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# 6 Rational Decisions: The Adaptive Nature of Context-Dependent Choice

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Although classical economic theory hinges on the assumption that rational actors should seek to maximize gains, psychologists and behavioral economists have recently collected a wealth of evidence challenging this premise. In violation of the principles of rational choice, context appears to dramatically influence human decision making. Like humans, numerous nonhuman animals, ranging from honeybees to primates, are sensitive to context, suggesting deep evolutionary roots for seemingly irrational decision-making. Many psychologists have suggested that such choices may stem from cognitive biases that result in errors. We contend, however, that labeling context-dependent choices as errors obscures the real issue. Natural selection does not create organisms that adhere to economic theory—it creates decision makers that maximize fitness. We review evidence that many species show context-dependence when making decisions and then present a framework for analyzing the adaptive consequences of these choices. We argue for an approach weaving psychological perspectives into an evolutionary framework to elucidate the nature of decision making.

Would you rather receive \$100 today or \$105 tomorrow? Often people are split 50/50 when facing this choice; some preferring the immediacy of the \$100, and others preferring the larger payoff of \$105. However, when given the option between \$100 in 30 days and \$105 in 31 days, an almost unanimous winner emerges: \$105. This switch is puzzling because, although both cases involve an additional \$5 for waiting an extra day, temporal context influences preferences. That is, immediacy provides a strong temptation to prefer the smaller reward, but pushing both options into the future makes waiting for the larger reward much easier. The standard economic model of this kind of intertemporal choice (Samuelson, 1937)

cannot account for these so-called ‘preference reversals’ (Strotz, 1955; Thaler, 1981).

Humans therefore appear to choose irrationally when making temporal decisions, at least according to classical economic theory. Behavioral economists have identified a number of decision-making ‘anomalies’ like this, which violate principles of rational choice (Camerer et al., 2004; Thaler, 1992). Psychologists have investigated these violations as ‘cognitive biases’ that lead to systematic errors in decision making (Kahneman et al., 1982; Kahneman and Tversky, 2000; Tversky and Kahneman, 1981). However, such investigations do not provide an explanation for the context-dependent decisions, only a description. More generally, why should decision makers value options differently depending on context? We argue that human choice behavior is not anomalous, but rather has deep evolutionary origins: context-dependent decisions occur across an array of animal taxa. This suggests that context-dependent decisions may provide adaptive responses to an organism’s environment (Gigerenzer et al., 1999; Kacelnik, 2006; Payne et al., 1993). Here we briefly review assumptions and predictions of rational choice theory and then examine decision making in nonhuman animals to identify the situations under which context-dependent choice arise. By doing so, we can begin to formulate an evolutionary framework to explore the ultimate consequences of such choices across species, including humans.

## 1 Rational Decisions

Rational choice theory derives primarily from the expected utility theory developed by von Neumann and Morgenstern (1947). This theory describes utility as an index of ‘goodness’ or goal achievement and assumes that decision makers attempt to maximize their expected utility. That is, individuals should prefer options that offer the highest utility weighted by the probability of acquiring that option. From a few basic assumptions, expected utility theory predicts how ‘rational actors’ should behave (von Neumann and Morgenstern, 1947).

Most fundamentally, expected utility theory assumes that utility is independently determined for each option—that is, decision makers assign a single value to an outcome that holds across all situations. Consequently, preferences between different options should be absolute: if the utility of option  $x$  exceeds the utility of option  $y$ , individuals should always prefer  $x$  to  $y$ . This model of decision making assumes that individuals possess an ordered list describing their complete set of preferences. For example, a piece of cauliflower might have a value of one, an orange a value of two, and an apple a value of four. Decisions then involve simply choosing the option with the highest value when presented with a particular choice. Some important principles follow from this framework. First, preferences should be *transitive*, with a consistent ranking of preference order. That is, if an individual prefers apples to oranges and oranges to cauliflower, then this same individual should also prefer apples to cauliflower. Second, decisions should be *independent of irrelevant alternatives*—adding low-quality alternatives to a set of options should not influence decisions (Luce, 1959; Rieskamp et al., 2006). For example, when given a choice between apples, oranges, and cauliflower, the presence or absence of the (least preferred and therefore irrelevant) cauliflower to the choice set should not affect relative preferences between apples and oranges.

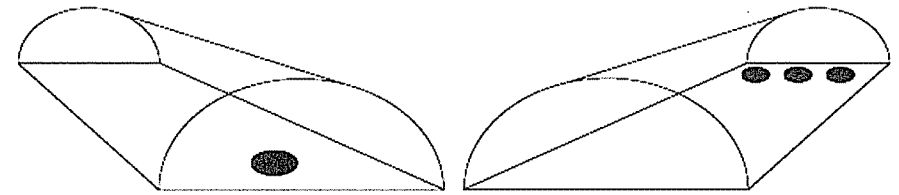


Figure 1. Waite (2001a,b) tested intransitivity and background context in gray jays by offering them a choice between food in two tunnels. By varying the amount of food and the distance it was placed in the tunnel, Waite could manipulate the value of each option.

Finally, preferences should be *invariant*—the same options should produce the same decision regardless of how the experimenter presents options (Tversky and Kahneman, 1986). That is, assuming identical outcomes for two sets of options, the manner in which the choices are framed should not influence preferences. Taken together, these principles above all predict consistent decision making: rational choice theory ignore how initial values are assigned to different options, but once they are assigned, decision makers should follow them.

Expected utility theory therefore represents a *normative* theory of choice, because it describes what a rational actor should do to achieve a norm of behavior, namely maximize utility. However, expected utility often does a poor job of predicting how humans actually behave (Camerer et al., 2004; Thaler, 1992). Context—including the decision maker’s previous experiences, the set of available options when they make their decisions, and the framing of these options—has a pervasive influence on human decision making (Kahneman and Tversky, 2000; Simonson and Tversky, 1992; Tversky and Kahneman, 1981). Here we show that content-dependent choice is also common across numerous animal taxa in the domains of transitive choice, background context, local context, framing effects, and temporal discounting.

## 2 Context-Dependent Choice in Animals

### 2.1 Transitive Preferences

Although all of rational choice theory emerges from a foundation of ordered, transitive preferences, empirical research shows that some animals violate even this most basic principle. For example, Waite (2001a) examined transitivity in hoarding gray jays (*Perisoreus canadensis*), using a paradigm in which these birds made tradeoffs between the number of food items available (raisins) and the travel distance necessary to acquire them (Figure 1). Over a series of choices, most jays consistently violated transitivity: although they preferred one raisin placed a short distance into a tube over two at an intermediate distance (1 short > 2 intermediate) and preferred the same two raisins over three placed at a long distance (2 intermediate > 3 far), they did not prefer the one close piece of food over the three far pieces (1 short < 3 far). In addition, Shafir (1994) presented honeybees (*Apis mellifera*) with forag-

ing decisions about a set of artificial flowers. The flowers varied in the amount of nectar they contained and their length, with shorter flowers containing a smaller volume of nectar. Some individual bees violated transitivity, although the effect was much smaller than with the jays. Together, these results imply that some organisms do not assign absolute utilities to various options in their environments. Instead, animals compare options using the relevant dimensions (e.g., food amount and travel distance) when the choice arises. If the dimensions are valued differently across different choices, then intransitive preferences emerge.

## 2.2 Background Context

Violations of rationality also occur in the presence of seemingly irrelevant alternatives. The principle of independence of irrelevant alternatives predicts that the broader set of options available to an individual should not influence valuation. As a specific example, the background context of a decision (an individual's past experiences or choices) should not alter current choices: choosing between pizza and a hamburger for lunch should not depend on whether one had eggs or bagels for breakfast. Again, if preferences are absolute, no choices before the current one should influence decision making—the preferences are already determined. However, the preferences of some animals appear to vary depending on previous choices.

Waite (2001b) examined the effect of background context on decisions by gray jays using the distance paradigm described previously (Figure 1). Half of the jays initially faced a background in which they chose between one raisin or three raisins; to acquire either option, the birds had to travel half-way into a tube. The other half of the jays faced a background context in which they chose between two identical options (one raisin located half-way into the tube). Following the background conditions, all subjects then faced a 'target choice' between one raisin located at the entrance to a tube (small benefit with a low cost) and three raisins located at the end of the tube (large benefit with a high cost). Background context influenced the birds' preferences in this situation: subjects experiencing the first background context preferred the single close raisin, but subjects in the second background condition chose the two options equally. Waite interpreted this result as a tradeoff between reward amount and the cost of traveling farther in the tube (potentially increasing predation risk). For jays in the first background condition, the larger reward became more costly in the target choice; in contrast, jays in the second background condition had no experience with the large reward and willingly accepted a higher cost to acquire it.

An animal's preferences can also depend on their own nutritional condition when they first learn about the new reward option. Kacelnik and colleagues (Marsh et al., 2004; Pompilio et al., 2006) introduced two novel food sources to European starlings (*Sturnus vulgaris*) and desert locusts (*Schistocerca gregaria*). Both food sources provided identical rewards, but individuals experienced the two options under different nutritional states: they encountered one option in a food-deprived state and the other when pre-fed. In subsequent choices between the two options, both species preferred the food source they had encountered while in a low nutritional state, regardless of their state when they made their choice. These findings indicate that valuation can depend not only on the intrinsic qualities of the

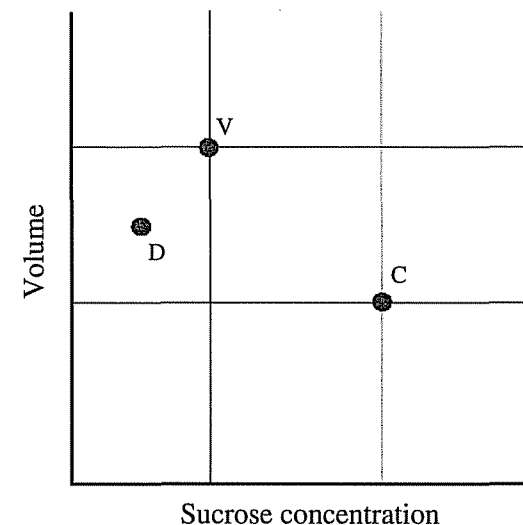


Figure 2. Most choices in human and nonhuman animal experiments involve two options which vary on at least two attributes (here, V is superior in volume and C is superior in sucrose concentration). When a third decoy option is included (D), the relative preference for the two options should not change, and the absolute preference should not increase. (Redrawn from Bateson et al. 2002).

reward but also on the animal's own physiological state upon encountering it.

## 2.3 Local Context

The principle of independence of irrelevant alternatives predicts not only that background context but also local context should not influence choice. That is, the addition of new but irrelevant alternatives to a set of options (such as the cauliflower mentioned previously) should not influence the relative preferences between the original options. In addition, the principle of regularity predicts that adding an option to a choice set should not increase the absolute preference for any of the previous options (Luce, 1959; Rieskamp et al., 2006). Despite these predictions, the influence of local context on choice behavior has been demonstrated in taxonomically diverse animal species. In these experiments, animals initially are given choices between two different foraging options. As in the examples described above, these options normally vary on two dimensions, such as total volume of food and percent sugar content (Figure 2). Subsequently, the animals receive a choice between three options: the original options, plus a new third option. This additional option is inferior to both the original options on at least one dimension; for example, hummingbirds might be offered a third nectar source with a lower sugar concentration at an intermediate volume (Figure 2). Rational choice theory predicts that adding this lower-quality food source to the choice set should have no effect on the level of preference between the two original options. Studies on hummingbirds (*Selasphorus rufus*), honeybees, and gray jays, however, demon-

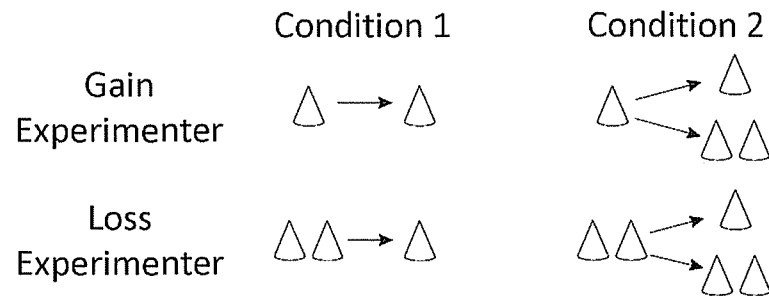


Figure 3. Chen et al. (2006) had two experimenters offer capuchin monkeys choices between pieces of apple. In the first condition, the 'Gain Experimenter' showed and offered the monkeys one piece, whereas the 'Loss Experimenter' showed two but only offered one. In the second condition, the Gain Experimenter showed one piece but offered either one or two with equal probability, and the Loss Experimenter showed two and offered either one or two with equal probability.

strate that animals frequently change their relative preferences between the original options, violating the principle of independence of irrelevant alternatives, and increase their preference for the highest quality option, thereby violating regularity (Bateson et al., 2003; Shafir et al., 2002).

## 2.4 Framing

The manner in which options are presented can profoundly influence choice behavior. Tversky and Kahneman (1981) originally demonstrated how framing violated the rational principle of invariance in human preferences. They presented equivalent choices to human subjects posed either in terms of subjective gains or losses and demonstrated that people avoid risk when making decisions framed as gains, but prefer risk when making decisions about losses. Marsh and Kacelnik (2002) tested an analogous scenario in starlings. They framed decisions as either losses or gains by first offering each bird either a very high or very low number of food pieces (one or seven). They then allowed the birds to choose between receiving four pieces or an equal probability of receiving either two or six pieces. Though the options had identical means, the risk associated with each option differed. For subjects who initially received a low number of food pieces, any of the three possible outcomes would increase their return and thus might be perceived as a gain. For subjects who initially received a large amount of food, however, any option resulted in a reduction in pellet number and thus a loss. Marsh and Kacelnik found that, like humans, the birds preferred the risky option in the loss condition and therefore exhibited an effect of framing. Chen, Lakshminarayanan, and Santos (2006) found similar results with capuchin monkeys (*Cebus apella*) by having experimenters show the monkeys food rewards but then potentially giving them different rewards. For example, one experimenter showed one food reward and gave one reward, whereas another experimenter showed two food rewards but then only gave one (Figure 3). Although the payoff was the same for both experimenters (and the principle of

invariance therefore predicts that subjects should be indifferent between the two options), the monkeys preferred the constant option in which they saw and received one food reward. In another condition (Figure 3), the monkeys preferred an experimenter that showed one food reward and gave either one or two rewards with equal probability (possible gain) over an experimenter that showed two rewards and gave one or two with equal probability (possible loss). Chen and colleagues interpreted these results as evidence that the monkeys exhibit reference-dependent choice by attending to losses and gains. The monkeys did not have absolute preferences for the outcome, because they were the same in both conditions. Instead, preferences depended on the reference point of the initial amount of food shown.

## 2.5 Temporal Discounting

Animals, including humans, constantly tradeoff between short-term preferences and future gains (Frederick et al., 2002; Kacelnik, 2003; Stevens and Stephens, in press), and many researchers have interpreted this as discounting, or devaluing, the future. Accordingly, economic theorists have developed a model of how reward value decreases over time: exponential discounting (Samuelson, 1937). Notably, exponential discounting predicts that decision makers should exhibit consistent preferences between two options. Any temporal component of a delay is treated as equivalent to any other interval, so preferences should remain the same with constant differences between the delays. Choosing between \$10 now or \$11 in a week, consequently, should be functionally equivalent to choosing between \$10 in a year or \$11 in a year and a week—in both decisions, a quantitative difference of one dollar is associated with the same temporal difference of one week.

Like other normative models of rational choice, exponential discounting also fails to accurately predict real choices. Empirical research has repeatedly demonstrated that humans and other animals exhibit preference reversals when discounting the future: preferences change as access to both options is pushed farther into the future. (Ainslie and Herrnstein, 1981; Green et al., 1981; Thaler, 1981). Other models of intertemporal choice such as rate maximization, hyperbolic discounting, and quasi-hyperbolic discounting (Laibson, 1997; Mazur, 1987; Stevens and Stephens, in press) predict these preference reversals and therefore effects of temporal contexts.

In humans, other types of context also influence discounting behavior, such as attention to the reward (Mischel et al., 1989), sleep deprivation (Reynolds and Schiffbauer, 2004), social context (Wilson and Daly, 2004), and temporal framing (Read et al., 2005). In contrast to the human temporal discounting literature, however, few systematic attempts have assessed whether animal discounting naturally varies across contexts. One exception is a study by Stephens and Anderson (2001), who tested blue jays (*Cyanocitta cristata*) in experimentally different but economically similar contexts (Figure 4). In the first context, the standard 'self-control' procedure, subjects made binary choices between smaller, sooner and larger, later food rewards (Ainslie, 1974). In the second context, the 'patch foraging' situation, subjects waited the shorter delay for the small reward and then could choose between continuing in the patch to receive the remaining food after a further delay or leaving the patch to end the trial. When continuing in the patch, the two reward amounts summed to the

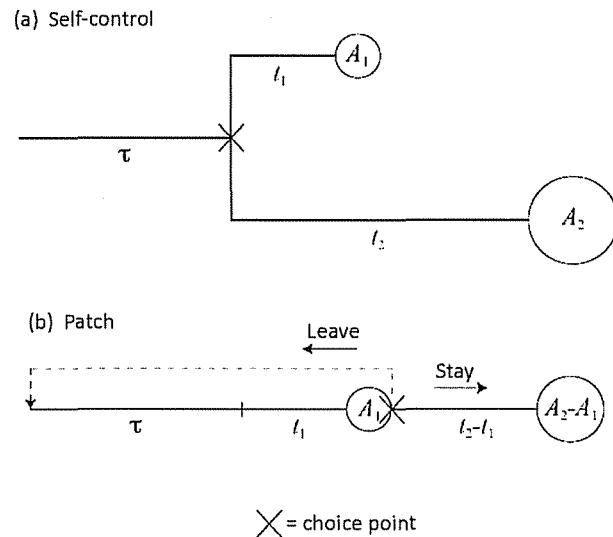


Figure 4. Stephens and Anderson (2001) tested how context influences temporal preferences by offering blue jays two economically equivalent foraging scenarios. In the self-control condition (a), the jays made a series of binary choices between a smaller, sooner reward (amount  $A_1$  after time  $t_1$ ) and a larger, later reward (amount  $A_2$  after time delay  $t_2$ ). Following each payoff was an intertrial interval  $\tau$ . In the patch condition (b), after the intertrial interval the jays received the small amount after the short delay and then chose to either leave the patch and begin the intertrial interval or stay and wait a bit longer ( $t_2 - t_1$ ) for more food ( $A_2 - A_1$ ). A choice for the smaller, sooner option in the self-control situation yielded the same reward amounts and delays as the leave option in the patch situation, and the larger, later option was equivalent to staying in the patch. (Redrawn from Stephens and Anderson 2001).

large reward and the two time delays summed to the longer delay in the self-control context. Therefore, the time delays and reward payoffs were equivalent between the two conditions, but the self-control context offered a binary choice and the patch context offered a stay-or-leave choice. Stephens and Anderson found that at long time delays, the jays chose the smaller, sooner reward more often in the self-control situation, despite its economic equivalence to the patch situation.

Another example explores how two species of primates assess temporal versus spatial decisions. Stevens and colleagues completed a pair of studies examining cotton-top tamarins (*Saguinus oedipus*) and common marmosets (*Callithrix jacchus*), two New World monkeys. In the first experiment, tamarins and marmosets faced the standard self-control situation, and tamarins chose more impulsively than marmosets (Stevens et al., 2005a). In the second experiment, the monkeys chose between spatially varying rewards—that is, they could select a smaller, closer reward or a larger, more distant reward (Stevens et al., 2005b). Tamarins traveled farther for rewards in the second experiment, suggesting that they are less impulsive than marmosets in the spatial context. This reversal of preferences across species indicates

that framing the choices in a temporal or a spatial context differentially influenced preferences in these monkeys.

### 3 Analyzing the Evolutionary Consequences of Context Dependence

These results demonstrate that the context in which a decision is made influences choices across a wide range of species: much like humans, other animals appear to violate a variety of economic principles when making decisions. Though context-dependent choice may violate economic rationality principles, few researchers have provided functional explanations for the violations (but see McKenzie, 2004). An evolutionary perspective, however, reveals that context dependence may prove *biologically* or *ecologically* rational (Gigerenzer et al., 1999; Kacelnik, 2006). Ecological rationality refers to decision mechanisms that are specifically tailored to the environment in which they operate (Todd and Gigerenzer, 2000). This suggests that the rationality of a decision is not absolute and invariant but must be judged according to the typical decision-making environment. Thus, rather than being sub-optimal and maladaptive, context-dependent choice may provide an adaptive response to the natural environments in which animals usually make decisions.

How can we assess the adaptive nature of context-dependent choice? Notably, all of the nonhuman results discussed thus far fit into a general foraging framework—animals making choices and tradeoffs about food. Indeed, this type of research often sits at the intersection of behavioral ecology and behavioral economics. However, although economic models and the foraging models used in behavioral ecology overlap (Hammerstein and Hagen, 2005; Kacelnik, 2006; Stephens and Krebs, 1986), these two approaches differ in how they treat the ‘currency’ of decisions. Economic models are concerned with the subjective utility that decision makers expect to receive from different possible outcomes. Evolutionary analyses, in contrast, focus on only one type of value: influence of the choice on fitness.

To determine the adaptive nature of context-dependent choice, we propose a three-prong approach that integrates cognitive mechanisms, evolutionary models, and the comparative method. First, realistic views of the abilities of boundedly rational agents focus our attention on the actual cognitive mechanisms that animals use to make decisions. Second, evolutionary models of the specific choice environment provide a critical check on what is considered ‘adaptive’—sometimes what is thought to be optimal or adaptive behavior is not. Finally, if context-dependent choices are shaped adaptively, then preferences should vary systematically when examined in a comparative perspective across species with different ecologies. The comparative method—one of the most important tools in evolutionary biology—may therefore provide crucial insights into understanding how animals make decisions.

#### 3.1 Bounded Rationality: Cognitive Mechanisms in Decision Making

From the perspective of bounded rationality, decision makers are not omniscient, computational machines that can instantly calculate the expected utility of all options present and

choose the optimum. Instead, real decision makers face imperfect knowledge and cognitive constraints such as limited or time-consuming information processing and low memory capacity and retrieval (Gigerenzer et al., 1999; Simon, 1955). Therefore, rather than use an optimizing process to maximize utility, decision makers might actually use a variety of heuristics or simple rules of thumb that generally succeed at identifying the best options (Gigerenzer et al., 1999; Hutchinson and Gigerenzer, 2005). This suggests that examining the cognitive rules and information that animals use when making decisions—rather than focusing solely on the behavioral outcomes of these rules—is necessary to assess the evolutionary consequences of their choices. A further advantage of examining the cognitive mechanisms supporting the observed behaviors is that, once the rules that guide animal's choices are known, the performance of such rules can be compared across different potential environments (e.g., Houston et al., 2007a).

This approach has been successfully applied to several types of choices that animals commonly face. For example, Stephens, et al. (2004) suggested that the context-dependent choice in temporal discounting found in blue jays (Stephens and Anderson, 2001) may result from a simple rule of maximizing the short-term food intake rate, rather than calculating a rate over a longer timeframe. Stephens and colleagues argued that the patch choice situation offers a more realistic foraging scenario, and stay-or-leave decisions—continue to deplete the current patch or move on to a fresh patch—may better represent the kinds of decisions upon which natural selection has acted (Figure 4). Because the short-term rule is equivalent to the long-term rule in the patch situation in terms of calculating intake rate, it may be used because it is computationally less expensive and therefore a simpler rule for animals to implement (Real, 1991). Applying this rule in the self-control context, however, results in more impulsive choice (and lower overall intake rates). Thus, the same rule can result in suboptimal outcomes in contexts that animals are less likely to face in the real world (Houston et al., 2007b).

A more broadly applicable choice rule is a comparative evaluation of options, rather than the absolute determinations of value that many economic models assume (Shafir, 1994; Tversky, 1969). This applies especially to choices between options that vary on multiple dimensions, because calculating a single overall utility value for each option may require difficult computations (Real, 1996). Tversky (1969) originally argued that this kind of comparative choice may provide a more cognitively efficient mechanism than assigning absolute utility because of the ease in evaluating within a dimension across options rather than to assign utility across dimensions for each option. Therefore, comparative choice mechanisms may provide simpler evaluation processes, though occasionally producing intransitive choices. Shafir (1994), however, pointed out that intransitive choice may occur only in restricted circumstances and therefore may not face strong selection pressure: the errors are too rare to have an important effect on fitness. Similar arguments have been made for local context effects (Bateson et al., 2003).

Valuation based on state-dependent learning may reflect another kind of cognitively efficient rule: organisms may attribute value to an option according to the marginal fitness gain associated with this option in the past (Kacelnik and Marsh, 2002; Marsh et al., 2004). This rule will select the highest-value reward under most normal circumstances. If, however, an

animal encounters an option in a low nutritional state, the calculated marginal gain will be higher than if they had encountered it in a high nutritional state. That is, the benefit provided by one piece of food is higher for a hungry animal than a satiated animal, so dissociations between an animal's state when it learns about an option and its state when it makes choices can therefore result in paradoxical preferences.

### 3.2 Context Dependence as Adaptive: Reassessing Optimality

Rather than being a misapplication of a decision rule or comparative decision strategy, context dependence could be optimal and provide adaptive benefits on its own: our assumptions about what is adaptive may not be correct! From this perspective, natural selection does not assign absolute values to options, so it is not an 'error' for animals to fail to make decisions according to an absolute metric. Rather, value is inherently relative—the selective value of a decision depends on the decision-making context, and the value of a decision for an organism may depend on previous decisions. Houston (1997) developed a model demonstrating how background foraging rates can produce different 'best options' in a novel choice situation. With a high background intake rate, time is very valuable, and thus spending time on activities that do not contribute to the rate is costly. Consequently, options with short handling times (and thus small gains) may offer the best payoff. If, however, the background rate is lower, time is not as important, and options with longer handling times (and therefore larger gains) could provide greater benefits. Houston's model can also account for intransitive choices. Because the best option for a forager depends on the background rate, and choosing an option must update the background rate, choices may alter the background rate over repeated decisions such that intransitive choices arise.

Another context that has important implications for adaptive choice is the state of the decision maker (Houston and McNamara, 1999). For instance, the energetic state of foragers may influence their risk preferences: hungry animals may prefer risky options and satiated animals avoid risk (Caraco et al., 1980; but see Kacelnik and Bateson, 1996). State dependence is important because of the likely concave nature of the fitness function—as the state of an individual increases, the fitness benefit received from that state experiences diminishing returns. Therefore, a gain of two food units has different influence on fitness depending on the state of the individual—it generates a larger increase in fitness at low states. At low states, options yielding higher fitness benefits may be more preferred than when at high states (Kacelnik and Marsh, 2002). Schuck-Paim et al. (2004) suggested that many of the local context effects reported in animals may result from changes in the states of the subjects. An experiment with starlings demonstrated that they could eliminate violations of regularity in local context conditions by controlling the food intake of the subjects. Therefore, the starlings implemented state-dependent rate maximizing rules rather than comparative mechanisms of choice in binary versus trinary choice situations.

Rate maximization itself may account for the preference reversal effect seen in temporal discounting in animals (raising the question whether it is really discounting). Bateson and Kacelnik (1996) show that starlings' performance in self-control tasks matches predictions of short-term rate maximization rules, and cotton-top tamarins demonstrate similar adher-

ence to rate maximization predictions (Stevens et al., 2005a; Hallinan, E. V., Stevens, J. R., and Hauser, M. D., unpublished data). Though neither study tested for them formally, preference reversals emerge from the hyperbolic nature of rate maximization. Thus, simple adaptive foraging rules may result in strategies depending on temporal context.

This kind of rate-maximization model, however, cannot account for preference reversals of all nonhumans: bonobos (*Pan paniscus*) appear to adhere to a long-term rate maximization rule, whereas the temporal choices of chimpanzees (*Pan troglodytes*) cannot be accounted for by either a short or long-term rate-maximization model (Rosati et al., 2007). This implies these two phylogenetic sister species may be making temporal choices in different ways. Notably, one explanation for this species difference and others (such as different performance of tamarins and marmosets in temporal and spatial discounting contexts described above) is that species-typical ecology served as a strong selective force shaping even closely related species in disparate ways (e.g., Stevens et al., 2005a; b). The comparative method provides a crucial test of whether context-dependent preferences are adaptive in some contexts.

### 3.3 The Comparative Method: How Do Context-Dependent Preferences Evolve?

One of the most powerful tools in evolutionary biology is the comparative method: examining the traits of different populations or species that have been shaped by differing ecological or social forces in order to better understand how natural selection proceeded (Clutton-Brock and Harvey, 1979; Mayr, 1982). As evolution normally occurs over historical time the comparative method thus allows us to reconstruct a phenomenon that often cannot be directly observed. Although species comparisons are used widely for understanding the evolution of physical characteristics and behavior in animals, they have been only more recently applied to the problem of cognitive evolution (Balda and Kamil, 1989; Bond et al., 2003; Clayton and Krebs, 1994).

We have used this approach to investigate economic choice in animals; growing evidence suggests that species differences in natural ecology may drive differences in decision-making and value-based preferences in experimental settings. As described previously, cotton-top tamarins and common marmosets show different patterns of choice in both temporal discounting (Stevens et al., 2005a) and spatial discounting (Stevens et al., 2005b) contexts. As tamarins and marmosets are closely related New World monkeys with similar body sizes, natural histories, and social systems, we hypothesized that differences in their dietary ecology may drive differences in their underlying decision-making mechanisms. Building off these results, we applied a similar approach to decision making in chimpanzees and bonobos. Although these species recently diverged (Won and Hey, 2005), they differ in their social systems and behavior, and feeding ecology is likely a major evolutionary factor driving these differences: chimpanzees are thought to live in less food-rich, more variable environments relative to bonobos (Malenky and Wrangham, 1994; White and Wrangham, 1988). We hypothesized that due to these same differences in feeding ecology, chimpanzees may be more willing than bonobos to pay high costs of obtain food. Two studies indicated that

these species showed different preferences when making choices about temporal delays (Rosati et al., 2007), as well as risk, or probabilistic variability in reward outcome (Heilbrunner et al., 2008). Namely, chimpanzees waited longer than bonobos to receive a large food reward and more often chose a 'risky' option.

These comparative studies, therefore, highlight the importance of assessing the role of species-typical environment in studying decision making. Applying the comparative method to the study of rational choice may provide similar insights as to when context-dependence is a successful strategy for animals to implement.

## 4 Conclusions

The myriad studies of context-dependent decision making in animals indicates that these purported anomalies or cognitive biases are not unique to humans but are shared with species as taxonomically diverse as honey bees and hummingbirds. The ubiquity of these types of decisions suggests that either the artificial experimental paradigms are generating spurious behavior (Houston et al., 2007b) or there are deep evolutionary roots to this behavior. Though an artificial environment may elicit some instances of context-dependent choice, this likely cannot explain all cases. Many of the studies on bees, hummingbirds, and gray jays use very natural settings to test subjects (Bateson et al., 2002, 2003; Shafir et al., 2002; Waite, 2001a, b). As pointed out by Schuck-Paim et al. (2004), however, it is critical that differences between contexts are evaluated carefully. What may appear to be a sophisticated discrimination between subtle contexts (such as the local context effects seen in hummingbirds) may actually result from more basic differences between the foraging scenarios, such as different intake rates. This provides a salient reminder that many instances of context-dependent choice probably result from adaptive benefits associated with different contexts, rather than resulting from simple cognitive biases.

This certainly does not mean, however, that *all* violations of rational choice can be construed as forms of adaptive behavior. Many of the results discussed in this paper fall under the general category of foraging decisions. Yet humans make many value-based decisions that are not so easily categorized as foraging behaviors, and recent work has begun to adapt these kinds of human economics experiments for animals. These results find similar consistencies between human and nonhuman choices. For example, both capuchin monkeys and four-year-old children behave as if they devalue options they had forgone in previous choices (e.g., they act as though they experience cognitive dissonance), even though no new information should lead them to change the value they associate with various options (Egan et al., 2007). Similarly, chimpanzees appear to show endowment-like effects, valuing something *more* if they physically possess it than if they do not (Brosnan et al., 2007). Although it might be possible to construct evolutionary scenarios for these kinds of decision biases, it is certainly more difficult to fit them in the kinds of foraging framework that seems most useful for the results discussed here.

In the end, it may be phenomena like these that are critical for understanding human market behavior and decision-making on an individual level. Though adaptive explanations



may account for context dependence in nonhumans, do these explanations apply to human decision making? Numerous psychological and economic studies have demonstrated context dependence in humans using only one-shot trials, and it seems unlikely that rate maximizing can account for these instances. So what is the role of adaptive considerations in the study of human decision making? Perhaps we misapply strategies that evolved in 'selection past' to current choice environments. Or perhaps, like other animals, we possess a comparative choice mechanism; such a mechanism can approximate optimal responses much of the time but leads to occasional suboptimal outcomes. To disentangle these possibilities and better understand the adaptive nature of decision making, we must analyze decision rules with reference to the environment in which they were designed to operate (Gigerenzer et al., 1999). This can be accomplished by constructing process models of decision making that specify how individuals search for information, when they stop searching, and how they implement decision rules (Gigerenzer et al., 1999; Hutchinson and Gigerenzer, 2005). The structure of the environment obviously affects the outcomes of these rules, so determining whether or not those rules are suboptimal must make reference to the problems decision makers normally encounter. From this perspective, context-dependent choice is built into a system of decision making tailored to specific situations for humans and animals alike.

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