact with someone at a different level of the social hierarchy; Nakao, 1987). As discussed earlier, it is becoming increasingly clear that those cultural experiences are not necessarily arbitrary from a biological perspective and that they are often linked to ecological factors.

Deci and Ryan (2000) argue that some needs do not require any form of external stimulation. Although we have stressed environmental triggers, it is totally consistent with our view that some people will sometimes (e.g., when no immediately pressing problems present themselves) go out of their way to seek opportunities not present in the immediate environment. We would speculate that the organism

may be relatively more internally motivated in seeking opportunities and more externally driven when it comes to avoiding threats.

Conscious, Unconscious, and Incidental Goals

Maslow believed that much of the operation of fundamental motives occurs at a nonconscious level, and we agree. On one level, this means that people are often not aware of the subtle influences on their behavior (e.g., Bargh & Williams, 2006; Cheng & Chartrand, 2003). At another level, fundamental motivational systems involve not only subtle and preconscious influences on behavior but also influences for which there is no awareness at any level. We earlier mentioned the example of birds migrating in response to changing day length and noted that those birds need make no connection between the migratory triggers and the ultimate purpose of traveling to obtain better food supplies and nesting sites. Human motives also likely respond to cues of which the person is neither consciously aware nor—even if those cues do penetrate conscious awareness—likely to understand the ultimate significance of (as in women's greater responsivity to symmetrical and masculine men during their fertile periods; e.g., Gangestad et al., 2007; Little, Jones, & DeBruine, 2008).

Besides having nonconscious triggers and consequences, motivated behaviors may also have incidental effects. This is because, as Maslow noted, a given behavior can serve more than one goal. For example, seeking companionship when feeling socially isolated after moving to a new city may result in the incidental, unintended consequences of finding a mate and improving one's chances of ascending the social hierarchy at work. This is connected to the issue of evolutionary by-products, which we discussed earlier and consider in more detail later in this article. Note that by-products of motivated behavior occur at the proximate and developmental levels as well.

Evolutionism, Humanism, and Positive Psychology

Besides his famous pyramid of needs, Maslow was influential as one of the founders of humanistic psychology. Maslow distinguished a humanistic approach from the two other perspectives influential in his time. The psychoanalytic approach was limited, Maslow argued, by its focus on the negative and pathological aspects of human behavior, viewing people as motivated by suppressed feelings of hostility and sexual desires, often directed at their parents. The behavioral approach was limited, in Maslow's view, by its assumption that general principles of behavior could be developed by studying rats. In contrast, the humanistic approach emphasized the positive side of behavior and its assumption that the traits that were most positive in humans (such as artistic creativity and scientific curiosity) were not to be found in rats. In this sense, Maslow presaged the modern movement toward examining positive aspects of human behavior (e.g., Diener, 2000; Diener & Biswas-Diener, 2008;

Lyubomirsky, 2008; Lyubomirsky, King, & Diener, 2005; Myers, 2000; Seligman & Csikszentmihalyi, 2000).

To what extent is an evolutionary perspective compatible with the distinguishing features of humanistic psychology? At first glance, it may appear that an evolutionary approach, à la Freud, adopts a view of humans as driven by base sexual and aggressive instincts and, à la Skinner, emphasizes the commonalities between humans and rats. First glances can be deceiving, however, and a more careful look reveals that a modern evolutionary approach is quite compatible with Maslow's dual emphases on the differences between humans and other animals, and on the importance of understanding positive as well as negative aspects of human behavior.

Positive aspects of human nature. Although an evolutionary perspective recognizes sexual and competitive motivations as undeniable aspects of human nature, it also emphasizes the roles of cooperation, love, and parental concern (e.g., Ackerman & Kenrick, 2009; Kameda & Tindale, 2006; Keltner, Haidt, & Shiota, 2006; Kenrick, 2006; Van Vugt & Van Lange, 2006). It is useful to keep in mind a point we made earlier: that sex is only a small part of human reproduction. Human beings devote great effort to lengthy courtship periods, which even for the sexiest among us usually involves more hours spent in platonic activities than copulation. Beyond initial courtship, humans, both males and females, devote a great deal of energy to maintaining their bond and to raising their children. And for the last few decades of their lives, they may devote great energy to helping their grandchildren. From this perspective, reproductive goals provide the ultimate driving force behind not only copulation but also much that is positive in human nature—creating music and poetry, devoting oneself to charitable endeavors, or working to improve the world for the next generation (Griskevicius, Cialdini, & Kenrick, 2006; Griskevicius et al., 2007). Our perspective is also compatible with a wide range of research and theory in developmental psychology suggesting that people move toward increasing concern for others' welfare with age (Krebs & Van Hesteren, 1994; Van Lange, Otten, DeBruin, & Joireman, 1997). Note that the top of our hierarchy is defined by taking care of others—not pursuing that which gives one idiosyncratic pleasure. Consistent with our analysis, Buss (2000) makes a good case that a full understanding of human nature and its links to the natural and social environment is essential to psychologists who desire to promote positive psychology.

Human uniqueness Although it is true that an evolutionary approach involves an attempt to search for broad principles that apply to all animals, the approach also involves careful attention to each species' unique adaptations. Evolutionists have dedicated much attention to the characteristics that separate humans from other primates (e.g., spoken language, bipedal gait, delayed reproduction, paternal investment in offspring), those that separate primates from other mammals (e.g., large brains, opposable thumbs), and those that separate mammals from other vertebrates (e.g., live birth, nursing, prolonged period of infant care). Animal behaviorists themselves have become increasingly evolutionary in their orientation, and this has led

to an exploration of how learning processes differ in rats, humans, and other animals (e.g., Wilcoxon et al., 1971). This is not to deny the search for broad general principles, but to appreciate that a full understanding of human behavior will come from exploring how those general principles apply specifically to our species. For example, paternal investment is not found in most other mammals (such as rats) but is found in some mammals (like gibbons and wolves) and is common in birds. Understanding the ecological and social factors that predispose paternal investment helps us understand that feature of humanity and how it links with other human features (Geary, 2000).

One of the defining features of our species is an unusually large cerebral cortex, and there are many theories about the specific fitness pressures that led to such a substantially increased brain size (e.g., Dunbar & Schultz, 2007). Whatever the evolutionary causes might have been, there are manifold consequences that transcend those adaptive origins, and those consequences are unique to human beings. For example, many different approaches to motivation suggest that people are characterized by a need to seek and maintain some sense of understanding, meaning, and purpose (e.g., Heine, Proulx, & Vohs, 2006; Koole, Greenberg, & Pyszczynski, 2006; Ryff, 1995; Stevens & Fiske, 1995). It is typically presumed that these needs are unique to humans, and this presumption is neither demanded nor denied by an evolutionary perspective on human motivation. Rather, an evolutionary perspective sharpens the discussion about the nature of these ostensibly unique needs. It does so by inviting specific kinds of questions: Are these cognitive needs simply nonadaptive consequences of underlying cognitive capacities (e.g., Boyer, 2003)? Or are they instead adaptive? If so, what exactly are their fitness-relevant consequences? And, regardless of whether they are adaptations or nonadaptive by-products, how might the expression of these needs, and their implications, change across the life span? An evolutionary perspective also suggests specific kinds of possible answers to those questions. For instance, in response to questions about developmental changes in the expression of cognitive strivings, an evolutionary life-history perspective suggests that what appear to be higher strivings in educated adults may stem from general motivational processes present much earlier in life (such as curiosity). This sort of suggestion resonates with—and substantiates—idiosyncratic speculations in Maslow's own work: "Acquiring knowledge and systematizing the universe have been considered as, in part, techniques for the achievement of basic safety in the world, or, for the intelligent man, expressions of self-actualization" (Maslow, 1943, p. 385).

Self-actualized people In an effort to redirect psychological research toward the positive side of humanity, Maslow (1970) studied a group of people he described as self-actualized. Besides manifesting the central feature of self-actualization motivation—striving to excel in their own unique area of expertise—these individuals also manifested a number of other characteristics Maslow viewed as highly desirable, including self-acceptance, independent thinking, a problem-solving orientation, an ability to form deep friendships, and a lack of prejudice. The individuals Maslow studied, such as

Albert Einstein, Eleanor Roosevelt, and Frederick Douglass, no doubt were highly accomplished and achieved very high levels of status as a function of their intellectual capacities and social intelligence. At one level, such individuals are manifesting the various aspects of "good genes" (Miller, 2000). Whether such highly functioning individuals reproduce more successfully than less self-actualized individuals is an empirical question, but it certainly seems likely that they would be attractive as mates. Their intellectual capacities and social skills would also be expected to translate into benefits for themselves and their relatives. Again, this is not to suggest that people who are striving to reach higher goals are consciously (or even unconsciously) intending to improve their fitness, only to suggest that any inclinations underlying such strivings are likely to be maintained within one's lifetime, and across generations, by adaptive consequences.

Conclusion

In light of developments at the interface of evolutionary biology, anthropology, and psychology, we have suggested some structural modifications to Maslow's classic hierarchy of human motives. A consideration of the ultimate functions of behaviors and of life-history development counsels the explicit inclusion of motivational levels linked to mating and reproduction. Reproduction for humans is not ultimately about self-gratification, but involves a considerable diversion of resources away from selfish goals and toward other human beings in our social networks. A consideration of life-history trade-offs also implies that later developing motive systems never fully replace earlier ones and that they continue to coexist, ready to be activated depending on current opportunities and threats in the environment, in interaction with individual differences. Thus, a key point of this revised perspective is the focus on the ongoing dynamic interaction between internal motives and their functional links to ongoing environmental threats and opportunities.

Notes

1. Evolutionary explanations can also examine the historical roots of a feature, trait, or behavior. For example, the human hand is quite similar to the hands of other great apes, and the differences between primates can be traced in the bones of now extinct species linking the current species. In this article, we focus on the functional, not the historical, aspect of evolutionary explanations.
2. Of course, there are transformations. Elderly people are less likely to devote attention to mating effort, and such effort in postmenopausal females would no longer have direct reproductive consequences.

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