

36 Decision Making in Animals

Rational Choices and Adaptive Strategies*

Francesca De Petrillo and Alexandra G. Rosati

Introduction

Humans face a myriad of choices every day, from simple decisions about what to eat for lunch or how much time to spend on leisure versus work, to more complex decisions like selecting between competitive jobs offers or deciding whether or not to get married. How do we make these choices? This question has spurred research in decision science across fields including economics, psychology, and biology. Here we will argue that we can gain important insights into these questions by examining how nonhuman animal species make choices. Animals constantly make decisions about many problems that are similar to those faced by humans: what food to eat, where to spend their time, and with whom to mate or to interact with. In doing so, they must account for both costs, such as delays and uncertainty, and the potential benefits of taking one course of action over another. By understanding *why* decision makers show certain preferences, we can better understand *how* these cognitive processes work.

We specifically argue that integrating biological perspectives can reshape how we understand rational decision making: while economists and psychologists often focus on logical processes that maximize utility, evolutionary biologists assume that decision makers are trying to maximize fitness. This evolutionary perspective can explain patterns of decision making that may appear puzzling at first glance. We first provide an overview of different theoretical frameworks for rational decision making from psychology, economics, and biology. Next, we synthesize empirical evidence examining how different species make decisions and whether their choice strategies accord with different conceptualizations of rationality. We conclude by showing how integrating psychological approaches with evolutionary theory and comparative data will help to generate more realistic models of the mechanisms underpinning decision making.

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What Does It Mean to Be Rational?

The question of how a rational decision maker should select between choice options has fascinated scholars from different disciplines, from economists predicting people's reactions to taxation, to biologists trying to understand how foraging animals decide what food to pursue. However, different disciplines have taken different approaches to how to answer this question, which have led to the proliferation of distinct normative models for ideal, "rational" decision making processes (Kacelnik, 2006).

Economic and Psychological Rationality

A predominant view in both psychology and economics is that decision makers are trying to maximize utility, which refers to the magnitude of satisfaction received from consuming a good or service (Bernoulli, 1738/1954; Baron, 2000). In other words, utility represents the degree of satisfaction associated with a particular outcome, like money or food. The fundamental assumption in economics is that individuals act rationally when they maximize their own expected utility (Baron, 2000). More generally, rational actors should prefer options that offer the highest utility weighted by the probability to obtain that option (von Neumann & Morgenstern, 1947). This theory therefore provides a powerful framework for assessing if people behave rationally.

However, empirical research shows that real-world people not only do not accord with the predictions of rational-choice theory, they systematically violate them in several ways, such as by avoiding risk even when it would pay off (Kahneman & Tversky, 2000; Weber & Johnson, 2009), preferring immediacy even when it would pay off to wait (Thaler, 1981), and shifting preferences based on the irrelevant framing of the problem (Kahneman & Tversky, 2000). This led to the important question of what are the evolutionary origins of these "irrationalities," and whether they are uniquely human or shared with other animal species.

The identification of many of these systematic, seemingly irrational choice patterns – sometimes called "anomalies" (Camerer et al., 2004; Kahneman & Thaler, 2006) – also led economists and psychologists to develop new models that better describe real-world behavior. For example, prospect theory represents a revision of classical rational-choice theory that integrated the idea that people make choices with respect to the status quo or a local reference point, rather than in terms of their overall utility. Since people dislike negative changes in the status quo (losses) much more than they like an equivalent positive change (gains), this model can account for framing effects. More recent extensions to prospect theory further account for how people subjectively overweight the probability of rare events but underweight the probability of common events (Tversky & Kahneman, 1992; Kahneman & Tversky, 2000;

Barberis, 2013). Overall, these newer models introduce more “psychological realism” into the normative approach from psychology by modifying the way in which utility is calculated to better align with real behavior (Barberis, 2013). However, although these models better describe people’s choices, it remains unclear why people are making choices in this seemingly biased way.

Evolutionary Rationality

In contrast to approaches from psychology and economics, work in biology is grounded in evolutionary theory and has developed a different set of normative models about how decision makers should act. Similar to classical economic models, biological models predict that individuals seek to optimize some metric of value. However, whereas economists approach this problem by assuming that individuals maximize their utility, biologists assume animals want to maximize their biological fitness, defined as the direct fitness stemming from the number of offspring produced by an individual as well as indirect fitness accrued from relatives (Krebs & Davies, 1978; Stephen & Krebs, 1986; Kacelnik, 2006). In this case, food or calories are therefore treated as proxy for fitness (MacArthur & Pianka, 1966; Charnov, 1976; Stephens & Krebs, 1986). Although biological models and economic models often have a similar structure, this crucial difference in how biological theories conceptualize the “goal” of decision-making processes results in predictions about optimal behavior that can stand in stark contrast to economic definitions of rationality.

One fundamental way in which biological ideas about rationality differ from those in economics is that the *context* of the decision is assumed to have a major impact on its fitness consequences (Houston & McNamara, 1999; Houston, McNamara, & Steer, 2007; Modeling Animal Decisions Group, Fawcett, Fallenstein, Higginson, & Houston, 2014). Thus, animals may show context effects that appear “irrational” from an economic perspective, but which in fact maximize their fitness (Kacelnik & Marsh, 2002; Schuck-Paim et al., 2004; Rosati & Stevens, 2009).

For example, risk-sensitivity theory proposes that the relationship between foraging gains and fitness depends on the energetic state of animals when making their choice (Caraco, Martindale, & Whittam, 1980; Stephens, 1981). As such, an animal’s state (an irrelevant aspect of context in classical economic theories) should have a predictable effect on preferences. For example, yellow-eyed juncos (*Junco phaeonotus*) are risk-seeking when in a poor energetic state, but risk-averse when in a positive state (Caraco et al., 1980). The adaptive logic for this is that pursuing a more constant reward is advantageous for a small animal in a positive energetic state because the payoff is enough to provide energetic reserves to survive. However, for the same animal in a negative energetic state – potentially on the verge of starvation – the payoff from the safe option is insufficient to survive, and only the risky option might provide enough energy to make it to the next day (Stephens, 1981).

This illustrates how the fitness benefit of one additional unit of food does not cleanly map onto one unit of fitness, but it is instead dependent on the state of the individual decision maker (Kacelnik & Marsh, 2002; Kacelnik & El Mouden, 2013). Similar work has shown that an animal's state shapes how they learn about different rewards in the first place, providing a potential mechanistic explanation for these effects (Marsh et al., 2004; Pompilio & Kacelnik, 2005; Pompilio et al., 2006). This economic violation of preference consistency may therefore be adaptive (Houston, McNamara, & Steer, 2007; Modeling Animal Decisions Group et al., 2014). As such, decisions that are context-dependent, and therefore economically irrational due to this inconsistency, may in fact appear perfectly rational from an evolutionary perspective.

Decision Making in Animals

Are animals rational? Given that many nonhumans face a variety of choices about benefits like food or mates and costs like time or effort, empirical studies in both biology and psychology have examined whether animals accord with the predictions of different perspectives on “rationality.” This has revealed that many animals often show the same kinds of choice biases that humans do, including *time preference reversals* (Ainslie & Herrnstein, 1981; Stevens & Stephens, 2010), *framing effects* (Marsh & Kacelnik, 2002; Chen, Lakshminarayanan, & Santos, 2006; Lakshminarayan, Chen, & Santos, 2008, 2011; Krupenye, Rosati, & Hare, 2015) and *endowment effects* (Brosnan et al., 2007; Lakshminarayanan et al., 2008). Here we review the evidence that these strategies, while sometimes seemingly irrational from an economic perspective, are in fact persistent and widespread in the animal kingdom (Figure 36.1).

Inter-Temporal Choices

Many decisions involve temporal tradeoffs, from choosing whether waiting for a fruit to ripen rather than eating it unripe (Stevens & Stephens, 2008) to saving money for the future rather than spending it immediately (Frederick, Loewenstein, & O'Donoghue, 2002). People tend to overvalue immediate rewards and devalue future rewards as a function of the expected delay before acquiring them – a phenomenon known as temporal discounting (Ainslie, 2001). This overvaluing of immediate rewards often results in preference reversals, in which people's preference for each option changes when they are both pushed into the future. For example, when people are asked to choose between \$100 today or \$105 tomorrow, about half prefer immediate gratification. However, when the choice is between \$100 in thirty days and \$105 in thirty-one days, almost everyone prefers the delayed option. Importantly, both decisions involve waiting for the same delay (one more

Economic bias	Intertemporal choice	Risk preference	Framing effects	Endowment effect	Counterfactual reasoning
Basic tasks					
Species					

Figure 36.1 *Measuring animal rationality. Empirical studies on economic choice in nonhuman animals use different methods to assess how and why animals make different kinds of decisions. This shows schematic representations of several important paradigms used to test animals’ decision strategies, as well as major taxonomic groups that have been tested in these setups.*

day) to get the same benefit (an extra \$5) – yet people show a preference reversal (Thaler, 1981) where they are willing to pay the temporal costs when all options are pushed into the future, but many succumb to temptation when there is the possibility of immediate rewards. These kinds of reversals are a key form of economic “irrationality.” Do animals exhibit this same bias?

This can be tested by presenting individuals with choices between a smaller, sooner option, and a larger option available in the future (i.e., delay choice tasks; Tobin & Logue 1994). Numerous studies have quantified discounting

rates across species – including several species of nonhuman primates (Stevens, Hallinan, & Hauser, 2005a; Stevens, Rosati, Ross, & Hauser, 2005b; Rosati, Stevensen, Hare, & Hauser, 2007; Addessi, Paglieri, & Focaroli, 2011; Stevens & Mühlhoff, 2012; Stevens, 2014), birds (Tobin & Logue, 1994; Green, Myerson, & Calvert, 2010; Platt, Wascher, Braun, Miller, & Bugnyar, 2012; Auersperg, Launer, & Bugnyar, 2013; Hillemann, Bugnyar, Kotschal, & Wascher, 2014; Thom & Clayton, 2014), dogs (Leonardi, Vick, & Dufour, 2012), rats (Tobin & Logue, 1994; Richards, Mitchell, De Wit, & Seiden, 1997) and even fish (Mühlhoff, Stevens, & Reader, 2011). In fact, all these species discount future rewards, but the degree to which they are tempted by immediate gratification, vs. willingness to wait for larger payoffs, can vary to a large extent: while pigeons or rats might wait up to 10 s to get the larger delayed options (Mazur, 1987; Tobin & Logue, 1994; Green, Fristoe, & Myerson, 1994; Green, Myerson, Holt, Slevin, & Estle, 2004), some monkeys might wait up to 40 s (Tobin, Logue, Chelonis, Ackerman, & May, 1996; Stevens et al., 2005a).

Indeed, some species can wait for even longer delays to obtain a better reward in the future. For example, capuchin monkeys (*Sapajus* spp.), chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) are able to wait for the larger reward in a range of 70 s to 2 min, much longer than many other animal species tested in a comparable way (Rosati et al., 2007; Addessi et al., 2011). Work using other tasks to assess abilities to delay of gratification similarly reveal species differences in preference, with apes, especially, exhibiting a willingness to wait (Evans & Beran, 2007; Evans, Beran, Paglieri, & Addessi, 2012; Parrish et al., 2014). For example, chimpanzees were willing to wait more than 10 min to increase their payoffs in an accumulation task, in which a reward accumulates continuously until it is accessed (Beran et al., 1999; Beran, 2002; Beran & Evans, 2006). In contrast, several monkey and bird species are willing to wait only about a minute in this situation (Vick, Bovet, & Anderson, 2010; Pelé, Micheletta, Ulrich, Thierry, & Dufour, 2011; Anderson, Kuroshima, & Fujita, 2010; Addessi et al., 2013; Hillemann et al., 2014). This suggests that species vary in their ability to overcome immediate temptation to acquire better outcomes (Rosati, 2017a).

Risky Choices

Decision making under risk, where there is probabilistic variation in payoffs, is another important choice context for humans and other animals. For example, when deciding between foraging patches, sleeping sites, or potential mates, animals must choose between options that differ in the variance of their returns. When presented with choices between a sure option with a certain outcome (such as getting \$10) and a risky option that varies in its outcome (such as a 50 percent chance of winning \$20), people generally show a strong preference for the certain option, even when both provide the same average

expected value (Tversky & Kahneman, 1992; Weber & Johnson, 2009). That is, humans tend to be averse to risk. Do other animals exhibit similar responses to risk?

Many studies have examined how diverse species make choices between food options with similar average payoffs: a “safe” or certain option yielding a reward that is constant in amount, and a “risky” or variable option yielding a reward that varies probabilistically around the mean. In a meta-analysis of more than fifty studies spanning twenty-eight species (including insects, fish, birds, and mammals), animals were broadly risk-averse for gains when making decisions about food (Kacelnik & Bateson, 1996). Yet as with temporal discounting, there is also important variation in preferences across different species. Even when tested in identical tasks, some species are more risk-averse than others – and may even actively prefer risk, a pattern that violates predictions about economic rationality in the opposite direction (McCoy & Platt, 2005; Hayden & Platt, 2007; Heilbronner, Rosati, Stevens, Hare, & Hauser, 2008; Stevens, 2010; Haun, Nawroth, & Call, 2011; Rosati & Hare, 2012, 2013; De Petrillo, Ventricelli, Ponsi, & Addessi, 2015; Rosati, 2017b). For example, wolves (*Canis lupus*) (Marshall-Pescini, Besserlich, Kratz, & Range, 2016), rhesus macaques (*Macaca mulatta*) (McCoy & Platt, 2005; Platt & Huettel, 2008), capuchins (De Petrillo et al., 2015), and chimpanzees (Heilbronner et al., 2008; Haun et al., 2011; Rosati & Hare, 2012, 2013) have all been shown to be fairly risk-seeking, whereas dogs (Marshall-Pescini et al., 2016), bonobos (Heilbronner et al., 2008; Rosati & Haun et al., 2011; Hare, 2012, 2013), cotton-top tamarins (*Saguinus oedipus*) (Stevens, 2010), and several species of lemurs (*Lemur catta*, *Eulemur mongoz*, *Varecia rubra*) (MacLean, Mandalaywala, & Brannon, 2012) are more risk-averse.

Framing Effects

Following the formulation of the prospect theory (Kahneman & Tversky, 1979), decades of research have revealed that humans exhibit framing effects when making choices: judging decisions involving losses differently from mathematically equivalent decisions that are perceived as involving gains. When presented with economically equivalent choices posed either in terms of subjective gains or losses – for example, judging a disease eradication program described in terms of lives saved vs. lives lost – people tend to avoid risk when making decisions framed as gains, but prefer risky options when decisions are framed as losses (see Kahneman & Egan, 2011 for a review). This kind of framing effect is one of the classic demonstrations that human decision makers do not make economically rational choices. Do animals treat economic gains differently from economic losses, similarly to what humans do?

Some initial evidence for framing effects in other animals comes from European starlings (*Sturnus vulgaris*). Marsh and Kacelnik (2002) examined

birds' preferences across contexts, so that the same rewards appeared to be either a gain or a loss relative to the status quo. They first manipulated birds' payoff history by offering them either a small payoff of one pellet or a large payoff of seven pellets, thereby establishing a "reference point" for later decisions. Then they presented starlings with a choice between a constant option of four pellets and a risky option corresponding to an equal probability of receiving two or six pieces. For birds that had regularly received only one pellet, any of the other options was perceived as a gain; in contrast, birds that received seven pellets now faced different outcomes, which all provided less than they were used to. Like humans, starlings became more risk-seeking when facing this loss than in the gain context.

Primates show similar patterns of "irrational" choices. For example, one series of studies evaluated whether capuchins show framing effects in a token exchange task (Chen et al., 2006, Lakshminarayanan, Chen, & Santos, 2011). These capuchins had been trained to trade tokens for rewards, which allowed for a novel assessment of their trading preferences. To establish a gain-vs.-loss frame, two experimenters initially offered different amounts of food for one token, but then would shift what they gave such that both provided the same average payoff. Capuchins preferred the experimenter initially displaying one food item and then sometimes augmenting that amount, so they sometimes gained an additional food item, compared to an experimenter who initially showing two food items, but sometimes subtracting one (Chen et al., 2006). When these token-trading decisions involved some level of risk or variability in payoffs, capuchins were more risk-seeking in response to a loss frame compared to a gain frame (Lakshminarayanan et al., 2011). Finally, chimpanzees and bonobos also exhibit reference-dependent choice, evaluating equivalent options as preferred when they are framed as a gain than a loss (Krupenye et al., 2015). Together, these results indicate that many species exhibit framing effects, suggesting that the psychological mechanisms underpinning this cognitive bias might have deep evolutionary roots.

Endowment Effects

Another important irrational bias or anomaly in human decision making is the endowment effect (Thaler, 1980; Kahneman, Knitsch, & Thaler, 1990, 1991). This effect concerns people's tendency to value things that they possess more than things they do not (Thaler, 1980; Kahneman et al., 1990). In one of the first investigations of the endowment effect, Kahneman et al. (1990) gave human participants a mug and then offered them the chance to sell or trade it for an equally priced object. They found that participants refused to trade their own mug and demanded approximately twice as much money to sell the mug as other participants were willing to pay for it. Yet according to rational-decision theory, individuals should be indifferent between keeping the item they currently have and

trading it for an equally valued item. Studies using this basic method have shown that people generally overvalue things in their possession and, consequently, they tend to behave irrationally when making decisions about their property (Kahneman et al., 1990, 1991; Johnson, Hershey, Meszaros, & Kunreuther, 1993; Franciosi, Kujal, Michelitsch, Smith, & Deng, 1996; see Morewedge & Giblin, 2015 for a review).

Many views suggest that the endowment effect stems upon special cognitive capacities, such as understanding of ownership or a well-developed sense of self (Franciosi et al., 1996; Lerner, Small, & Loewenstein, 2004; Morewedge, Shu, Gilbert, & Wilson, 2009), and animals appear to lack human-like conceptions of property (Rossano, Rakoczy, & Tomasello, 2011). Yet comparative research has indicated that this bias is nonetheless present to some degree in some primates, including chimpanzees, gorillas, orangutans, and capuchin monkeys (Brosnan et al., 2007; Flemming et al., 2012; Drayton et al., 2013; Lakshminarayanan et al., 2008). For example, primates are often reluctant to exchange food items they have in their hand for other food items, even when the new reward is much more preferred (Lakshminarayanan, Chen, & Santos, 2008; Brosnan et al., 2007; Flemming, Jones, & Mayo, 2012; Drayton et al., 2013). However, unlike humans, primates seem to primarily show this bias for food, but not other kinds of objects, such as toys or tools (Brosnan et al., 2007; Kanngiesser, Santos, Hood, & Call, 2011; Brosnan, Jones, Gardner, Lambeth, & Schapiro, 2012; Flemming et al., 2012). Indeed, although chimpanzees seem to exhibit an endowment effect for tools that they can use immediately to obtain food, they do not show such effect for tools when the food is inaccessible (Brosnan et al. 2012). Thus, nonhuman animals do behave irrationally when making decisions about their “property,” but this bias appears to be specific to food in their possession and therefore less elaborated than in humans.

Are Animals Irrational?

The previous section examined instances when animals are error-prone or biased when making decisions – and thus may seem to be behaving irrationally from an economic or psychological perspective. Why do animals show these biases? One possibility is that animals, indeed, do not possess the cognitive capacities that are necessary to correctly evaluate each option when making decisions (Stevens, 2008). For example, when presented with a choice between risky gambles, a decision maker needs to compare the probability of receiving each outcome. On the other hand, decades of research demonstrate that animals can be quite skilled in inferential reasoning (see following, Völter & Call, 2017), suggesting that these “biases” may reflect a deeper biological function. Here we explore whether such biases are either failures of rationality vs. whether they rather align with biological rationality.

Are Animal Biases Failures of Logic?

One possibility is that animals lack the ability to make decisions guided by logical principles, resulting in failures of rationality. This kind of “process-based” conception of rationality is common in some psychological views emphasizing that rational actions or decisions are those that emerge from a logical process (Kacelnik, 2006). Along these lines, some theories propose that the ability to make logical inferences is a unique human ability and may be strictly dependent on language or formal pedagogy (Csibra & Gergely, 2009). If animals are much more limited in their ability to combine information flexibly or to think abstractly, they may then lack the ability to represent logical concepts or engage in logic-based reasoning when making decisions (e.g., Carruthers, 2002, Spelke, 2002; Premack, 2007; Penn, Holyoak, & Povinelli, 2008).

However, recent comparative research does not support this view, as non-human animals can make many complex logical inferences (Völter & Call, 2017). For example, chimpanzees (*Pan troglodytes*), gorillas (*Gorilla gorilla*), orangutans (*Pongo pygmaeus*), bonobos (*Pan paniscus*), and capuchin monkeys (*Sapajus* spp.) can use information about probability to select options that are most likely to provide a high-value reward (Rakoczy et al., 2014; Tecwyn, Denison, Messer, & Buchsbaum, 2017; Eckert et al., 2017; Eckert, Call, Hermes, Herrman, & Rakoczy, 2018a; Eckert, Rakoczy, Call, Herrmann, & Hanus, 2018b). In the basic setup for these studies, primates are presented with two containers of food, which differ in their ratio of preferred and non-preferred foods. One item is then drawn from each container, without the primate seeing its exact identity. Across several trials, primates can use information about the proportion of their preferred item in the container to select the container most likely to provide a high-value reward.

Work on primate risky-decision making similarly shows that animals can adjust their preferences according to the relative value of different options, suggesting that their cognitive process for making choices in decision making tasks follows a logical course. For example, even though chimpanzees show an overall preference for risk (Heilbronner et al., 2008), they appropriately adjust their risk preferences based on the relative value of the risky option by choosing risk more often when it provides a higher relative payoff (Rosati & Hare 2011, 2012, 2013, 2016; Proctor, Williamson, Latzmann, de Waal, & Brosnan, 2014). Capuchins show a similar ability to modulate their choices based on relative payoffs (De Petrillo et al., 2015). That is, these species show biases that do not accord with normative economic models, yet their patterns of choices nonetheless seem internally consistent across different situations.

Are Animal Biases Biologically Rational?

If animals appear to be rational in terms of the psychological processes that generate their decisions, why do they exhibit these choice biases? One possible

explanation is that animals' choice strategies are designed to maximize a biological currency (such as fitness) rather than an economic currency such as expected utility. Biological models of decision making are in many ways analogous to economic models, in that they are derived from first principles about how rational individuals should act. However, they fundamentally differ from economic models in that they hinge on the idea that the best strategies are those that maximize fitness rather than expected utility, for example by using long-term rate of energy intake as a fitness proxy (Bateson, 2002; Stephens & Krebs, 1986).

Crucially, biological theories inherently assume that the context of the decision shapes its fitness consequences, and thus animals may show the kinds of preference inconsistencies discussed above and yet still maximize their fitness (Houston & McNamara, 1999; Houston et al., 2007; Modeling Animal Decisions Group et al., 2014; Kacelnik & Marsh, 2002; Rosati & Stevens, 2009; Schuck-Paim et al., 2004). For example, similar to prospect theory for human risky choice (Kahneman & Tversky, 1979), risk-sensitivity theory predicts risk aversion when (small-bodied) animals are in a positive energy budget (e.g., face a "gain" situation) but risk-seeking when they are in a negative energy budget (e.g., losses). From this perspective, risk-sensitivity theory provides an explanation of how reference points – here rooted in an animal's energetic state – may affect risky choice in species like birds (Stephens, 1981; Stephens & Krebs, 1986; Kacelnik & Bateson, 1996; see also Kacelnik & El Mouden, 2013). In contrast, this perspective suggests that in larger animals – where short-term energetic requirements do not represent a significant threat to survival – risk-seeking behaviors may emerge more often when they are in a positive energetic state (Gilby & Wrangham, 2007). Along these lines, several large-bodied primate species in captive contexts show marked preferences for risk in several contexts (Heilbronner et al., 2008; Haun et al., 2011; Rosati & Hare, 2012, 2013; De Petrillo et al., 2015). Thus, the broad lesson is that evolutionary explanations for a given species' pattern of decision-making need to account for how that strategy plays out for specific species in their specific ecological context.

One way to test this idea is to examine how animals living in different kinds of environments make decisions. Since the structure of the environments play a crucial role in determining the fitness impacts of different decisions, animals typically living in different kinds of environments should show different kinds of preferences. In fact, primate species often show wide variation in how they respond to different kinds of decisions, as described previously. This natural variation in "irrationality" provides a new route for a biological understanding of why animals make decisions the way they do. For example, many studies of inter-temporal choice suggest that organisms can often maximize their utility by waiting for the larger reward, and thus overweighting immediate returns is considered irrational. However, this may not be the case for animals foraging in the real world, since waiting is costly and does not always

represent the absolute best strategy (e.g., Stephens, 2002; Stevens, 2010; Fawcett et al., 2012). During the delay, the food could be stolen by a competitor (*interruption risk*, Stephens, 2002) or a predator may force the individual to abandon it (*termination risk*, Stephens, 2002). There is also the cost associated with all the lost opportunities to invest in an option that is not yet available (*opportunity costs*, Fawcett, McNamara, & Houston, 2012; Stephens, 2002; Stevens, 2010). From this perspective, some animals might prefer immediate options for biologically rational reasons (Kacelnik, 2003; Stephens, Kerr, & Fernández-Juricic, 2004; Fawcett et al., 2012).

In some sense, the biological views on rational preferences can sometimes also align with a psychological or economic perspective focusing on rationality as choices that emerge from a logical process. Considering that animals often face uncertain environments, individuals that are able to fill in what they do not know through inference have a higher chance of finding resources than individuals that are not able to make such inferences. For example, tracking statistical regularities concerning where or when food is likely to be found will allow animals to be more effective foragers, and, therefore, to increase their energy intake, which in turn increases their fitness. This suggests that to fully understand the processes of animal decision making, it is necessary to look at rationality through an evolutionary lens and to appreciate the problems that animals face in the wild.

Integrating Biological, Economic, and Psychological Approaches

One tool that can be used to assess the evolutionary function of different cognitive abilities for decision making is the comparative method. By comparing the traits of different species that inhabit different socio-ecological environments, it is possible to reconstruct the evolutionary history of a particular trait, and to identify which selective pressure may have shaped it (Clutton-Brock & Harvey, 1979; Mayr, 1982). Comparative approaches have been widely used to understand what kinds of specific ecological or social environments promote the emergence of specific morphological, behavioral, or cognitive characteristics across species. A well-known example of the comparative method to understand and explain natural phenomena comes from Darwin's finches. In particular, finches in the Galapagos Islands possess beaks of differing length and breadth, allowing different species to feed on different types of food (Darwin, 1854; Weiner, 2014).

This approach has recently also been used to investigate patterns of decision making in animals. Empirical evidence from comparative studies suggests that some differences in species decision-making strategies map onto differences in these species' wild ecology. For example, cotton-top tamarins (*Saguinus oedipus*) and common marmosets (*Callithrix jacchus*) are closely related, with similar body sizes and social-group structures, but they show a major difference in their wild diets. Whereas marmosets are obligate gummivores, using

specialized dental adaptations to gouge holes in trees and then waiting for sap to exude, tamarins rely more on ephemeral and widely distributed fruit and insects (Rylands & de Faria, 1993; Garber, 1993). Experimental comparisons have shown that, in line with these differences in their natural ecology, these species also exhibit different preferences when making decisions about the temporal and spatial distribution of rewards (Stevens et al., 2005a, b; Rosati, Stevens, & Hauser, 2006): marmosets waited almost twice as long as tamarins to obtain a larger quantity of food in temporal discounting tasks, whereas tamarins were willing to travel longer distances than marmosets to obtain more food, lining up with their larger ranging patterns to obtain fruits and insects (see also Platt, Brannon, Briese, & French, 1996).

Differences in the decision-making patterns of chimpanzees and bonobos similarly map onto their wild foraging ecology. Compared to bonobos, chimpanzees exploit more seasonally variable and widely distributed fruit resources, exhibit high rates of risk hunting, and engage in temporally costly tool use to extract food (Rosati, 2017d; Malenky & Wrangham, 1994; Stanford, 1999). Bonobos, in contrast, eat more temporally and spatially homogenous terrestrial herbs, rarely hunt, and do not use tools in the wild to extract food (Surbeck & Hohmann, 2008; Furuichi et al., 2015). This means that chimpanzees frequently face delays in food consumption and invest energy in pursuing risky outcomes, whereas bonobos do so less often. In experimental comparisons, chimpanzees accordingly wait longer to obtain a larger reward in an inter-temporal choice tasks (Rosati et al., 2007; Rosati & Hare, 2013), and are also more risk-seeking than bonobos (Heilbrunner et al., 2008; Haun et al., 2011; Rosati & Hare, 2012, 2013, 2016).

Further evidence that a species' natural history shapes decision-making strategies come from instances of convergent evolution, whereas species that face similar ecological problems show similar preferences (De Petrillo & Rosati, 2019). For example, chimpanzees and capuchin monkeys both live in wild ecological niches centered in the exploitation of temporal costly and risky foods, with extensive hunting and extractive tool use (Brewer & McGrew, 1990; Wrangham, Conklin, Chapman, & Hunt, 1991; Wrangham et al., 1993; Perry & Rose, 1994; Stanford & Wrangham, 1998; Fragaszy, Visalberghi, & Fedigan, 2004; Spagnoletti et al., 2012; Gilby et al., 2017; Rosati, 2017b). Studies comparing capuchin and ape decision making in matched contexts found that capuchins and chimpanzees both exhibit high degrees of patience and risk-seeking compared to other more closely related taxa (Rosati et al., 2007; Addessi et al., 2011; Rosati & Hare, 2012, 2013; De Petrillo et al., 2015).

Taken together, these findings support the proposal that decision making can be shaped by a species' natural history and show how comparisons of decision making across diverse species that vary in their ecological characteristics can test the evolutionary implications of different choice strategies in the real world. Indeed, individuals' decisions that appear to be violations of

economic rationality in experimental settings might actually represent rational strategies evolved in response to a given species natural history. This evolutionary approach to rationality, therefore, provides a new explanatory framework for understanding why humans and animals do not always conform with classical notions of economic rationality. Such work with animals can reveal the evolutionary contexts that favor some kinds of decision-making strategies over others (Santos & Rosati, 2015; Rosati, 2017c). Extending this approach to also include humans can further provide a new framework for understand human economic behavior.

Conclusions

We have argued that different conceptualizations of decision-making processes across economics, psychology, and biology can lead to conflicting views on rationality. Humans and animals alike often deviate from classical rational-choice theories and seem to fall prey to cognitive biases, even though they are able to follow logical processes when making decisions. One approach to address this is to consider that from an evolutionary point of view, animals' inconsistent and context-dependent choices may in fact maximize their fitness and thus, what appears to be economically irrational might actually be biologically rational. We have argued that an evolutionary approach to rationality can elucidate the ultimate origins of variation in decision-making strategies across species and provide a new framework for understanding why humans and animals do not conform to classical notions of economic rationality. Only by integrating economic theory with biological information about the consequences of different choices strategies in the real world – and therefore accounting for what the real world looks like for different species – is it possible to understand the origins of human and animal economic behavior.

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