

Decision-Making Under Risk: Integrating Perspectives From Biology, Economics, and Psychology

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Abstract

Decision-making under risk has been variably characterized and examined in many different disciplines. However, interdisciplinary integration has not been forthcoming. Classic theories of decision-making have not been amply revised in light of greater empirical data on actual patterns of decision-making behavior. Furthermore, the meta-theoretical framework of evolution by natural selection has been largely ignored in theories of decision-making under risk in the human behavioral sciences. In this review, I critically examine four of the most influential theories of decision-making from economics, psychology, and biology: expected utility theory, prospect theory, risk-sensitivity theory, and heuristic approaches. I focus especially on risk-sensitivity theory, which offers a framework for understanding decision-making under risk that explicitly involves evolutionary considerations. I also review robust empirical evidence for individual differences and environmental/situational factors that predict actual risky decision-making that any general theory must account for. Finally, I offer steps toward integrating various theoretical perspectives and empirical findings on risky decision-making.

Keywords

evolutionary psychology, judgment/decision-making, risk, motivation/goals, individual differences

The study of decision-making under risk is of notable importance to all of the behavioral sciences, for good reason: Almost every human and non-human animal decision is made under some consideration of risk, where risk is defined as known variance in outcomes. Trading commodities on the stock market involves risk, as does searching for food, asking someone out on a date, or aggressing toward others (Holton, 2004). In everyday vernacular, risk usually refers to a chance of a negative outcome occurring. Other terms that have been used more or less synonymously with risk include uncertainty, exposure to danger, and hazard, among other more discipline-specific terms (e.g., Winterhalder, Lu, & Tucker, 1999).

Although risk has been widely studied in various disciplines, in a wide array of species, and in various social and environmental contexts, relatively little progress has been made toward developing a general interdisciplinary theoretical framework for examining decision-making under risk in the behavioral sciences. In particular, biological approaches to understanding decision-making, such as risk-sensitivity theory, have been largely ignored in the economics and psychology literature. Furthermore, such classic theories of decision-making as expected utility theory and prospect theory have not been significantly reconceptualized or updated in light of the growing body of empirical evidence on how individuals actually make decisions under risk. This article

reviews various theories of decision-making from multiple behavioral science disciplines and integrates them under the broad meta-analytic framework of evolution by natural selection.

I seek to accomplish several specific objectives in this review. First, I explicate the distinction between normative and descriptive understandings of decision-making under risk, and explain why both are necessary for any broad theory of decision-making. Second, I critically review four of the most influential frameworks that have been used to study decision-making under risk in the behavioral sciences: expected utility theory (from economics), prospect theory (from economics/psychology), risk-sensitivity theory (from biology), and heuristic approaches (from psychology). Third, I explain why any understanding of decision-making under risk requires engaging with evolutionary theory and integrating explanations from multiple levels of analysis (i.e., proximate and ultimate). In support of this approach, I provide an evolutionary normative framework for broadly understanding decision-making under risk. Fourth, I review robust

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empirical findings that any general theory of decision-making must account for. In doing so, I provide a descriptive basis for a broad theory of decision-making under risk. Finally, I suggest steps toward integrating various theoretical perspectives and empirical findings on decision-making under risk, with a specific emphasis on the importance of the frameworks of risk-sensitivity theory and evolutionary theory more generally.

Normative and Descriptive Theories

Theories from different disciplines variably adopt normative and/or descriptive approaches to understanding decision-making under risk. As a consequence, it is important to compare and contrast both approaches and to emphasize that they are in large part complementary. Before doing so, however, it is necessary to clarify a definition of risk. Researchers in economics, biology, and psychology have largely converged on a definition of risk as outcome variance, where the riskier of two options with the same expected value is that with higher outcome variance (e.g., Bernoulli, 1738; Daly & Wilson, 2001; Friedman & Savage, 1948; Real & Caraco, 1986; Rubin & Paul, 1979; Winterhalder et al., 1999). For example, a 50% chance of receiving \$100 is riskier than receiving \$50 with 100% certainty. In this example, both decision options have the same expected value but differ in outcome variance (receiving \$50 for sure vs. receiving either \$0 or \$100). Other conceptions of risk include unpredictability, uncertainty, and exposure to danger or hazard. Although they appear to be different, these conceptions of risk all involve real or perceived outcome variance. Given that individuals exhibit systematic preferences for risk in various different environmental and social contexts, explaining decision-making under risk therefore requires explaining why decision makers sometimes prefer high variance options to low variance options and vice versa.

Several theoretical frameworks for examining decision-making under risk have been developed in disparate fields. In economics, “rational” models of risky behavior have dominated (e.g., expected utility theory; Friedman & Savage, 1948, 1952). Psychological conceptions of risky decision-making have been broader, involving risk-taking as a product of cognitive processes (e.g., prospect theory, heuristic approaches; for example, Gigerenzer & Gaissmaier, 2011; Kahneman & Tversky, 1979; Todd & Gigerenzer, 2012; Tversky & Kahneman, 1981), and more recently, a product of evolutionarily adaptive mechanisms (e.g., Aktipis & Kurzban, 2004; Daly & Wilson, 2001; Kenrick & Griskevicius, 2013; Mishra & Lalumière, 2008; Rode & Wang, 2000; Todd & Gigerenzer, 2012). Biologists have developed risk-sensitivity theories based on the idea that organisms ultimately behave to enhance reproductive success or fitness (e.g., Stephens, 1981; Stephens & Krebs, 1986).

These various theories take very different approaches to explaining decision-making under risk. Normative theories

of decision-making involve a top-down approach concerned with identifying the most “rational” decision in a given situation, where rationality is typically defined by decisions that maximize a currency of interest. Normative theories attempt to describe what organisms *ought* to do in a given decision-making situation. Many theories of decision-making under risk in economics and psychology explain decisions in terms of the currency of utility, where utility (broadly defined) is a measure of happiness, gratification, or satisfaction derived from a behavior (in economics, usually the consumption of a good or a service; Friedman & Savage, 1952). Theories of decision-making in biology have focused on the universal biological currency of fitness, where fitness refers to the differential reproductive success of individuals possessing certain heritable characteristics (Williams, 1966).

In contrast to normative theories, descriptive theories involve a bottom-up approach concerned with identifying proximate mechanisms involved in decision-making. That is, descriptive theories tend to begin with empirical observations of actual behavioral. Descriptive theories have mostly been constructed from apparent violations of the predictions of normative theories and describe *how* organisms actually make decisions, rather than *why* they make decisions. Although descriptive theories are often argued to be superior to normative theories of decision-making because they are, on average, more empirically driven, descriptive theories still require normatively defining some currency of decision-making. It is difficult to conceive of a theory of decision-making with sufficient predictive power that does not specify goals or aspirations that motivate decision-making, and specifying such goals or aspirations requires defining a currency of decision-making, even if it is a functional abstraction or conceptualization.

A comprehensive, interdisciplinary, and convergent approach to understanding decision-making under risk must therefore contain two components. The first component is a normative rationale for decision-making under risk involving a clear definition of a currency. The second component is some conception of the mechanisms underlying decision-making driven by empirical observation of actual behavior. It is not enough to argue that decision makers seek to enhance outcomes associated with a currency of interest; some elucidation of perceptual and cognitive mechanisms is necessary to address how decision makers perceive and compare decision options and make choices. Throughout this article, I advocate for the integration of both normative and descriptive approaches to decision-making under risk.

Theories of Decision-Making Under Risk

In this section, I summarize some of the most influential normative (expected utility theory, risk-sensitivity theory) and descriptive (prospect theory, heuristic approaches) theories of decision-making under risk in the behavioral sciences.

These theories are reviewed in roughly chronological order of development: (1) expected utility theory, (2) prospect theory, (3) risk-sensitivity theory, and (4) heuristic approaches.

Expected Utility Theory

Expected utility theory stems from Bernoulli's (1738) proposed solution to the St. Petersburg paradox. Consider a game in which an individual must decide the maximum amount of money he or she is willing to pay as an entry fee. The game is played by flipping a fair coin until it comes up heads, and the total number of flips (n) determines the amount of the prize, $\$2^n$. If the coin shows a heads on the first flip, the coin can be flipped again until a tails shows up. The player then earns $\$2^n$, where n is the number of heads that show up in a row. The expected value of the game is infinite, and thus, any "rational" player should wager any finite amount for the opportunity to play (Bernoulli, 1738):

$$(1/2) \times \$2 + (1/4) \times \$4 + (1/8) \times \$8 \\ + (1/16) \times \$16 + (1/n) \times \$2^n = \infty.$$

Most people, however, would not even wager \$25 to play the game, and the actual probability of winning more than \$4 is less than 25% (Hacking, 1980).

Bernoulli (1738) proposed a solution the St. Petersburg paradox, and in doing so, provided the first conception of expected utility theory. Bernoulli proposed that money has diminishing marginal utility: A single dollar is not worth much to someone who is wealthy, but to someone who is poor, a dollar is extremely valuable. Thus, in addition to the absolute value of a decision outcome (e.g., dollars earned), decision makers may identify some additional subjective value, or *utility*, to any decision outcome. Expected utility is computed as the utility of any decision outcome multiplied by its probability. Expected utility theory predicts that decision makers seek to maximize utility in all decisions, where utility is broadly defined as a measure of happiness, gratification, or satisfaction derived from a behavior (Friedman & Savage, 1952).

Early conceptions of expected utility theory posited three types of utility functions describing the relationship between the expected value of a decision and perceived utility. These three curves summarize risk-indifference, risk-aversion, and risk-preference (von Neumann & Morgenstern, 1944). Each of these utility curves differs in its quantification of *marginal utility*, defined as the change in utility that occurs for every unit change in reward. The risk-indifference curve describes a linear relationship between marginal utility and wealth (or some other currency associated with happiness or gratification). The risk-averse, concave-down function exemplifies the law of diminishing returns, where each additional unit of reward is less valued than the last. The risk-preferring, concave-up curve provides an example of a utility curve that describes a situation where each individual unit of reward is valued more than the last.

It was originally argued that these three utility curves describe consistent patterns of behavior among individuals (von Neumann & Morgenstern, 1944). For example, a risk-averse individual's decision-making would be consistently characterized by a concave-down function. Changes in the environment of decision-making were suggested to influence the steepness of the curve, but the general shape was argued to remain stable for individuals. This conception of stability in risk, however, is problematic. Decision-making behavior is characterized by what appears on the surface to be inconsistency: for example, people who purchase lottery tickets (exhibiting risk-proneness) also purchase insurance (exhibiting risk-aversion).

Another problem with expected utility theory is its conception of utility. Utility as a currency is difficult to operationalize because utility can take many forms. For humans, these forms may include wealth, happiness, opportunity, or any other positive reward in various domains of life. As a consequence, any decision is easy to justify *post hoc* as being utility maximizing; it was famously stated, "[u]tility is the quality in commodities that makes individuals want to buy them, and the fact that individuals want to buy commodities shows that they have utility" (Robinson, 1962, p. 48). This phenomenon has been described as discovered preference (e.g., Cubitt, Starmer, & Sugden, 2001). Consequently, it is possible to claim under expected utility theory that all decisions are utility maximizing. Expected utility theory therefore offers little predictive value for a normative theory of decision-making.

The most important criticism of expected utility theory, however, stems from its inability to explain actual patterns of decision-making under risk. In their original conception of expected utility theory, von Neumann and Morgenstern (1944) suggested that decision-making under risk conforms to five preference axioms: completeness (decision makers can always rank preferences between outcomes), transitivity (preferred rank ordering of options is always consistent), continuity (there is some possibility that decision makers are indifferent between best and worst outcomes), monotonicity (for outcomes with equal expected values, higher probability outcomes are preferred), and independence (if paired choices are mixed with another set of paired choices, preferences remain independent). From these assumptions, it is possible to construct consistent utility curves for individuals that conform to the predictions of expected utility theory.

A crucial problem with this approach, however, is that it ignores actual preference behavior as it manifests in the real world. A very large body of evidence shows that most of the axioms of expected utility theory are consistently violated in real-world decision-making, in many different ways (e.g., Aktipis & Kurzban, 2004; Allais, 1953; Barrett & Fiddick, 1999; Ellsberg, 1961; Kahneman & Tversky, 1979; Rode & Wang, 2000; Starmer, 2000; reviewed in Wu et al., 2004). Although expected utility theory can, in principle, predict decisions in perfectly consistent environments with fully

available and known parameters—environments that Savage (1954) called “small worlds”—it is not robust in predicting decision-making under risk in more general and realistic conditions (Savage, 1954; reviewed in Gigerenzer & Gaissmaier, 2011). As a consequence, alternative theories of decision-making arose to try to account for systematic violations of the axioms of expected utility theory. These violations and criticisms of expected utility theory are discussed in the context of alternative theories of decision-making throughout this article.

Prospect Theory

Prospect theory arose from expected utility theory in the late 1970s to address growing concern with the inability of expected utility theory to predict actual decision-making in most situations. The best-known violation of expected utility theory is the framing effect (Kahneman & Tversky, 1979; Tversky & Kahneman, 1981). Kahneman and Tversky demonstrated that people tend to be risk-prone when faced with a decision framed as a loss and risk-averse when faced with a decision framed as a gain, even if both decisions have identical expected values. Consider the classic Asian disease problem (Tversky & Kahneman, 1981):

Imagine that the U.S. is preparing for the outbreak of an unusual Asian disease, which is expected to kill 600 people. Two alternative programs to combat the disease have been proposed. Assume that the exact scientific estimates of the consequences of the programs are as follows. (p. 453)

In the standard version of the Asian disease problem, participants are provided with a decision scenario involving a choice between two options, either presented in a positive (gain) or a negative (loss) frame. The positive frame states,

1. If Program A is adopted, 200 people will be saved.
2. If Program B is adopted, there is a 1/3 probability that 600 people will be saved, and 2/3 probability that no people will be saved.

In this positive frame, both options are phrased in terms of the possibility of saving people, and thus, in terms of gains. When presented with this positively framed scenario, Tversky and Kahneman (1981) found that 72% of participants preferred the certain option (Program A) over the risky option with higher outcome variance (Program B), thus exhibiting risk-aversion on average. The negative frame states,

1. If Program C is adopted, 400 people will die.
2. If Program D is adopted, there is a 1/3 probability that nobody will die, and 2/3 probability that 600 people will die.

Here, both options are negatively framed in terms of the number of possible deaths, and thus, in terms of losses.

Tversky and Kahneman found that when presented with this loss scenario, participants' risk-preferences reversed: only 22% of participants preferred the certain option (Program C), thus exhibiting risk-acceptance on average. This finding that people exhibit risk-preference reversal in mathematically identical decisions made in loss and gain frames has received substantial empirical support (reviewed in Levin, Schneider, & Gaeth, 1998; for a meta-analysis, see Kühberger, 1998).

Kahneman and Tversky (1979) conceived prospect theory to explain the systemic violations of expected utility theory they observed in conducting empirical studies with human subjects. Specifically, prospect theory addresses the framing effect described above, in addition to the certainty effect and the isolation effect. The certainty effect describes decision makers' tendency to overweight outcomes that are certain (e.g., sure gains or sure losses) over those that involve probability, regardless of expected value. The isolation effect describes decision makers' tendency to ignore common components of decision alternatives in order to simplify decisions (Kahneman & Tversky, 1979).

Kahneman and Tversky (1979) proposed that two phases—the editing and evaluation phases—describe how individuals make decisions under risk. The editing phase serves to reformulate and organize all of the possible decision options to simplify evaluation (Kahneman & Tversky, 1979) and involves several different operations (coding, combination, segregation, and cancellation; Kahneman & Tversky, 1979; Tversky & Kahneman, 1981). The most important of these operations—and the most influential contribution of prospect theory—is coding. Kahneman and Tversky suggested that decision makers code gains and losses around a reference point, where outcomes below the reference point represent losses, and outcomes above the reference point represent gains. Reference points are derived from an individual's present state but can change based on expectations or biases of decision makers (Tversky & Kahneman, 1981). The other operations in the editing phase describe how decision makers combine separate decisions with identical outcomes and probabilities into single decisions (combination), clarify riskless and risky components (segregation), and simplify multistep decisions by ignoring similar decision elements (cancellation).

The second phase of a decision, according to prospect theory, is the evaluation phase, where an individual assesses all of the edited options and makes a decision. The evaluation phase consists of a value function and a weighting function. The value function assigns specific values to certain outcomes. Here, the law of diminishing returns applies: The difference between \$1 and \$2, for example, is perceived as greater than the difference between \$500 and \$501. Because of the law of diminishing returns and the differential subjective values placed on gains and losses, the utility curve for prospect theory preferences (analogous to a utility function) is concave-down above a reference point (i.e., exhibiting risk-aversion for gains), and concave-up below a reference

point (i.e., exhibiting risk-proneness for losses). The reference point refers to the origin of the utility function, around which gains and losses are defined.

The weighting function describes the overweighting of small probability events and underweighting of medium and high probability events (i.e., emphasizing the salience of certain and/or rare events, Kahneman & Tversky, 1979; Tversky & Kahneman, 1992). In prospect theory, the value of each outcome is multiplied by the decision weight of that particular outcome, leading to some quantification of the utility of decision options. This operation is similar to that involved in computing utility in expected utility theory (Bernoulli, 1738; Friedman & Savage, 1952). Here, individuals engage in processing of decisions involving both the editing and evaluation phase prior to making a final decision, leading to a subjective evaluation of utility.

Prospect theory is an amendment to expected utility theory, albeit a significant one, and so suffers from many of the same problems. Although prospect theory addresses some commonly observed violations of expected utility theory (e.g., intransitivity of preferences), utility remains the currency of decision-making under risk, and its definition is unchanged from that used in expected utility theory (Kahneman & Tversky, 1979). Although prospect theory describes mechanisms of decision-making that take into account some systemic empirical violations of expected utility theory preferences (e.g., framing effects), it still suffers from the shortcomings of a poorly defined currency. Other theories of decision-making, such as biologically derived risk-sensitivity theory, have more concretely defined currencies and so avoid many of the problems that plague expected utility theory and prospect theory.

Risk-Sensitivity Theory

Risk-sensitivity theory is a normative theory developed by behavioral ecologists to explain food acquisition decisions in foraging animals. Instead of focusing on the broad (but vague) goal of maximizing utility, risk-sensitivity theory was conceived to more narrowly explain risky decisions in the context of foraging. In risk-sensitivity theory, decision-making is characterized as a behavioral response designed to seek foraging returns in stochastic environments that allow for survival, with the ultimate goal of enhancing reproductive success or fitness (Bednekoff, 1996; Hurly, 2003; Stephens, 1981; Stephens & Krebs, 1986; Weber, Shafir, & Blais, 2004).

Caraco, Martindale, and Whittam (1980) provided the first conception of risk-sensitivity theory based on experimental examination of the foraging behavior of yellow-eyed junco birds. Birds had to choose between two food patches with the same expected value, but one risky (high variance) and the other certain (low variance). Caraco et al. constructed utility curves (similar to those used in expected utility theory) for individual juncos based on their risk-preferences but

did so under two different energy budgets: positive and negative. A bird in a positive energy budget experienced foraging returns at a rate that would allow it to meet its energy requirements, whereas a bird in a negative energy budget experienced foraging returns at a rate that would not allow it to meet its energy requirements. Caraco et al. found that juncos in negative energy budgets were substantially more risk-prone compared with those in positive energy budgets. A subsequent study showed the same pattern of findings in white-crowned sparrows (Caraco, 1983). This pattern of behavior is more specifically known as the energy-budget rule (Stephens, 1981; Stephens & Krebs, 1986).

The adaptive logic for this shift in risk-preferences is simple. Consider a foraging bird that must consume 1,000 calories before dusk to survive the night. This bird seeks food from one of two different food patches. Both offer the same mean payoff (120 calories), but differ in payoff variance: Patch 1 ranges from 110 to 130 calories (low variance), and Patch 2 ranges from 40 to 200 calories (high variance). Foraging in Patch 2 is riskier due to its higher outcome variance. The patch chosen by the bird should depend on its budgetary needs. If the bird had already acquired 900 calories through the day and required 100 more calories to meet its energy need for the night (a positive energy budget), its survival is guaranteed if it forages from the low-risk patch (Patch 1). If the bird has acquired 800 calories through the day and required 200 more calories to survive the night (a negative energy budget), it effectively guarantees its death if it forages from the low-risk patch (Patch 1). As a consequence, the high-risk patch (Patch 2) should be favored in this situation because it at least allows for a chance of survival. At baseline, most organisms are risk-averse when making decisions between high and low variance reward amounts (Daly & Wilson, 2001; Kacelnik & Bateson, 1996, 1997). Risk-aversion switches to risk-preference, however, when a need (like a negative energy budget) must be fulfilled that cannot be satisfied with a low-risk option.

Risk-sensitivity theory therefore formally predicts that decision makers shift from risk-aversion to risk-preference in situations of need, where need describes disparity between an individual's present state and desired (or goal) state (Ermer, Cosmides, & Tooby, 2008; Mishra & Fiddick, 2012; Mishra & Lalumière, 2010; Rode, Cosmides, Hell, & Tooby, 1999; Stephens, 1981; Stephens & Krebs, 1986). For example, in human context, someone with a pressing \$5,000 debt should prefer a gamble offering a 10% chance of winning \$5,000 over earning \$500 with certainty. Although both options have the same mean payoff, the riskier option at least allows for a chance to meet one's need. According to risk-sensitivity theory, decision makers do not necessarily seek to maximize desirable outcomes but rather seek to avoid outcomes that fail to meet their needs (Stephens, 1981; Stephens & Krebs, 1986). In this sense, risk-sensitive decision-making is a form of satisficing—actors make decisions that are “good enough” to meet one's needs at any given time (Simon, 1956).

As a biological theory of decision-making, risk-sensitivity theory is necessarily tied to survival, reproductive success, and fitness. Each risk-sensitive decision that meets an immediate foraging need serves to guarantee survival, and in part addresses the larger overarching biological imperative of enhancing reproductive success and fitness. After all, reproduction is impossible if survival is not first assured. Twin-threshold models of risk-sensitivity have been developed to explain how risk-sensitivity theory can account for both survival- and reproduction-based decisions under risk by considering multiple needs in different domains (e.g., Bednekoff, 1996; Hurly, 2003). Specifically, these models suggest that organisms should focus on meeting their survival needs first, and then seek to maximize reproductive outcomes. A more detailed life history account of how organisms (especially humans) may prioritize needs in different domains is provided in more detail later in the article.

Although risk-sensitivity theory has enjoyed substantial empirical support, it too suffers shortcomings, mostly arising from its historically rigid application to non-human animal behavior. Most criticisms of risk-sensitivity theory that have been identified thus far are applicable only to foraging animals and not to more general human decision-making under risk. For example, animals appear not to adhere to the predictions of risk-sensitivity theory when making decisions involving variance in delay of rewards (as opposed to variance in the magnitude of rewards; e.g., Reborada & Kacelnik, 1991). Furthermore, the energy-budget rule has also been inconsistently supported (reviewed in Bateson & Kacelnik, 1998; Kacelnik & Bateson, 1996, 1997; Kacelnik & El Mouden, 2013). Despite the shortcomings of risk-sensitivity theory noted in the behavioral ecology literature, however, recent attempts to import and generalize risk-sensitivity theory to understanding human decision-making under risk have proven remarkably successful (e.g., Deditius-Island, Szalda-Petree, & Kucera, 2007; Ermer et al., 2008; Mishra & Fiddick, 2012; Mishra, Gregson, & Lalumière, 2012; Mishra & Lalumière, 2010; Pietras & Hackenberg, 2001; Pietras, Locey, & Hackenberg, 2003; Rode et al., 1999; Wang, 2002; reviewed in Mishra & Fiddick, 2012; Mishra, Gregson & Lalumière, 2012; Mishra & Lalumière, 2010). These findings and their implications are described in greater detail later in the article.

Heuristic Approaches

Heuristics are “rules of thumb” devised to allow for quick and efficient decision-making. They are typically the products of inductive reasoning from actual patterns of decision behavior. As a consequence, heuristics represent a descriptive approach to explaining decision-making (reviewed in Gigerenzer & Gaissmaier, 2011; Gigerenzer, Hertwig, & Pachur, 2011; Gigerenzer, Todd, & the ABC Research Group, 1999; Thorngate, 1980; Todd & Gigerenzer, 2000, 2012).

The heuristic approach to understanding decision-making first gained prominence when Tversky and Kahneman (1974) popularized understanding heuristics as misapplied cognitive processes that give rise to so-called irrational cognitive biases. These cognitive biases were defined as violations of rational choice as dictated by expected utility theory. This understanding still dominates today (e.g., Krueger & Funder, 2004). However, heuristics are not necessarily manifestations of maladaptive cognitive biases. Rather, heuristics can be better understood as products of adaptive evolutionary processes that solve problems that would have been recurrent over human ecological and evolutionary history (e.g., Hutchison & Gigerenzer, 2005; Todd & Gigerenzer, 2012). Traditional economic theories of decision-making, including expected utility theory and prospect theory, suffer from an important limitation in that they assume that decision makers have an unlimited capacity for processing information related to decision options (i.e., they reflect a conception of “unbounded” perfect rationality). However, most real-world decisions are made quickly with incomplete information. Therefore, any compelling theory of decision-making under risk must acknowledge the limitations of cognitive processing and available information (i.e., acknowledge “bounded” rationality; for example, Gigerenzer & Gaissmaier, 2011; Gigerenzer et al., 1999; Todd & Gigerenzer, 2000, 2012).

Several amendments to traditional utility theories have been proposed in an attempt to model observed decision-making behavior under more realistic conditions of constraint. Optimization under constraint approaches, for example, suggest that decision makers formulate stopping rules that dictate when to cease searching for reasonable decision options. Specifically, it has been hypothesized that decision makers calculate the best possible decision by weighing the costs and benefits of searching for further information about alternative decision outcomes, and stop searching for alternatives as soon as costs exceed benefits (e.g., Gigerenzer et al., 1999; Todd & Gigerenzer, 2000, 2012). However, optimization under constraint approaches still in part reflect a concept of decision-making as unbounded and are therefore unrealistic.

In most real-world situations, it is impossible to arrive at an optimal or maximizing outcome given the sheer number of decision options available and the amount of uncertainty inherent in the environment (where uncertainty describes the degree to which decision outcomes are unknown; Knight, 1921). Satisficing is an alternative, bounded approach to decision-making that is characterized by the seeking of outcomes that are “good enough,” as opposed to the seeking of optimal outcomes (i.e., optimization or maximization; Simon, 1956). Satisficing, unlike optimization, does not require complete information and can be used effectively in situations of uncertainty. Specifically, “fast and frugal” heuristics are satisficing heuristics that can be applied quickly and with a minimum of informational input.

Fast and frugal heuristics are defined by their efficiency regarding time, knowledge, and computational requirements for decision-making. An example of a fast and frugal heuristic is one-reason decision-making, where a single piece of information is used to make a decision (e.g., in searching for a mate, stopping a search once a mate taller than oneself is found; Gigerenzer et al., 1999; Todd & Gigerenzer, 2000, 2012). Using a single piece of information to make a decision avoids the pitfalls of having to combine multiple different potential currencies (e.g., height and income potential, or height and intelligence).

Fast and frugal heuristics are also necessarily constrained by environments of decision-making. To construct simple decision rules, it is necessary to take into consideration how information is structured in the environments most regularly encountered by decision makers (e.g., foraging patches tend to consist of clumped resources at distance from each other; Wilke, Hutchinson, Todd, & Czienskowski, 2009). In this sense, fast and frugal decision-making reflects ecological rationality, which describes robust fit between decision-making mechanisms and the recurrent structure of regularly encountered environments (Todd, 2000; Todd & Gigerenzer, 2012). Ecologically, rational decision-making must necessarily be robust to allow for decision rules to be broadly used in multiple different environments. Rigid fit of decision-making mechanisms to specific environments would be implausibly cognitively expensive given the enormous array of heuristics that would be required to solve specific problems in multiple specific environments. One-reason decision-making, for example, has only two requirements to be effective: a domain of decision-making (e.g., mate choice, hunger), and a threshold of satisfaction (i.e., a need level). Because of their flexibility with limited information, fast and frugal heuristics are robust in facilitating effective decision-making in multiple different environments. Furthermore, fast and frugal heuristics have been shown to be remarkably effective in explaining substantial variance in actual decision-making behavior in a wide variety of contexts (reviewed in Todd & Gigerenzer, 2012; Gigerenzer & Gaissmaier, 2011; Gigerenzer, Hertwig, & Pachur, 2011; Gigerenzer, Todd, & the ABC Research Group, 1999; Todd & Gigerenzer, 2000, 2012).

In sum, the heuristics approach to understanding decision-making under risk involves explicating simple rules that describe how decision-making actually takes place (e.g., Berg & Gigerenzer, 2010; Brandstätter, Gigerenzer, & Hertwig, 2006; Katsikopoulos & Gigerenzer, 2008; but see Johnson, Schulte-Mecklenbeck, & Willemsen, 2008). Heuristics describe the manner in which decision makers perceive their environment, collect information regarding a decision, and choose between decision options. Of course, more deliberative decisions involving careful consideration of decision options and potential outcomes may work through less efficient and more optimization-focused means. However, an ecologically rational conception of decision-making that

seeks to explain most decision-making behavior must account for the speed and efficiency of decision-making, as well as the structure of information in the environment, both of which are accounted for in the fast and frugal heuristic approach.

The Functional Basis of Decision-Making Under Risk

In the first portion of this article, I briefly summarized four of the most dominant approaches that have been used to study decision-making under risk in the behavioral sciences. In the remainder of the article, I seek to integrate these different theories into a more unified understanding of decision-making under risk. In this specific portion of the article, I address issues of levels of analysis and explanation (proximate and ultimate), with a focus on emphasizing the importance of the ultimate level of analysis (also known as the functional or evolutionary level of analysis). Humans, like all other animals, are products of evolution by natural selection. Consequently, any framework for understanding decision-making under risk must necessarily engage with evolutionary explanations of behavior. I specifically argue for a biological, fitness-based currency of decision-making, and for a general understanding of risk-relevant motivation centered on the concept of need from risk-sensitivity theory.

Levels of Analysis

Tinbergen (1963) famously proposed that the causes of behavior can be broadly understood at two levels: the proximate level and the ultimate level. Proximate explanations describe *how* a behavior occurs by describing the causes of behavior in a mechanistic way. Proximate explanations include both immediate causal mechanisms (e.g., hormones, immediate situational/environmental factors, emotions) and developmental or ontological influences (e.g., gestational environment, maternal nutrition, childhood social environment). Ultimate explanations provide an evolutionary explanation of *why* a behavior occurs. That is, why did a species evolve the traits that it possesses? Ultimate explanations include both phylogeny (i.e., understanding how similar/different traits evolved in different species) and function (i.e., How does a trait solve a problem in a way that facilitates reproductive success or fitness?).

It is important to note that ultimate evolutionary explanations are not about understanding how (or whether) organisms are “optimally” biologically designed. Rather, evolutionary theory is about understanding adaptive fit of organisms to the environments in which they adapted. Optimal design is therefore biologically impossible because environments (and environmental inputs) are constantly changing. This clarification is key—understanding the behavioral products of natural selection necessarily requires understanding environments of decision-making (and more specifically, mechanism-environment fit, that is, ecological

rationality). Evolutionary explanations are as much about the environment as they are about biological products. This point is often lost, given that many perceive evolutionary explanations as exclusively “biological” or “genetic” at the exclusion of any environmental considerations. Genes and environment necessarily interact to produce behavior; neither genes nor the environment can exert their influence on behavior without the other.

Another key point is that proximate and ultimate levels of explanation are not at odds with each other (Scott-Phillips, Dickins, & West, 2011; Sherman, 1988; Simpson & Gangestad, 2001; Tinbergen, 1963). Rather, both levels of explanation combine to provide a richer description of the causes of behavior. Many arguments and controversies in the behavioral sciences can be resolved by understanding that valid explanations arise from both proximate and ultimate questions (Scott-Phillips et al., 2011). However, most approaches to understanding behavior (and more specifically, decision-making under risk) have largely ignored ultimate explanations in accounting for behavior (Buss, 1995).

Interestingly, the proximate/ultimate distinction in large part mirrors the descriptive/normative distinction used to characterize decision-making theories. Descriptive theories can give rise to proximate explanations of the causes of decision-making and often stem from systematic violations of normative theories. A solely descriptive approach, however, lacks the primary virtue of normative approaches: The ability to offer ultimate functional explanations of *why* particular patterns of decision-making occur. However, of established normative theories, only risk-sensitivity theory explicitly acknowledges the pursuit of reproductive success and fitness as an overarching goal for decision-making behavior under risk.¹ Other normative theories actually focus on proximal goals (e.g., maximization of utility, usually monetary in nature) rather than ultimate functional goals. As argued earlier, a general theory of decision-making under risk (and theories of behavior more generally) requires both normative and descriptive components. A behavior can never be fully explained by focusing on only the proximate and/or ultimate level of explanation.

The Currency of Decision-Making

An important difficulty in reconciling various frameworks of decision-making under risk is deriving an operational currency of decision-making. It is difficult to understand the perceived or actual costs and benefits of any given decision without describing a single common currency (Daly & Wilson, 2001). Economic and psychological accounts of risky decision-making tend to focus on the maximization of utility, broadly defined. Biological models such as risk-sensitivity theory are concerned with survival and the ultimate enhancement of reproductive success or fitness.

The currency of utility suffers from the problem of being vague and ill defined. It is too easy to argue that utility is

always being maximized in decisions *post hoc* because utility can take many forms (e.g., happiness, monetary outcomes, a feeling of well-being). The currency of fitness at first glance appears to suffer from a similar problem of being difficult to quantify and operationalize in the context of everyday decisions. Fitness strictly refers to the average contribution of a particular individual’s genotype to the gene pool of the next generation (Williams, 1966). However, both human and non-human animals make decisions, on average, as if they were at least somewhat aware of the costs and benefits of a particular course of action with regard to fitness consequences (reviewed in Daly & Wilson, 2001; Kenrick, Griskevicius, Neuberg, & Schaller, 2010). How can individuals make decisions that appear to be, on average, adaptive—seeking to enhance reproductive success and fitness—without being explicitly aware of this motivation?

Both non-human and human decision makers are the functional products of evolution by natural selection. As a consequence, it is necessary to acknowledge the ultimate underlying fitness-relevant motivations that drive all behaviors, including decision-making under risk (reviewed in Buss, 2009a; Confer et al., 2010; Duntley & Buss, 2008). Because all organisms have necessarily evolved to enhance reproductive success and fitness, decision-making mechanisms must be in part calibrated to support this goal (e.g., Aktipis & Kurzban, 2004; Barrett & Fiddick, 1999; Buss, 1995; Daly & Wilson, 2001; McDermott, Fowler, & Smirnov, 2008; Mishra & Lalumière, 2008; Rode & Wang, 2000; Winterhalder et al., 1999).

This functional, evolutionary approach to decision-making is assumed in heuristic approaches centered on ecological rationality. Ecological rationality necessarily reflects the adaptive fit between decision-making tendencies (i.e., fast and frugal heuristics) and environments of decision-making (Todd, 2000; Todd & Gigerenzer, 2012). Recently, some psychologists have called this phenomenon “deep rationality,” referring to the fact that much of decision-making appears to be influenced by evolutionarily relevant motivations (e.g., Kenrick et al., 2009).

Through the lens of natural selection, resources associated with reproductive success or fitness are of utmost importance; these include material resources, social status and respect, and quality mates (Daly & Wilson, 2001).² Throughout evolutionary history, individuals who had plenty of resources, high social status, and quality mates were more likely to reproduce and generate high-quality offspring that were likely to survive compared with those who possessed few resources, low social status, or no mates. Individuals sensitive to these correlates, or proxies, of fitness likely left more descendants than those who were not. Thus, over time, acquiring resources, social status, and mating opportunities have become, through evolution by natural selection, *de facto* goals (or needs) that animals, including humans, aspire to meet.

Because proxies of fitness were necessarily associated with actual fitness in ancestral environments, natural selection

would have facilitated the evolution of psychological systems that were incentivized and motivated by such proxies, thus guiding decision-making. This statement is not controversial in non-human animals, but it is more difficult for many to accept in regard to human behavior. This is not to say that all (or even most) decision-making in the present modern environment is directly (or indirectly) fitness-motivated, or that people continually make explicit cost/benefit calculations about the functional consequences of their behavior. However, it is necessarily true that over the course of evolutionary history, natural selection would have shaped many of the implicit motivations underlying decision-making in both humans and non-human animals, even if they take place in a modern environment that differs from that of ancestral environments. That is, natural selection, on average, would have favored decision-making strategies that enhance reproductive success and fitness over time, without necessarily endowing decision makers with the capacity to be explicitly aware of these underlying functional, evolutionary goals. It is very difficult to quantify and operationalize fitness in the context of people's everyday decisions in modern environments. It is a safe assumption, however, that functional, evolutionary motivations underlie many of the proximate mechanisms that guide everyday decision-making, and that these proximate cues would have been statistically associated with fitness over evolutionary history.³ These proximate cues form the basis of risk-sensitivity theory as it is reconceptualized below.

Needs, Goals, and Motivation: Explicating Risk-Sensitivity Theory

Of the influential theories of decision-making under risk reviewed in this article, only risk-sensitivity theory has received broad and robust empirical support from both human and non-human animal studies (reviewed in Kacelnik & Bateson, 1996, 1997; Mishra & Fiddick, 2012; Mishra & Lalumière, 2010). In spite of this cross-taxa evidence, risk-sensitivity theory has been largely neglected in psychology. This portion of the article seeks to clarify in more detail key mechanisms that comprise risk-sensitivity theory and explicate why they are important for broadly understanding decision-making under risk. In particular, I use life history theory—a framework for understanding how organisms allocate time and energy to essential biological functions—to examine how and when organisms should make risk-sensitive decisions.

Risk-sensitivity theory posits that need motivates decision-making behavior. Need describes disparity between a present state and a goal or desired state (Ermer et al., 2008; Mishra & Fiddick, 2012; Mishra & Lalumière, 2010; Rode et al., 1999; Stephens, 1981). If the disparity between a goal state and a present state increases, individuals should make decisions that seek to bridge that disparity. This is the fundamental mechanism underlying risk-sensitivity theory: If an organism cannot meet its needs with a safe, low-risk

behavioral option, then it should choose a high-risk behavioral option that at least offers a *chance* of meeting that need. Risk-sensitivity theory is a satisficing theory of decision-making, focused on understanding how actors make decisions that meet one's need at any given time as opposed to making "optimal" or maximizing decisions (Mishra & Lalumière, 2010).

Defining need. "Need" may describe either an aspiration level (or goal; Heath, Larrick, & Wu, 1999) or a minimal acceptable threshold (or survival point; March & Shapira, 1992). Some preliminary research has shown that when these two potential motivational levels are pitted against each other, humans prioritize minimal acceptable thresholds (Mishra & Fiddick, 2012). However, both aspirational levels (i.e., wants) and minimal acceptable thresholds (a concept closer to the canonical understanding of "need") have been shown to motivate decision-making in a manner consistent with risk-sensitivity theory: Those at distance from either a want or a need engage in greater risk-taking in pursuit of their goal (Heath et al., 1999; Larrick, Heath, & Wu, 2009; Mishra & Fiddick, 2012). As a consequence, the term *need* is used here and throughout this article simply to describe disparity between a present and a desired (or goal) state (as this definition has been used previously; Ermer et al., 2008; Mishra & Fiddick, 2012; Mishra & Lalumière, 2010; Rode et al., 1999; Stephens, 1981).⁴ Risk-sensitivity theory is therefore broadly relevant to understanding decision-making both for wants (i.e., non-essential motivations; for example, consumer purchases) and canonical needs (essential motivations; for example, survival).

The simple mechanism of risk-sensitivity theory—engage in risk-taking when needs cannot be met with safe, low-risk behavior—is generalizable enough to explain and predict patterns of decision-making under risk under many different circumstances and in many different environments. As a consequence, it is an ecologically rational theory of decision-making. Almost every decision is made under some consideration of need (i.e., disparity between where an individual is, and where they want to be). This conception of need is relevant to individual goals in any of a number of domains, ranging from physical (e.g., bridging the gap between hunger and satiety) to social (e.g., bridging the gap between one's own resources and those of a rival). The concept of need also dovetails well with the currency argument provided earlier: Need represents a proxy of fitness, in that organisms that satisfy their proximate needs would enjoy greater reproductive success and fitness, on average.

Life history theory and domains of need. How do individuals compute and weigh needs in different domains? Life history theory can shed some light on motivational priorities. Life history theory seeks to explain how individuals allocate limited time and energetic resources to various biologically important functions, including survival, growth, reproduction, and parental investment. Life history theory can also

explain how motivations are sequenced across development (Kaplan & Gangestad, 2005; Kenrick & Keefe, 1992; Kenrick & Luce, 2000; Stearns et al., 2008).

A key concept in life history theory is trade-off: Individuals have a finite amount of effort or energy, and so must allocate effort to endeavors that constrain each other, such as number of offspring and degree of parental investment in each offspring (Stearns, 1992). Natural selection favors the allocation of effort or energy contingent on the features of a particular environment (Kaplan & Gangestad, 2005). The end life history product is a developmental plan that determines relative energy and resource allocation to survival, growth, reproduction, and parental investment.

Integral life history tasks follow a relatively rigid developmental hierarchy. For example, survival is imperative before somatic investment (e.g., growth to maturation). Somatic investment must precede reproductive efforts. Reproductive efforts must precede parental investment in offspring. Because of the relatively strict developmental ordering of these biological motivations, it is possible to construct a hierarchy of needs according to developmental timing (Kenrick et al., 2010). “Higher” motivations do not necessarily supplant “lower” motivations in this functional approach: It is possible to continue investing in somatic effort, for example, without sacrificing survival (a key distinction from canonical theories of hierarchical needs, for example, Maslow’s hierarchy of needs; Maslow, 1943). Kenrick et al. (2010) proposed the following functional hierarchy of needs based on life history theory, with more essential needs preceding later needs: (1) immediate physiological needs/survival, (2) self-protection, (3) affiliation, (4) status/esteem, (5) mate acquisition, (6) mate retention, and (7) parenting. In this hierarchy, later needs (e.g., parenting) cannot take place before earlier needs are initially met (e.g., mate acquisition, survival).

This evolutionarily informed hierarchy of needs provides a basic framework for understanding how and when needs motivate decision-making under risk. It is important to reemphasize that allocation of energy and effort is contingent on the features of one’s situation or environment. There are situations in which higher needs will supplant lower ones given the cost–benefit calculus determined by one’s present situation or environment. For example, Wilson and Daly (1997) showed that in Chicago neighborhoods with relatively low life expectancy, women reproduce earlier in life, and men engage in significantly more risk-taking and criminal conduct. In this particular environment, investment in reproduction and survival trade-off, and people behave as if they have calculated that there are greater benefits to reproducing early compared with investing in long-term survival (which, given their local environment, was likely an adaptive pattern of behavior).

The link between life expectancy, reproductive timing, and risk-taking is an example of a well-documented life history trade-off between long-term survival and current

reproduction (Stearns, 1992; Kaplan & Gangestad, 2005). Reproduction is costly both in terms of opportunities and resources. Spending limited energetic resources on reproduction might mean reduced resources for evading predators, finding food, or migrating, for example. The twin-threshold model of risk-sensitivity theory incorporates predictions about decision-making regarding both survival and reproduction (Bednekoff, 1996; Hurly, 2003). This model suggests that decision makers are sensitive to both survival needs and reproductive needs. Risk-proneness may thus be observed when an individual is close to a reproductive threshold: Taking a risk to ensure reproduction may be more beneficial than engaging in risk-averse behavior and potentially losing the opportunity to reproduce at all, even if taking a risk compromises survival (Bednekoff, 1996; Hurly, 2003).

Humans and non-human animals appear to make effective and accurate calculations that take into account different motives and the costs and benefits associated with each in a given environment, leading to attention being paid to different problems at different times (e.g., Ackerman et al., 2009; Neuberger, Kenrick, Maner, & Schaller, 2004; reviewed in Daly & Wilson, 2001; Kenrick et al., 2010). For example, if the potential benefits of immediate reproduction outweigh those of long-term survival, then reproduction motives are favored at the present moment (e.g., Geronimus, 2003; Wilson & Daly, 1997). If one experiences proximate feelings of hunger, it will activate motivational systems associated with satiating immediate physiological needs (in conjunction with other motivations that are ongoing—for example, growth, parental investment). At a higher level, proximity of one’s own children would activate motivational systems associated with parental investment. A comprehensive review of proximate triggers of various motivational systems can be found in Kenrick et al. (2010).

These attentional and motivational mechanisms are relevant to understanding when risk-sensitivity would be invoked in decision-making. Life history theory provides some direction as to when certain needs would be prioritized over others. Regardless of the motivational domain in focus, the mechanism of risk-sensitive decision-making remains the same: If one is far from a desired goal, and cannot reach this goal with a safe, low-risk option, they should engage in increased risk-taking behavior. For a more comprehensive review of the relevance of life history theory to risk-taking behavior, see Mishra and Lalumière (2008).

Relative outcomes. Fitness is relative: To have one’s genes disproportionately expressed in the next generation, it is necessary to outcompete others. As a consequence, proximate motivations underlying decision-making should also be relative. Risk-sensitivity theory by its fundamental structure emphasizes sensitivity to relative outcomes. Specifically, need describes disparity between one’s present and desired states. This calculation of need is necessarily about relative outcomes for an individual. One important commonality

between many of the motivational domains described above is relative social competition. Perception of need can therefore stem not only from consideration of relative outcomes for an individual but also from the comparison of one's present social condition with the social condition of others in a population.

Needs in evolutionarily salient social domains—obtaining material resources, gaining social status, and obtaining mating opportunities—should be primarily defined relative to the accomplishments of others. In humans, evidence suggests that people are particularly sensitive to relative disparity in social domains. For example, most people would prefer a smaller 2,000 square foot house in a neighborhood full of 1,000 square foot houses than a twice-as-large 4,000 square foot house in a neighborhood full of 6,000 square foot houses (Frank, 2000). Similarly, Luttmer (2005) showed that higher earnings of neighbors are associated with lower levels of self-reported happiness (controlling for own income). Relative outcomes should be privileged in decision-making, and the perception of need—disparity between one's present and desired state, where one's desired state is dictated by the state of others—captures this sensitivity to relative standing well, especially in the domain of social competition.

Summary. The historical pursuit of reproductive success and fitness has shaped motivations underlying decision-making in both humans and non-human animals. Decision makers seek to obtain material resources, social status, and mating opportunities that have been correlated with fitness over evolutionary history. Acquiring these correlates of fitness have become needs that individuals aspire to meet. Life history theory can provide a framework for understanding when certain needs are prioritized over others. Risk-sensitivity theory suggests that decision makers should elevate risk-acceptance in situations of need, when low-risk options are unlikely to meet one's needs. Because success in competition is relative, decision makers' levels of perceived need are in part dictated by their relative position compared with others.

Individual Differences and Environmental/Situational Factors

In this section, I review well-validated empirical findings regarding decision-making under risk while operating under the more general overarching frameworks of risk-sensitivity theory and evolutionary theory. The findings reviewed here represent evidence of the causes of risk-taking from both the ultimate and proximate levels of analysis.

Individual differences interact with environmental and situational factors to produce behavior (Dall et al., 2012). Individual differences are largely products of genetics and development. Environmental and situational factors are largely proximate causes of behavior. For ease of exposition, I divide this review of empirical evidence into sections focused on (1) individual differences and (2) environmental/

situational factors. I conclude this section with a discussion of the domain-general and domain-specificity of risk-taking. Given that it would be impossible to review the vast literature on the causes of risk-taking comprehensively, I focus on key findings that have been demonstrably robust, well validated, and replicated.

Individual Differences

Traditional models of decision-making under risk do not adequately address individual differences in risk-propensity. Some conceptions of expected utility theory acknowledge that utility curves can vary in their steepness and degree of curvature. Friedman and Savage (1948), for example, suggested that individual utility curves could change concavity based on income, where decision makers should hypothetically be risk-averse at high and low incomes, and risk-seeking at middle incomes. Others have proposed amendments to expected utility attempting to account for why decision makers are sometimes risk-averse and risk-prone (e.g., rank-dependent expected utility theory; Quiggin, 1982). Regardless, these theories do not provide a normative rationale for why decision makers vary highly in their risk-propensities across different contexts. Here, I review various sources of individual differences, including personality traits, developmental influences, embodied capital, and age and sex differences.

Personality traits. Variability in personality traits such as low self-control, impulsivity, and sensation-seeking has been consistently associated with various forms of risky behavior, including gambling and crime (Blaszczynski, Steel, & McConaghy, 1997; Blaszczynski, Wilson, & McConaghy, 1986; Langewisch & Frisch, 1998; McDaniel & Zuckerman, 2003; Mishra, Lalumière, Morgan, & Williams, 2011; Skitch & Hodgins, 2004; reviewed in Quinsey, Skilling, Lalumière, & Craig, 2004; Toneatto & Nguyen, 2007; Zuckerman, 2007). Furthermore, these individual differences have been demonstrated to exhibit a fair degree of stability over time (Roberts & DelVecchio, 2000), suggesting that personality traits may facilitate, to some degree, stable individual differences in actual risky behavior (Mishra & Lalumière, 2011). Behavioral ecology research further supports this hypothesis, with evidence suggesting that stable individual differences in risk-taking exist in a variety of species (Gosling & John, 1999; Sih, Bell, Johnson, & Ziemba, 2004; reviewed in Mishra, Logue, Abiola, & Cade, 2011).

How do stable individual differences in risk-acceptance arise? Because environments are heterogeneous, there may be many different adaptive optima for various behaviors in any particular environment (Buss, 2009b). For example, variation in selection pressures over time or in different environments may give rise to individual differences in the degree to which a personality trait is expressed. If individual differences in personality traits are relatively stable, then

individual differences in such traits may reflect an attempt to establish different behavioral niches in a stochastic environment (e.g., McDermott et al., 2008; Wolf, van Doorn, Leimar, & Weissing, 2007). Other stable individual differences seem to be under stronger genetic control, perhaps representing facultative strategies in particular social environments (e.g., psychopathy; Lalumière, Mishra, & Harris, 2008; Mishra & Lalumière, 2008).

Developmental influences and embodied capital. Stable individual differences in risk-propensity may also arise as a product of early developmental environments. In humans, cues of poor developmental environments, including poor maternal malnutrition, early head injuries, and other forms of neurodevelopmental perturbation, have been associated with elevated and persistent risky behavior (e.g., Neugebauer, Hoek, & Susser, 1999; reviewed in Anderson, 2007; Harris, Rice, & Lalumière, 2001; Lalumière, Harris, & Rice, 2001; Mishra & Lalumière, 2008). Unpredictable early environments (especially in the first five years of life) have also been shown to predict later risk-taking behavior (E. Hill, Ross, & Low, 1997; Simpson, Griskevicius, Kuo, Sung, & Collins, 2012). These developmental factors typically interact with other social factors to facilitate even more elevated levels of risk-taking (e.g., single-parent upbringing, low socioeconomic status, parental abuse; Griskevicius, Tybur, Delton, & Robertson, 2011; Rutter, 1997). Other cues associated with the social environment, including divorce, lack of social and familial support, high interpersonal competition and inequality, and the lack of a mate, have been associated with various forms of risk-acceptance, including gambling, criminal engagement, promiscuous sexual behavior, school dropout, and substance abuse, among others (reviewed in Mishra & Lalumière, 2008, 2009).

More permanent environmental effects such as neurodevelopmental perturbations (e.g., early head injuries) and poor nutrition during development may serve as cues of disadvantage to a mother and her fetus, facilitating the development of psychological mechanisms calibrated to produce risk-accepting strategies (Mishra & Lalumière, 2008). Variation in risk-acceptance may thus be in part due to variation in embodied capital, which refers to intrinsic attributes such as health or attractiveness that allow for successful competition with others for resources, social status, and mates. Individuals who possess low embodied capital may persistently experience situations of high need, where they are consistently at competitive disadvantage relative to others and must therefore engage in persistent risky behavior to compete effectively. For example, some evidence suggests that life-course persistent offenders (i.e., criminals who show signs of antisocial conduct early in life and persist in antisocial conduct across the life span) exhibit low embodied capital (e.g., Anderson, 2007; Harris et al., 2001; Mishra & Lalumière, 2008; Moffitt, 1993). Experimental studies support these findings, demonstrating that inducing the perception of

competitive disadvantage relative to others in important domains of social competition (e.g., social status, intelligence) facilitates increased risk-taking (Ermer et al., 2008; S. E. Hill & Buss, 2010; Mishra, Barclay, & Lalumière, 2014).

Of course, embodied capital (and other individual differences) necessarily interact with situational and environmental factors to facilitate engagement in risky behavior, and it is always necessary to consider both embodied capital and situational/environmental factors when seeking to explain risk-taking (and behavior more generally). Studies of embodied capital and risk-taking sometimes confound low embodied capital with often-correlated poor social environments (e.g., low socioeconomic status, high inequality, social stress). What appears to be a relationship between embodied capital and risk-taking may therefore instead be a situation where risky behavior is consistently evoked by stable but poor-quality environments (i.e., enduring situational evocation; Buss & Greiling, 1999). If it makes sense for one to engage in risk-taking in poor environments and one is unable to escape a poor environment (regardless of embodied capital), then risky behavior may be engaged in as a recurrent contingent response (e.g., Mishra, Daly, Lalumière, & Williams, 2012).

Age and sex differences. Males are significantly more risk accepting than females in both humans and non-human animals. In a meta-analysis, Byrnes, Miller, and Schafer (1999) found that men engaged in significantly more risk-taking than women in 14 of 16 domains studied. Age also plays an important role in the engagement of risky behavior. The classic age-crime curve shows that individuals age 16 to 24 are substantially more likely to engage in criminal and risky behavior, especially men (Hirschi & Gottfredson, 1983; Wilson & Daly, 1985). Furthermore, risky behavior is largely normative in adolescence and early adulthood in males (Moffitt, 1993).

Wilson and Daly (1985) suggested that young males are particularly likely to engage in risk-accepting behavior because competition for social status, mates, and resources during that period reaches its peak—a phenomenon they termed *young male syndrome*. Furthermore, young males not only compete with each other but also with older males who have had more time to accumulate skills, resources, and social status, all features important to obtaining mating opportunities. Young males are at competitive disadvantage relative to other males (because of youth and relative inexperience) and are in situations of interpersonal competition, and so experience conditions of high need (i.e., disparity between their own position and the position of more privileged others). Thus, risk-taking may be engaged in to try to meet one's social needs in particularly competitive circumstances. In support of this hypothesis, research shows that people are more likely to engage in risky aggressive and criminal conduct if they are unsuccessful at economic competition (e.g., if they are unemployed or expect poor future

economic outcomes; S. E. Hill & Buss, 2010; Raphael & Winter-Ebmer, 2001; Wohl, Branscombe, & Lister, 2014) or at mating competition (e.g., if they are single or less attractive; Campbell, 1995; Daly & Wilson, 1990; Harris et al., 2001; Mishra & Lalumière, 2008; Moffitt, 1993; Wilson & Daly, 1985).

Risk-taking tends to decrease in early adulthood, reflecting changes in the costs and benefits of risky behavior. As risk takers meet their resource, social status, and mating needs, the necessity of risky behavior is reduced. For example, marriage and stable work are reliable correlates of desistance from risky behavior (reviewed in Mishra & Lalumière, 2008). Interestingly, those who lose this stability (e.g., through divorce or being widowed) subsequently exhibit elevated risk-acceptance, suggesting that risk-propensity is plastic and heavily contingent on the environment and perceived situations of need (Daly & Wilson, 2001). Experimental studies have also shown that relatively acute changes in the perception of competitive (dis)advantage facilitate parallel changes in risk-taking behavior (Ermer et al., 2008; S. E. Hill & Buss, 2010; Mishra et al., 2014).

Sex differences in risk-taking, both during adolescence and across the life span, can be similarly explained with a consideration of the costs and benefits of risky behavior in the context of life history theory. In most species, males have a substantially higher potential reproductive rate than females. A male can produce offspring with an almost unlimited number of females, whereas females in most species bear the brunt of parental investment costs and are thus limited by physiology and other constraints (Trivers, 1972). Consequently, the sex that must invest more time and energy into reproduction (usually female) becomes a valuable resource for which members of the other sex (usually male) compete (Clutton-Brock & Vincent, 1991). Furthermore, because pregnant and lactating females are effectively removed from a pool of potential mates, the operational sex ratio is often heavily skewed toward males, facilitating increased male–male competition for the limited number of available females.

Risk-sensitivity theory can explain both age and sex differences in risky behavior. Young males in highly competitive environments tend to escalate risky behaviors in various domains. Because of this highly competitive environment, males often experience relative disparity between their present and desired states, where their desired state is derived from the relative successes of competitors in the domains of resource holding potential, social status, and mating opportunities. Furthermore, young males are disproportionately sensitive to status disparities, and risk-taking often represents a “badge of honor” (Daly & Wilson, 1990, 2001; Wilson & Daly, 1985). Consequently, young males are usually in a situation of higher need compared with females and engage in elevated risk-taking behavior as a consequence. With changing circumstances, the costs and benefits of risky behavior shift, motivating different patterns of risk-acceptance.

Of course, males are not always riskier than females. Although males face circumstances that lead to risk-taking more frequently, certain social environments can create similar circumstances for females. Campbell (1995) demonstrated that females in environments with a scarcity of resource-rich men and high competition from rival women engaged in greater delinquent and risk-taking behavior. This is powerful evidence in support of risk-sensitivity theory: Situations of need predict risk-taking, even if they run counter to typical sex differences in behavior.

Summary. Within most species, some individuals take more risks than others (reviewed in Mishra, Logue, et al., 2011). These individual differences in risk-taking can be explained by risk-sensitivity theory: Those in situations of need engage in greater risk-taking. Developmental influences and social environments dictate that some individuals are more or less competitively advantaged relative to others. Those who are competitively disadvantaged are more likely to take risks because they are less likely to succeed by lower risk means. That is, they are in conditions of high need because they experience disparity between their present state and their desired or goal state (usually determined by the superior competitive ability of others). Individuals who are competitively disadvantaged may be unable to meet their interpersonal, social, reproductive, or resource needs using low-risk options, and may thus have much to gain and little to lose from engaging in risky conduct.

Environmental and Situational Factors

Although stable individual differences clearly play a role in facilitating risky behavior, environmental and situational factors also have a significant role in motivating risk-taking. The ability to change behavior in response to environmental variation can facilitate an adaptive fit between behavior and environment more consistently. Mishra and Lalumière (2010), for example, demonstrated that in situations of low need, individual differences in personality—specifically, self-control, impulsivity, and sensation-seeking—are predictive of risk-prone behavior. In situations with greater need, however, where making a “wrong” decision is particularly costly, individual differences in personality do not significantly account for variance in risky choice. These results suggest that individual differences in risky personality may manifest only when there are low costs. In situations with the potential for high costs, most people, regardless of their personality, behave in a manner predicted by risk-sensitivity theory, exhibiting elevated risky choice in situations of high need (Mishra & Lalumière, 2010).

In non-human animals, a large body of evidence has shown that state-dependent conditions of caloric need (i.e., positive and negative energy budgets) predict risk-taking (reviewed in Kacelnik & Bateson, 1996, 1997). More persistent environmental effects, such as developmental environment, also play

a role in motivating risky behavior. Mishra, Logue, Abiola, and Cade (2011) demonstrated that the quality of hissing cockroaches' developmental environment predicted the emergence of individual differences in risk-acceptance as adults. In other animal studies, researchers have shown that risk-preference is affected by ecology and the structure of resources in the environment. For example, chimpanzees are significantly more accepting of risk than closely phylogenetically related bonobos (Heilbronner, Rosati, Stevens, Hare, & Hauser, 2008). This divergence may be due to differences in foraging sources: Compared with bonobos, chimpanzees forage from riskier and relatively less abundant food sources due to greater intraspecific competition and interspecific competition with gorillas that are prevalent in chimpanzee environments. Evolution by natural selection facilitates adaptive fits between individuals and their environment, and it is absolutely necessary to emphasize the key role of the environment in producing patterns of behavior.

Other research provides evidence for plastic responses in risk-sensitivity in humans based on social environment. Mishra, Daly, et al. (2012) recently demonstrated that participants living in situations of high need (i.e., situations of competitive disadvantage relative to more privileged others) made risk-sensitive decisions that were just as "rational" as more privileged, competitively advantaged people when doing so outside of their everyday impoverished environments. That is, in a neutral laboratory environment, they engaged in risk-taking when they were far from a goal and were risk-avoidant when risk was unnecessary (Mishra, Daly et al., 2012). These results suggest that although those in impoverished environments appear to be risk-persistent decision makers, they may actually be making "rational", risk-sensitive, environmentally contingent decisions that are modifiable with a simple change in environment (i.e., they are in environments that facilitate enduring situational evocation of particular behaviors; Buss & Greiling, 1999).

Environmental parameters unique to humans such as macroeconomic inequality have been shown to lead to increased risk-taking behavior in a number of different domains, including sexual promiscuity (Gold, Kennedy, Connell, & Kawachi, 2002), violence (Morenoff, Sampson, & Raudenbush, 2001), drug and substance abuse (Room, 2005), and crime (Daly, Wilson, & Vasdev, 2001; Wilson & Daly, 1997; reviewed in Wilkinson & Pickett, 2006, 2007, 2009). For example, Wilson and Daly (1997) demonstrated that Chicago neighborhoods with higher local income disparities also experienced higher homicide rates. Individual-level evidence also suggests that victims of income inequality engage in greater risk-taking (Mishra, Son Hing, & Lalumière, 2013). These results are consistent with risk-sensitivity theory. At the individual level, inequality facilitates the perception of need in that victims of inequality are at distance from the desired or goal state of more privileged others. Inequality also captures sensitivity to relative outcomes (as discussed earlier).

Cognitive biases. Cognitive biases are so named because according to canonical understanding, they represent "mistakes" that violate what is considered to be "rational" judgment and decision-making from an expected utility perspective (Tversky & Kahneman, 1974). Tversky and Kahneman argued that cognitive biases were systematic, maladaptive errors that were products of misapplied heuristics. Of course, this understanding did not take into account the idea of ecological rationality. A consideration of human cognition as a product of evolutionary processes leads to a very different understanding of cognitive biases and of "rationality" more generally. In an evolutionary framework, cognitive biases (and the heuristics that give rise to them) can be considered adaptive, ecologically rational responses to recurrent biological problems.

Many different cognitive biases related to decision-making have been described, including framing effects, the salience of certain and rare events, anchoring/focusing effects, availability, and representativeness, among several others. A substantial body of evidence suggests that these effects are robust and replicable, suggesting that any generally applicable theory of risk must be able to account for their observance. Here, I summarize some of the most widely demonstrated cognitive biases and explain how they fit within an evolutionary framework. A full review of cognitive biases in light of evolutionary thinking is beyond the scope of this article, but see Haselton and Nettle (2006); Haselton, Nettle, and Andrews (2005); and Haselton et al. (2009). This section is included under environmental and situational influences because many cognitive biases represent adaptive solutions to recurrent environmental problems.

Framing and loss-aversion. One of the most widely studied cognitive biases is the framing effect. The framing effect describes the phenomenon whereby decision makers shift risk-preference for mathematically identical options that are either framed positively or negatively (e.g., in gain vs. loss frames). Generally, it has been observed that negative frames lead to risk-preference, and positive frames lead to risk-aversion (reviewed in Kühberger, 1998; Levin et al., 1998). Substantial evidence suggests that framing effects in humans are highly replicable, with people reliably exhibiting elevated risk-acceptance in situations of loss and risk-aversion in situations of gain (reviewed in Kühberger, 1998; Levin et al., 1998). Framing effects have also been demonstrated in the behavioral ecology literature: Elevated risk-acceptance in loss situations has been shown in starlings and capuchin monkeys (Chen, Lakshminarayanan, & Santos, 2006; Marsh & Kacelnik, 2002) and full framing effects have been shown in capuchin monkeys (Lakshminarayanan, Chen, & Santos, 2011).

Why do decision makers exhibit different levels of risk-acceptance in differentially framed but mathematically identical problems? As described earlier, fitness-related motivations likely drive much of behavior, and individuals

should make decisions that are sensitive to such motivations. In the context of fitness and survival, marginal losses are significantly worse than marginal gains: Not reproducing (or not surviving due to lack of calories) is substantially worse than increasing fitness slightly (or being slightly more satiated). As a consequence, individuals should have evolved to be particularly sensitive to the prospect of facing losses compared with facing gains. A large body of animal and human evidence suggests greater sensitivity to losses compared with gains, and indeed, such an observation is coded into prospect theory (e.g., Ariely, Huber, & Wertenbroch, 2005; Kahneman & Tversky, 1984; Marsh & Kacelnik, 2002).

Loss-aversion may also account for anchoring or focusing effects in decision-making, whereby decision makers emphasize particular dimensions of a decision and discount others. For example, people tend to focus on the negative aspects of a decision over positive aspects. Negative outcomes are more salient in decision-making than positive outcomes. As a consequence, both the anchoring/focusing effect and negativity bias may represent manifestations of loss-aversion or cost-avoidance.

Loss-aversion may also explain decision makers' tendency to overestimate the salience of both certain and rare events (e.g., Hertwig, Barron, Weber, & Erev, 2004). High probability events should be treated as salient because near-certainty is particularly valuable in stochastic environments. Rare events should also be disproportionately influential in decision-making because of the potential of experiencing a very large gain or a very large loss. For example, people consistently overestimate the probability of winning the lottery and the probability of such catastrophic events as terrorist attacks (Armantier, 2006; Taleb, 2010).

Availability and representativeness. Two of the most widely known heuristics that have been argued to lead to cognitive biases are the availability heuristic and the representativeness heuristic. The availability heuristic describes the phenomenon whereby people tend to assess the probability of the occurrence of an event based on the ease with which an example can be brought to mind (e.g., the likelihood of a plane crash; Tversky & Kahneman, 1973). The representativeness heuristic describes the phenomenon whereby people tend to assess the probability of the occurrence of an event based on how representative an exemplar is compared with the general population (i.e., ignorance of base rates; Kahneman & Tversky, 1972). The representativeness heuristic has been argued to be the source of both the gambler's fallacy (the perception that certain probabilistic outcomes are "due"; for example, obtaining tails from a series of coin flips after a number of heads) and the "hot hand" phenomenon (the perception that outcomes are clumpy; for example, a basketball player being perceived to be successfully making a high percentage of shots in a period of time because of "momentum").

Wilke and Barrett (2008) argued that because natural resources tend to be clumpy (e.g., food resources such as

berries or potential prey), the representativeness heuristic (especially the "hot hand" phenomenon) reflects an evolved default assumption that natural resources in the world occur in clumps and are not truly random. Wilke and Barrett empirically demonstrated that people assume "clumpiness" of resources in foraging analogues involving fruits, coin tosses, and other resources that were actually distributed randomly. Similarly, Scheibehenne, Wilke, and Todd (2011) showed that people betting on binary events predicted more streaks than would be expected by chance. Furthermore, people exhibited what appeared to be a win-stay/lose-shift strategy, which is adaptive in clumpy environments (as shown in behavioral ecology research; e.g., Nowak & Sigmund, 1993). The availability heuristic may also similarly represent cognition tuned to ancestral environments where events were likely to happen in clusters; for example, a fatality due to a predator attack was probably likely to recur in a short amount of time in a given geographical area. Together, this growing area of research suggests that various cognitive biases may not be "irrational" errors of judgment and decision-making. Rather, such biases may instead represent adaptive manifestations of cognitive defaults sensitive to the structure of information in historical natural environments (reflecting ecological rationality; Todd, 2000; Todd & Gigerenzer, 2000, 2012).

Emotions. Normative theories of decision-making under risk have largely neglected the role of emotions in decision-making, and it has been argued that emotions distort "rational" decision-making processes.⁵ However, emotions have systematic effects on decision-making behavior. Negative emotional states have been generally associated with increased risk-taking (e.g., Fessler, Pillsworth, & Flamson, 2004; Leith & Baumeister, 1996; Mishra, Morgan, Lalumière, & Williams, 2010), and positive emotional states have been generally associated with risk-aversion (albeit inconsistently; De Vries, Holland, & Witteman, 2008; Hills, Hill, Mamone, & Dickerson, 2002; Isen & Patrick, 1983). Isen and Patrick (1983) introduced the mood-maintenance hypothesis to explain these findings. Specifically, they suggested that people in a positive mood avoid risk to maximize the likelihood of maintaining their positive mood, and people in a negative mood seek risk in an attempt to obtain gains that might ameliorate their negative mood (Arkes, Herren, & Isen, 1988; Isen, Nygren, & Ashby, 1988).

Other research, however, suggests that the effects of emotions on decision-making cannot be neatly separated based on positive and negative valence. Rather, different emotions may impact cognitive appraisals of various decision options in specific ways (Lerner & Keltner, 2000, 2001; Loewenstein, Weber, Hsee, & Welch, 2001). An evolutionary approach suggests that emotions guide decision-making in ways that would have been associated with biological fitness (Ekman, 1992; Fessler et al., 2004). In this sense, it is not necessarily useful to separate the effects of positive and negative

emotions (e.g., happiness vs. sadness) but rather to examine which emotions might motivate decision-making and behavior to solve adaptive problems. For example, fear and anger are both negative emotions. However, fear is designed to heighten sensitivity to threat, motivating escape in the search for safety and thus facilitates risk-aversion (Levenson, 1999; Oehman & Mineka, 2001). In contrast, anger is a response to social transgressions, motivating aggression and elevated risk-acceptance more generally (Fessler et al., 2004; Levenson, 1999; McGuire & Troisi, 1990).

In the context of risk-sensitivity theory, what emotions would be most important? Need describes disparity between a present and a desired state. People in a state of need should therefore feel relatively deprived, where relative deprivation describes subjective feelings of resentment, dissatisfaction, and anger associated with the perception of being deprived of a deserved outcome relative to others (Bernstein & Crosby, 1980). In support of this hypothesis, feelings of relative deprivation have also been associated with increased gambling behavior (Callan, Ellard, Shead, & Hodgins, 2008; Callan, Shead, & Olson, 2011; Mishra, Daly, et al., 2012). The valence components of relative deprivation—specifically, frustration, resentment, and anger—have also all been associated with increased risk-taking behavior (e.g., Fessler et al., 2004; Leith & Baumeister, 1996). Other negative emotions that are not as closely linked with relative deprivation, such as sadness (and its more extreme form, depression), have not been linked with increased risk-taking but rather risk-aversion (e.g., Yuen & Lee, 2003).

Individuals in situations of need may also perceive the relative costs and benefits of decision options in different ways due to differential affect. People in conditions of high need may de-emphasize the high probability of losses and emphasize the small possibility of large gains involved in a high-risk decision. This change in perceived cost-benefit ratio may in turn change the affective properties of a particular decision option (e.g., Loewenstein et al., 2001). People in conditions of high need may “feel” better about risky decisions and consider them more attractive as a result. Some risky decisions, such as choosing to engage in property or violent crime, may not necessarily “feel” like a pleasant option, but rather, they may feel exciting, or at least “less worse” than other less risky options. As such, decision-making motivated by affect may facilitate making the best of particular circumstances (i.e., satisficing).

Summary. Numerous environmental and situational factors that reliably affect risk-taking have been identified. These factors generally represent proximate causes of risk-taking behavior. Using an evolutionary framework, it is possible to understand such phenomena as cognitive biases and emotional reactions as adaptive responses to recurrent environmental problems. More specifically, cognitive biases (e.g., loss-aversion) and emotions associated with relative deprivation (e.g., anger, frustration, resentment) appear to facilitate

adaptive patterns of decision-making largely consistent with risk-sensitivity theory.

Domain-Specificity of Risk-Taking

Many evolutionary psychologists subscribe to the view that the mind consists of a collection of domain-specific adaptations, each designed to solve a different problem (e.g., Barrett & Kurzban, 2006; Cosmides & Tooby, 1994). Others argue that human problem-solving capacities are so flexible because domain-general cognitive machinery (e.g., learning) exists alongside more constrained domain-specific adaptations (e.g., incest avoidance, social exchange; Cosmides, 1989; Lieberman, Tooby, & Cosmides, 2007). Is risk-taking a domain-general or domain-specific phenomenon?

Substantial evidence suggests that various forms of risky behavior, including crime, gambling, substance use, dangerous driving, sexual risk-taking, and antisocial behavior tend to co-occur within individuals (e.g., Bartusch, Lynam, Moffitt, & Silva, 1997; Donovan & Jessor, 1985; Hirschi & Gottfredson, 1994; Jones & Quisenberry, 2004; LeBlanc & Girard, 1997; Lussier, LeBlanc, & Proulx, 2005; Mishra & Lalumière, 2009; Mishra, Lalumière, Morgan, & Williams, 2011; Mishra, Lalumière, & Williams, 2010; Osgood, Johnston, O'Malley, & Bachman, 1988). Furthermore, individuals who regularly engage in various forms of risk-taking (including gambling and crime) consistently score higher than others on measures of poor self-control, impulsivity, and sensation-seeking (reviewed in Zuckerman, 2007). In non-human animals, stable individual differences in boldness (analogous to individual differences in risk-propensity in humans) have been also largely been shown to be domain-general (reviewed in Sih et al., 2004). Although these findings suggest that risk-taking is domain-general, a growing body of evidence suggests that risk-taking is instead domain-specific (e.g., Blais & Weber, 2006; Hanoch & Gummerum, 2011; Hanoch, Johnson, & Wilke, 2006; Johnson, Wilke, & Weber, 2004; Kruger, Wang, & Wilke, 2007; Wang, Kruger, & Wilke, 2009; Weber, Blais, & Betz, 2002; Weller & Tikir, 2011). How can the domain-general and domain-specific views of risk-taking be reconciled?

Proponents of the domain-specific view argue that risk-taking can be best understood using a risk-return framework (Weber, 2001; Weber & Milliman, 1997). The risk-return framework posits that risk-taking is a function of the perceived costs and benefits of risk-taking, with the acknowledgment that decision makers vary in their individual propensities for risk (e.g., via personality traits such as impulsivity or self-control). Because individuals vary in their perceptions of the costs and benefits of risks in different domains (e.g., financial vs. recreational; Weber et al., 2002), it is therefore argued that decision makers exhibit domain-specific patterns of risk-taking (Hanoch et al., 2006).

The risk-return argument for the domain-specificity of risk-taking can be reconciled with empirical evidence

suggesting that risk is domain-general by considering the role of competitive (dis)advantage. Unnecessary risk-taking is costly. Therefore, an individual's risk-taking would be maximally adaptive if it was attuned to specific environmental and situational circumstances. For example, someone competitively disadvantaged in Environment A, but not in Environment B, should engage in greater risk-taking in Environment A and not in Environment B (given the downside costs of risky behavior). This hypothesis has been supported by research suggesting that as perceptions of competitive advantage change within individuals, so too does their risk-propensity (Ermer et al., 2008; S. E. Hill & Buss, 2010; Mishra et al., 2014; Wohl et al., 2014). This argument can be extended to address domain-specificity: If in Domain A the benefits of risk-taking outweigh its costs, and in Domain B the costs of risk-taking outweigh its benefits, then it would be most adaptive for one to be risk-prone in Domain A and risk-averse in Domain B.

Possessing low embodied capital may lead someone to be consistently competitively disadvantaged in numerous domains relevant to reproductive success, leading to what appears to be domain-general risk-taking. Poor developmental environments are associated with lower overall embodied capital (e.g., Gluckman & Spencer, 2004; Gluckman, Hanson, & Spencer, 2004; Lummaa, 2003; Mishra & Lalumière, 2008), and low embodied capital is associated with domain-general criminal and risk-taking behavior (e.g., Harris et al., 2001; Mishra & Lalumière, 2008; Moffitt, 1993; but see psychopathy as an exception; Lalumière et al., 2008). Research also suggests that various facets of embodied capital tend to covary with each other (e.g., intelligence and attractiveness; Case & Paxson, 2006; Kanazawa, 2011; Langlois et al., 2010). Even more time-limited explanations for risk-taking (e.g., the "young male syndrome") are consistent with this process: Young males are at competitive disadvantage relative to more established, older males in a number of domains (e.g., resource holding potential, social status, embodied capital) and consequently engage in what appears to be domain-general risk-taking (Daly & Wilson, 1990; Wilson & Daly, 1985; reviewed in Quinsey et al., 2004), although this condition will typically dissipate over developmental time as disparities in competitive (dis)advantage diminish.

If, however, decision makers were not consistently competitively disadvantaged relative to others in multiple domains, or experienced competitive disadvantage in some domains but not others, then domain-specific risk-taking would be expected. For example, people with higher economic need (i.e., people who are poor compared with relevant others, or victims of inequality) are more likely to engage in pathological gambling, a risky behavior that exposes one's financial resources to high variance outcomes (e.g., Callan et al., 2008; Callan et al., 2011). Those with lower incomes relative to others are also significantly more likely to spend a large proportion of their income on more general gambling behavior, including the purchase of lottery

tickets (e.g., Blalock, Just, & Simon, 2007; MacDonald, McMullan, & Perrier, 2004; Welte, Wieczorek, Barnes, & Tidwell, 2006). Such individuals may be competitively disadvantaged in a financial sense but not necessarily in other domains (e.g., attractiveness, intelligence) and may thus show domain-specific risk-taking.

The theoretical perspectives and evidence reviewed above suggest that risk-taking is by default domain-specific but can manifest as being domain-general. This approach is fully consistent with risk-sensitivity theory: If decision makers find themselves to be in a condition of need (i.e., experiencing disparity between where they are and where they want to be), they will engage in risk-taking. This can manifest in a domain-specific manner (e.g., economic need leading to economic risk-taking; Wohl et al., 2014) or in a domain-general manner (e.g., low embodied capital leading to domain-general competitive disadvantage and subsequent domain-general risk-taking; Mishra & Lalumière, 2008).

Evidence from the behavioral ecology literature suggests that non-human animals exhibit both stable individual differences in risk-propensity (i.e., "behavioral syndromes"; Mishra, Logue, et al., 2011) and sensitivity to environmental and situational factors that lead to increases or decreases in risk-taking (e.g., Kacelnik & Bateson, 1996, 1997; Stephens, 1981; Stephens & Krebs, 1986). Stable individual differences may lead to domain-general risk-taking (Mishra, Logue, et al., 2011), whereas situational factors may lead to what would appear to be domain-specific risk-taking (Kacelnik & Bateson, 1996, 1997). As argued earlier, for both humans and non-human animals, individual differences should interact with situational and environmental factors to produce risk-taking behavior. The domain-specific/domain-general nature of risk-taking is a relatively nascent area of research, however, and further research is required to shed light on these mechanisms. Importantly, the theoretical perspectives and evidence reviewed here suggest that domain-general and domain-specific interpretations of risk-taking are not necessarily at odds with each other, and both are consistent with risk-sensitivity theory.

Summary

Both individual differences and environmental/situational factors associated with risk-taking behavior have been identified. Stable individual differences in risk-preference can arise from personality traits associated with risk (e.g., low self-control, impulsivity, sensation-seeking), developmental influences and individual differences in embodied capital, and age and sex differences. All of these mechanisms giving rise to individual differences are consistent with risk-sensitivity theory, in that individuals who are competitively disadvantaged or in situations of high need relative to others tend to engage in greater risk-taking.

Various environmental and situational factors have also been identified that consistently influence risk-taking

behavior. These include developmental environment, immediate social environment, cognitive biases, and emotions. In all cases, risk-taking behavior appears to be plastic and largely sensitive to environmental inputs. This is consistent with risk-sensitivity theory, in that circumstances that facilitate the perception of need should also be associated with greater risk-taking (e.g., loss-aversion, inequality, feelings of relative deprivation, and many other proximate factors). Finally, evidence suggests that risk-taking can be considered both domain-specific and domain-general. Risk-sensitivity theory suggests that decision makers should elevate risk-taking in response to conditions of need in a domain-specific manner. However, domain-general risk-taking may be observed if individuals experience conditions of need in multiple different domains simultaneously (e.g., because one possesses low embodied capital) and subsequently engage in risk-taking in multiple different domains.

Reconciling Theories of Decision-Making

Given the necessity of integrating normative evolutionary/functional explanations for decision-making under risk, and given the large body of descriptive evidence for actual patterns of decision-making under risk, how can various theories of decision-making be reconciled? Risk-sensitivity theory is the only theory of decision-making under risk that explicitly integrates the ultimate-level pursuit of reproductive success or fitness into its goal structure. As a consequence, it is an excellent starting point for building an integrated, comprehensive theory of decision-making. However, there is significant overlap between the predictions of risk-sensitivity theory and other dominant theories of risk from other disciplines. The definition of utility used in expected utility theory and prospect theory, for example, can be reconceptualized to be more ecologically valid and more specific and thus more compatible with risk-sensitivity theory (Okasha, 2011). Similarly, various mechanisms of decision-making in prospect theory dovetail nicely with mechanisms explicated in risk-sensitivity theory. In this section, I examine the overlap between risk-sensitivity theory and other theories of decision-making under risk in the search for general integration.

Expected Utility Theory

Expected utility theory posits that decision makers seek to maximize utility in all decisions, where utility is broadly defined as a measure of happiness, gratification, or satisfaction derived from a behavior (Friedman & Savage, 1952). Expected utility theory suffers from three primary problems. First, the theory uses a vague currency of decision-making in the form of utility. It is possible to describe any decision as being utility-maximizing *post hoc* by highlighting different

axes or dimensions of utility, and thus expected utility theory is not predictive. Second, although there are some stable individual differences in decision-making under risk, these individual differences interact with environmental and situational factors to produce behavior (as reviewed above). Consequently, the same individuals can be risk-prone or risk-averse in different situations. This observation is a key tenet of other theories of decision-making. Expected utility theory, however, suggests that individuals make decisions that are perfectly consistent with a single utility curve (i.e., they are consistently risk-seeking or risk-averse) and with several rigid preference axioms. Third, decades of research have shown that decision makers behave in ways that are not perfectly “rational,” as expected utility theory would predict. Instead, decision makers appear to make decisions that are consistent with the notion of bounded rationality, where decision-making mechanisms reflect the realities of time and cognitive resource constraints.

Given these shortcomings, how can expected utility theory be contemporized and integrated with other theories of decision-making and reconciled with the large body of evidence on actual descriptive patterns of decision-making? A key step would be to reconceptualize what utility means. An ecologically relevant, functional conception of expected utility theory would distill the currency of utility from various different domains of behavior into their effect on reproductive success or fitness (Daly & Wilson, 2001; Kenrick et al., 2009). Maximizing utility can thus simply be conceptualized as seeking outcomes that have been historically correlated with enhanced reproductive success and fitness—specifically, the pursuit of social status, material resources, and mating opportunities. This definition is not necessarily at odds with the economic definition of utility but rather reframes it into a more ecological and broadly relevant context (e.g., Okasha, 2012; Orr, 2007; Stearns, 2000). Using this conception of utility, the examples provided at the beginning of the article—trading commodities on the stock market, animal foraging, asking someone out on a date, or aggression between individuals—all involve utility maximization in that they all have some association with proxies of fitness (in these examples, manifesting through resource acquisition, mate choice, and interpersonal competition; Daly & Wilson, 2001).

Some aspects of expected utility theory, however, cannot be reconciled with actual patterns of decision-making under risk or other theories of decision-making under risk. For example, the rigidity of utility curves simply does not hold—decision makers are not consistently risk-prone or risk-averse. Decision makers also do not consistently conform to the five preference axioms put forth by von Neumann and Morgenstern (1944). As a consequence, expected utility theory is necessarily limited in its explanatory scope, even with a reconceptualization of utility in more relevant and concrete ecological terms.

Prospect Theory

Risk-sensitivity theory dovetails nicely with prospect theory and can provide a normative account for loss-aversion and framing effects more generally. In fitness terms, marginal losses are much more significant than marginal gains of a similar magnitude; the prospect of not reproducing at all is substantially worse than increasing fitness slightly (Aktipis & Kurzban, 2004; McDermott et al., 2008). A marginal gain in resources may increase the probability of reaching some higher reproductive threshold (Bednekoff, 1996; Hurly, 2003) or experiencing a longer survival time horizon (Aktipis & Kurzban, 2004; McDermott et al., 2008), but a marginal loss could push an organism closer to death or being unable to reproduce (Stephens, 1981; Stephens & Krebs, 1986). As a consequence, it would be adaptive for individuals to be significantly more sensitive to resource losses than to resource gains. This mechanism would explain the function of such cognitive biases as loss-aversion, the focusing effect, and the negativity bias, all of which facilitate sensitivity to outcomes involving loss.

Risk-sensitivity theory predicts that individuals switch from risk-aversion to risk-proneness in circumstances of high need. This finding is compatible with prospect theory, in that risk-proneness is observed in situations of potential loss (a situation analogous to high need) and risk-aversion is observed in situations of potential gain (a situation analogous to low need). As a consequence, the utility curve that arises from prospect theory can be similarly used to describe risk-sensitive behavior in situations of low need (a domain of marginal gains) and situations of high need (a domain of marginal losses).

Risk-sensitivity theory posits that decision makers seek certain outcomes (i.e., meeting one's needs) while also seeking to minimize the probability of experiencing outcomes that fail to meet their needs (Rode et al., 1999; Stephens, 1981). This prediction mirrors the logic of prospect theory, where decision makers engage in risk-taking to seek gain but not at the cost of loss (Tversky & Kahneman, 1981). Tversky and Kahneman suggested that reference points (around which gains and losses are defined) are derived from an individual's present state but can change based on expectations or biases of decision makers. As a consequence, the reference point in prospect theory may be considered analogous to a need threshold, in that it represents a desirable boundary condition.

If an individual is presently below a reference point, they may perceive themselves to be in a situation of high need. If an individual is presently at or above a reference point, they may perceive themselves to be in a situation of low need (see Mishra & Fiddick, 2012). Thus, the classic finding that decision makers are risk-averse in the face of gains and risk-prone in the face of losses in framed decision scenarios may be a by-product of decision makers seeking to minimize the possibility of experiencing a negative outcome that does not

meet their needs. Decisions framed in terms of losses confer the perception of high need, supporting this hypothesis (Mishra & Fiddick, 2012; Wang, 2002).

Heuristic Approaches

Most decision-making is quick and efficient. Therefore, any broad theory must acknowledge that decision-making is made under time and cognitive constraints (i.e., decision-making must reflect bounded rationality). Furthermore, most decisions are made in domains that were recurrently important over evolutionary history (i.e., involving mates, resources, and social status; Kenrick et al., 2010). The reality of these constraints suggests that most decision-making is likely heuristic based and that the heuristics used are fast and frugal. Finally, decision-making mechanisms must necessarily be ecologically rational. Ecologically rational decision-making must (1) exploit the structure of information in the environment, increasing the efficiency of decision-making, and (2) be simple and generalizable enough to be robust in stochastic environments (Todd & Gigerenzer, 2000, 2012). These are necessary conditions for any broad theory of decision-making under risk, and these two conditions are well met by risk-sensitivity theory.

Many decision-making paradigms used to model choice behavior in humans are not particularly ecologically valid, in that they only reflect decision-making from description. Decision-making from description involves providing decision makers with explicit information about the parameters of different choice options (e.g., mean, variance, probability). However, most real-world decision-making involves decisions from experience, where decision makers implicitly learn the yield characteristics of a wide array of decision options through interaction with their environments (Hertwig et al., 2004). Therefore, any broad theory of decision-making must be predictive of behavior involving decision-making from experience.

Recent research indicates that people can effectively make risk-sensitive decisions under need involving decision-making from experience (e.g., Mishra, Daly, et al., 2012; Mishra, Gregson, & Lalumière, 2012; Mishra & Lalumière, 2010). More importantly, risk-sensitivity theory is the only theory of decision-making under risk that enjoys substantial support in both human and non-human animal populations (reviewed in Bateson & Kacelnik, 1998; Kacelnik & Bateson, 1996, 1997; Stephens, 1981; Stephens & Krebs, 1986). Non-human animal decision preferences must necessarily reflect decision-making from experience, and as such, this evidence represents strong support for the ecological rationality of risk-sensitivity theory. Together, this cross-taxa body of evidence shows that risk-sensitive decision-making conforms to the first requirement of ecological rationality, whereby decision makers consider different options by exploiting the natural structure of information in the environment.

The second tenet of ecological rationality is robustness in the face of stochastic and variable environments. Decision makers have to make decisions across various domains and in situations with incomplete decision information (i.e., most ecologically relevant decisions involve some notion of uncertainty). Therefore, the most effective decision-making heuristics must balance environmental specificity with domain-generalizability. Specific decision-making rules and heuristics typically require several precise decision parameter inputs and are often specifically fixed to particular types of decisions (e.g., only framed decisions; Brandstätter et al., 2006). Although domain-specific heuristics may be effective in explaining choice behavior under specific constrained situations, they generally fail in explaining behavior across various contexts or in situations where only incomplete information is available (i.e., domain-specific heuristics are typically “overfitted” to specific problems; Gigerenzer et al., 1999; Todd & Gigerenzer, 2000, 2012).

Need-based decision-making as specified by risk-sensitivity theory is a heuristic approach that accomplishes a balance between environmental fit and flexibility. According to risk-sensitivity theory, decision makers acquire environmentally specific information about decision options from experience (i.e., discovering mean and variance of outcomes through implicit learning) and must simply choose an option that is likely to meet their needs in a particular domain (where needs are constructed with some consideration of life history and social comparison; see earlier). This risk-sensitive satisficing heuristic centered around meeting one’s needs is able to explain choice behavior in numerous domains, including foraging (Kacelnik & Bateson, 1996, 1997), mate choice (Baker & Maner, 2008), and status-seeking behavior (Ermer et al., 2008; S. E. Hill & Buss, 2010). Need-based risk-sensitive decision-making fulfills the goal of elucidating a mechanism of decision-making under risk that is able to explain choice in both human and non-human animals across various domains.

Summary

Although decision-making under risk has been variably studied in multiple different disciplines, these different perspectives are generally more consilient than they are different. This is not particularly surprising given that effective theories of decision-making under risk must necessarily converge if they accurately explain observed patterns of real-world behavior. Risk-sensitivity theory serves as an excellent starting point for an integrated theory of decision-making because it (1) acknowledges the pursuit of reproductive success and fitness as a fundamental motivation, (2) is supported by a broad body of evidence in both humans and non-human animals, and (3) reflects ecological rationality. Risk-sensitivity theory can be reconciled in part with expected utility theory if the currency of utility is reconceptualized as the pursuit of reproductive success and fitness. Prospect theory and risk-sensitivity theory make identical predictions if reference

points are considered analogous to need levels. Ecologically rational heuristic approaches are inclusive of the mechanisms of risk-sensitivity theory. Together, an integrated, interdisciplinary approach to decision-making should be productive in shedding light on real-world patterns of decision-making in multiple contexts.

Risk-Sensitivity Theory and Future Research

The primary virtue of the risk-sensitivity theory approach to understanding decision-making under risk is its broad generality and fit in multiple environments for all individuals. As described above, substantial evidence suggests that risk-sensitivity theory can account for patterns of decision-making in a wide array of domains. However, risk-sensitivity theory may be criticized as being *too* general, which in principle makes it difficult to falsify. However, risk-sensitivity theory is valuable precisely because of its generality—a simple mechanism of risk-taking when an organism is at distance from a desired goal or outcome can account for a broad array of behavior in many different domains. Furthermore, this central mechanism is easily operationalizable, testable, and falsifiable because of its simplicity.

Operationalization of risk-sensitivity theory for empirical examination requires three components. First, researchers must identify a domain (or domains) of need relevant to risk-preference. Need is strictly defined as disparity between one’s present and desired (or goal) states, so some measurement of perception of the components that make up need (or some direct experimental manipulation of need) is necessary. Second, researchers must identify or provide potential decision options that differ in risk (i.e., variability in outcome). Third, researchers should examine whether risk-preference is higher in situations of high need versus those of low need. Risk-sensitivity theory is general in its potential explanatory scope. However, this is a strength of the theory: With a few simple parameters, it is possible to make precise predictions about expected behavior regarding preferences for risk in a given context. Furthermore, because need is strictly defined as disparity between one’s present and desired (or goal) states, but can manifest in multiple domains, there is freedom in how to manipulate and measure perceptions and objective manifestations of need. Together, these well-defined parameters allow for the generation of a wide array of empirically testable and falsifiable hypotheses.

The most valuable theories of behavior allow for the generation of hypotheses that lead to research that reveals new, unexpected, and otherwise “invisible” phenomenon. This is the primary virtue of evolutionary theory in explaining human behavior, for example—phenomenon as broad as menstrual cycle influences on behavior (e.g., Gangestad & Thornhill, 2008), kin recognition (e.g., Krupp, DeBruine, Jones, & Lalumière, 2012), and adaptive perceptual biases for heights (e.g., Jackson & Cormack, 2007) would have

gone otherwise undiscovered without the use of an evolutionary framework (reviewed in DeBruine, 2009). Similar novel predictions are possible from risk-sensitivity theory.

For example, earlier, I summarized a study where it was demonstrated that people from poor socioeconomic backgrounds who appear to persistently engage in high levels of risk-taking (e.g., problem gamblers, ex-convicts, drug addicts) are actually risk-sensitive decision makers (Mishra, Daly, et al., 2012). The typical lay assumption is that risk-persistent individuals are “fixed” into a stable and persistent pattern of reckless and maladaptive risk-taking as a consequence of biological, developmental, or social influences. However, risk-sensitivity theory suggests that taking should be an adaptive, plastic response to situations of need and should be sensitive to changing environmental and situational factors. In this study, risk-persistent people who were brought into a neutral environment (away from their typical environments of decision-making) made risk-sensitive decisions that did not differ from more privileged risk-averse populations. That is, people who appeared to be risk-persistent based on their day-to-day behavior made “rational” risk-sensitive decisions independent of their socioeconomic background. These results suggest that real-world risk-taking may in part be the result of a flexible behavioral response sensitive to modifiable costs and benefits in the environment. This research has important implications for policy and for understanding patterns of decision-making, but may have otherwise gone uninvestigated without the theoretical framework of risk-sensitivity theory.

Research directly examining risk-sensitivity preferences in humans is still scarce. However, early research is promising: Some studies have shown that risk-sensitivity theory can account for remarkably high variance in decision-making under risk (e.g., Mishra & Lalumière, 2010; Rode et al., 1999). Because risk-sensitivity theory is so broad, however, it is important to test the predictive and explanatory bounds of the theory. Important limitations to risk-sensitivity theory have already been noted in the behavioral ecology literature (e.g., Kacelnik & Bateson, 1996, 1997; Kacelnik & El Mouden, 2013). Given the preliminary state of risk-sensitivity theory research in humans, the explanatory bounds of the theory have not yet been determined. These bounds will only be discovered through future research. For example, no research has yet examined how developmentally determined, stable individual differences in embodied capital interact with more transient environmental/situational needs to influence decision-making under risk. Our understanding of risk-sensitivity theory (and decision-making under risk more broadly) will certainly improve as a more comprehensive body of research centered on risk-sensitivity theory develops.

General Summary

Various theories of decision-making under risk have been developed in disparate fields. However, little attempt has been

made to integrate these different theories and find common explanatory ground. This review and integration suggests that various influential theories of decision-making under risk share many important features and can be understood together using an evolutionary framework conceptualizing utility as a measure of proxies of reproductive success and fitness. Although expected utility theory and prospect theory remain influential theories of decision-making under risk, more effort must be invested to try and contemporize these theories with a modern understanding of behavioral motivations shaped in large part by natural selection. Risk-sensitivity theory serves as an excellent framework for understanding decision-making under risk, in that it explicitly acknowledges the pursuit of proxies of fitness in its goal structure, and provides a simple, ecologically relevant mechanism to describe patterns of decision-making in a wide array of contexts.

To summarize:

1. Expected utility theory, prospect theory, risk-sensitivity theory, and heuristic approaches are four of the most influential frameworks for understanding decision-making under risk in the behavioral sciences. All suffer shortcomings, but have varied strengths in predicting and explaining real-world decision-making under risk.
2. Humans, like all other animals, are products of evolution by natural selection. As a consequence, decision-making under risk must necessarily be in part understood as a product of functional, evolutionary processes.
3. Decision makers do not explicitly seek to maximize reproductive success and fitness itself but rather seek to achieve goals that have been historically correlated with reproductive success and fitness, such as obtaining quality mates, resources, social status, and reputation.
4. Proximate goals associated with reproductive success and fitness are relative. Instead of seeking to maximize absolute outcomes in various evolutionarily relevant domains, decision makers seek to maximize the probability of meeting their needs in these domains.
5. In social competition, individuals make satisficing decisions that render them in an advantaged position relative to others whenever possible.
6. Life history theory can provide a hierarchical understanding of what needs (e.g., survival, affiliation, reproduction) should be prioritized in different developmental, environmental, and social contexts. An individual's present physiological or psychological state and the relative condition and possessions of others both play an important role in determining need perception in various domains.
7. Both stable individual differences and situational/environmental factors are associated with consistent

patterns of risk-taking. Both can be effectively understood through the lens of risk-sensitivity theory.

8. Need derived from low embodied capital and perceived competitive disadvantage can explain some commonly observed patterns of risk-taking, including individual differences in risk-preference. Need in the context of competitive disadvantage can also explain patterns of risk-taking that are both domain-specific and domain-general.
9. Such environmental and situational factors as cognitive biases and emotions play an important role in decision-making. Specifically, loss-aversion and many other cognitive biases are consistent with decision-making motivated by conditions of need.
10. If utility is defined by proxies of fitness, and fitness is enhanced by meeting one's needs in evolutionarily salient domains (where needs are analogous to reference points), then both expected utility theory and prospect theory make similar predictions about decision-making behavior as risk-sensitivity theory.
11. Decision-making designed to maximize the probability of meeting one's needs is compatible with the notion of ecological rationality. Specifically, need-based decision-making uses cognitive mechanisms that are sensitive to the structure of information in the environment and are simple enough to allow for generalization.

Risk-sensitivity theory emphasizes that risk-taking is not necessarily irrational, reckless, self-defeating, or pathological, as it is typically conceived. Everybody engages in risk-taking to some degree. Risk-sensitivity theory suggests that risky behavior is, in fact, an adaptive response to various environmental and social circumstances, taking into account developmental influences and individual differences. This approach has some important implications. Utilizing an evolutionary approach—where risk-taking is conceived as potentially adaptive under some circumstances—may lead to a more productive understanding of the causes of, and solutions to, societal issues such as crime, gambling, and other forms of harmful risky behavior. Future research should be informed by a more integrated and interdisciplinary approach to understanding decision-making under risk.

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Notes

1. Life history theory (reviewed later in the article) also takes a functional, evolutionary approach to explaining behavior (including decision-making), but it is not specifically a theory of decision-making under risk.
2. "Social status" here and throughout the article is used broadly to refer to an individual's relative position compared with others in relevant domains of competition (Cummins, 2005). In humans, this includes competition for social capital (education, income, occupational status, and other social forms of prestige). Status more generally can also be gained from embodied capital (attractiveness, personality traits, intellectual abilities), but these are largely biologically determined traits.
3. A common criticism of evolutionary psychology is that it consists of constructing *post hoc* "just-so" stories. Although this is a legitimate criticism of some evolutionary research, evolutionary theory, like any other theory, can be used to generate hypotheses about behavior that can be rigorously and empirically tested (and falsified) in the present environment (reviewed in Confer et al., 2010, Duntley & Buss, 2008). Furthermore, evolutionary theory can lead to novel predictions and explanations for behavior (reviewed in DeBruine, 2009). Research showing that risk-sensitivity theory broadly applies to human decision-making in multiple domains is an example of this hypothesis generation and testing process leading to novel research outcomes.
4. This definition of need is difficult to operationalize in non-human animals given that it is impossible to measure desired or goal states in organisms that do not possess consciousness. Perceptual control theory provides an account of how organisms seek to maintain homeostasis and engage in behavior to minimize disparity between one's present state and a homeostatic baseline state (e.g., behaving to minimize disparity between the perception of hunger and the perception of satiety). This perceptual control theory mechanism is fully parsimonious with the concept of need defined in this article without invoking consciousness or more complex perceptual mechanisms. A detailed account of perceptual control theory is beyond the scope of this article (given that it focuses largely on human decision-making), but see Powers (1973) for an introduction.
5. Emotions—shorter term feelings that stem from reactions to people, places, or things—are distinguished from affect and mood, which are longer lived, less intense, and more diffuse (Batson, Shaw, & Oleson, 1992). In the psychological literature, emotions, affect, and mood have often been used interchangeably.

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