Ecological rationality: Convergent decision-making in apes and capuchins

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A B S T R A C T

Humans and other animals appear to defy many principles of economic 'rationality' when making decisions. Here, we use an *ecological rationality* framework to examine patterns of decision-making across species to illuminate the origins of these strategies. We argue that examples of convergent evolution—the independent emergence of similar traits in species facing similar environments—can provide a crucial test for evolutionary theories of decision-making. We first review theoretical work from evolutionary biology proposing that many economically-puzzling patterns of decision-making may be biologically adaptive when considering the environment in which they are made. We then focus on convergence in ecology, behavior, and cognition of apes and capuchin monkeys as an example of how to apply this ecological framework across species. We review evidence that wild chimpanzees and capuchins, despite being distantly related, both exploit ecological niches characterized by costly extractive foraging and risky hunting behaviors. We then synthesize empirical studies comparing these species' decision preferences. In fact, both capuchins and chimpanzees exhibit high tolerance for delays in inter-temporal choice tasks, as well as a preference for risky outcomes when making decisions under uncertainty. Moreover, these species exhibit convergent psychological mechanisms for choices, including emotional responses to decision outcomes and sensitivity to social context. Finally, we argue that identifying the evolutionary pressures driving the emergence of specific decision strategies can shed light into the adaptive nature of human economic preferences.

1. Introduction

One of the most surprising empirical findings in the last 50 years of research in the social sciences is that people are not rational—or at least, do not often follow the axioms of rational choice theory as defined by economists. Models of economic decision-making provide a principled way for understanding what choices maximize a decision-maker's *expected utility,* a measure of satisfaction or 'goodness' provided by different choice outcomes (Baron, 2000; von Neumann and Morgenstern, 1974). However, empirical studies from psychology and behavioral economics, examining how people actually make choices in the real world, have revealed that people often deviate from economically rational expectations in systematic ways, for example by reversing preferences across seemingly-relevant contexts (Camerer et al., 2011; Kahneman and Egan, 2011; Kahneman and Tversky, 2000; Rieskamp et al., 2006; Thaler, 1992). Yet it is not only humans that show these patterns: many animals also show the same kinds of choice biases (Ainslie and Herrnstein, 1981; Bateson, 2002; Chen et al., 2006; Krupenye et al., 2015; Lakshminarayanan et al., 2011; Marsh and

Kacelnik, 2002; Stevens and Stephens, 2010; Waite, 2001). Biologists take a different view of these kinds of 'biases' because evolutionary theories assume animals act to maximize a different currency: their *biological fitness.* Since context can have crucial impacts on fitness, these kinds of preference reversals can be biologically rational even when violating economic axioms.

Yet comparative patterns of decision-making have also revealed important variability across different species' decision-making strategies. For example, while many species seem broadly averse to risk, other species show a pronounced preference for risk even when tested in identical contexts (De Petrillo et al., 2015; Hayden and Platt, 2007; Heilbronner et al., 2008; Haun et al., 2011; Kacelnik and Bateson, 1996; MacLean et al., 2012; McCoy and Platt, 2005; Rosati and Hare, 2012, 2013; Rosati and Hare, 2016; Stevens, 2010). Why do many species deviate from rational choice predictions, and what governs the variation in decision-making strategies seen across the natural world? Comparative research—linking variation in decision-making traits to variation in species' natural history—can reveal the evolutionary contexts that favor some kinds of decision-making strategies over others

(Rosati, 2017a; Santos and Rosati, 2015). By probing the origins of variation in other species' decision-making, we can also better understand how and why humans make the kinds of decisions we do.

Here we argue that evolutionary approaches to rationality provide key insights into the adaptive nature of different decision-making strategies. To integrate economic and biological approaches to decision-making, we focus on two fundamental components of value-based decision-making: inter-temporal choices about time, which involve a trade-off between the value of a reward and the time necessary to acquire it (Frederick et al., 2002; Stevens and Stephens, 2010), and choices about risk, which involve a trade-off between options that differ in the variance of their potential outcome (Kacelnik and Bateson, 1996). Both of these kinds of decisions are ubiquitous in the lives of humans and non-humans, as well as key bases for theoretical models in these different fields. We first provide an overview of theoretical proposals aimed at understanding rational decision-making from a biological perspective. We then synthesize recent empirical research comparing decision-making strategies in non-human primates, showing how a species' wild ecology—their particular diet, and the features of the environment that shape how they seek out food resources—can be a major force shaping patterns of decision-making. We argue that examples of convergent evolution are a crucial tool for understanding the origins of different decision-making strategies. Here we focus specifically on patterns of decision-making in chimpanzees (*Pan troglodytes*) and capuchin monkeys (*Sapajus apella*). These species are particularly well-suited for such comparisons because they are distantly related to each other but uniquely share important aspects of their wild ecology. We therefore show how this shared ecological niche predicts the emergence of convergent decision strategies that are not seen in other taxa. We finally discuss how understanding the evolutionary mechanisms that shape decision-making across species can help us to understand the origin of human choices.

2. Defining rationality

Normative or prescriptive models of decision-making address what an ideal decision-maker *should* do when faced with a decision: what is the best strategy for a rational actor to adopt? Ideas about rationality in economics and psychology assume that individuals act rationally when they maximize their own personal *expected utility* (Baron, 2000; von Neumann and Morgenstern, 1974), a subjective measure of goodness. Here, preferences are independently determined for each option allowing decision-makers to rank their preferences and then decide their best course of action in any given situation. To be economically rational, decision-makers should therefore follow a few simple rules to maximize their utility.

First, decision-makers should have well-defined preferences between different potential options (the *completeness axiom*). Second, decision-makers should show transitive preferences (the *transitivity axiom*): if an individual prefers cookies over apples and apples over oranges, then they should also prefer cookies over oranges. Third, decision-makers' preferences can be represented by a continuous utility function (the *continuity axiom*): if an individual prefer cookies over apples, there should be a probability when receiving an apple for sure is treated as equivalent to gambling for a chance of getting a cookie. Finally, decisions should reflect independence from irrelevant alternatives (the *independence axiom*): the choice between cookies and apples should not be affected by the presence of a much less-preferred option, such as broccoli. Taken together, this set of principles provides a normative model that predict what a rational decision-maker should do to maximize their own utility, and violations of these principles are classed as irrational.

However, empirical research shows that people rarely confirm to the predictions of these classic models (Allais, 1953; Ellsberg, 1961; Kahneman and Tversky, 2000), leading economists and psychologists to develop descriptive models that more accurately describe real-world behavior, but are not necessarily based on 'first principles' reasoning about ideal rational behavior. In another line of work, behavioral ecologists and biologists have used evolutionary theory to make new predictions about optimal strategies grounded in biological reasoning, in order to explain why both humans and non-human animals deviate from these definitions of economic rationality (Gigerenzer, 2001; Houston et al., 2007; Houston and McNamara, 1999; Kacelnik, 2006; Modeling Animal Decision Group et al., 2014; Rosati and Stevens, 2009). Here we first describe some of the empirical evidence that people and animals do not accord with traditional assumptions of rationality, and then examine evolutionary approaches to rationality.

2.1. Rational decisions about time and risk

One important violation of economic rationality concerns people's preference about the timing of rewards. According to classic economic models, decision makers should exhibit consistent preferences in decisions between a smaller reward that is available earlier and larger reward available later—preferences that depend only on the relative delay between rewards, not the absolute delays involved. This principle is called *exponential discounting* (Samuelson, 1937). Yet, there is overwhelming evidence that people do not show this predicted pattern of consistent time preferences. 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 30 days and $105 in 31 days, almost everyone prefers the delayed option. Importantly, both decisions involve waiting one more day to get 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 subjective 'over-valuing' of immediate rewards and 'devaluing' of delayed rewards is a phenomenon known as temporal or delay discounting (Ainslie, 2001).

Importantly, intertemporal choices between smaller, immediately available rewards and larger, delayed rewards are ubiquitous for non-human animals as well (Stevens and Stephens, 2009). While many humans face routine monetary decisions about whether to save money for the future or spend it immediately (Frederick et al., 2002), animals face analogous problems when making foraging decisions, for example concerning whether to travel to a distant patch where high-quality food is available, versus foraging on a closer, low-quality food patch (Stephens, 2008; Stephens and Anderson, 2001; Stevens and Stephens, 2010; Stephens et al., 2004; Stevens, 2010). Extensive work quantifying discounting rates across numerous species—including humans (Green et al., 1999; Kirby et al., 1999; Mazur, 1987; Rachlin et al., 1991), several species of primates (Addessi et al., 2011; Stevens, 2014; Stevens and Mühlhoff, 2012; Stevens et al., 2005a, 2005b; Rosati et al., 2007), several species of birds (Auersperg et al., 2013; Dufour et al., 2012; Green et al., 2010; Hillemann et al., 2014; Thom and Clayton, 2014; Tobin and Logue, 1994), dogs (Leonardi et al., 2012), rats (Richards et al., 1997a, 1997b; Tobin and Logue, 1994) and even fish (Mühlhoff et al., 2011)—show that many diverse species discount future rewards. While there is variation across species—humans can sometimes tolerate delays of weeks or months, whereas non-human animals usually tolerate delays of seconds or minutes at most—all species examined to date show this characteristic pattern of over-valuing of immediate rewards to some extent.

Similar violations of standard notions of rationality can be found in decisions involving risk, or probabilistic variation in payoffs. People often exhibit a strong aversion to risk even when expected average outcomes are equivalent or higher for the risky option. For example, 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% chance of winning $20), people generally strong preference the certain option even though both provide the same expected value (Tversky and Kahneman, 1992; Weber and Johnson,

2009). While expected utility theory does predict some level of risk aversion, these models are better at accounting for risk aversion when stakes are small and do not obviously capture the full scope of risk attitudes people exhibit. The degree of risk aversion seen in humans is therefore considered another economic 'anomaly' by many theorists (Rabin, 2000; Rabin and Thaler, 2001). As such, alternative psychological explanations such as loss aversion or probability weighting are often invoked to explain aspects of risk aversion that do not accord with expected utility theory (O'Donoghue and Somerville, 2018).

When deciding between foraging patches, sleeping sites or potential mates, animals must also choose between options that differ in the variance of their potential outcomes—and animals tend to share an aversion to variability in payoffs with humans. Many studies have examined how diverse species make risky choices, or situations in which the outcome is unknown, but the probabilities associated with each possible outcome are known. In such studies, animals are presented with repeated 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 50 studies spanning 28 species (including insects, fish, birds and mammals), animals were broadly risk-averse for gains when making decisions about food (Kacelnik and Bateson, 1996). Yet as with temporal discounting, there is also variation in preferences across species. Even when tested in identical tasks, some species are more risk-averse than others, and some even show a preference for risk (De Petrillo et al., 2015; Hayden and Platt, 2007; Heilbronner et al., 2008; Haun et al., 2011; McCoy and Platt, 2005; Rosati and Hare, 2012, 2013; Stevens, 2010).

2.2. 'Bounded' rationality

Why do decision-makers not accord with standard economic notions of rationality? One proposal focuses on the idea that humans and other animals are not omniscient beings with infinite time and unlimited computational power to find the optimal solution to a decision problem—unlike the assumptions of many normative economic models (Simon, 1990). From this perspective, decision makers with cognitive limitations should rather use 'approximate' strategies to solve problems—strategies that may be less than ideal, but which perform pretty well within certain environmental structures. Thus, rather than trying to optimize decision-making processes to maximize value across all situations, decision-makers have evolved a variety of fast and simple 'heuristics.' These rules of thumb quickly identify the best option with the minimal amount of cognitive work (Gigerenzer et al., 1999; Hutchinson and Gigerenzer, 2005).

If it is effectively impossible for real decision-makers to collect all the information necessary to arrive at an optimal choice, fast and frugal heuristics may represent an efficient and adaptive tool to identify outcomes that are 'good enough' (Gigerenzer et al., 1999; Simon, 1956). However, since the structure of these heuristics are adapted to an organisms' typical decision-making environment (Gigerenzer and Todd, 1999), there may also be a mismatch between rules that work well in natural situations and the rules required to make economically rational decisions in novel experimental contexts. For example, Stephens and Anderson (2001) compared blue jays' decision patterns in two situations: a typical experimental self-control task, and a patch exploitation paradigm in which birds could decide if staying or leaving a food patch; this second task was designed to better mimic the birds' natural foraging problems. They found that blue jays made more irrational choices (i.e. they chose the smaller sooner option even if choosing the larger later option led to larger food intake) in the self-control paradigm, whereas they behaved much more 'rationally' by maximizing their long-term food intake in the patch situation. This suggests that blue jays have evolved a simple rule of maximizing immediate food intake, instead of calculating the food intake in the long-

term (the more 'optimal' strategy). Crucially, the simple rule well-approximates the optimal strategy in these birds' typical foraging situations.

This example illustrates how a heuristic may work well in the situations that are similar to those encountered by animals in their natural environments—and can be cognitively simpler to implement—but can also lead to impulsive mistakes in the more artificial situations. Thus, a simple rule can function well in the wild, but also can lead to apparently irrational choices in new contexts that animals seldomly encounter in the real world (Fawcett et al., 2014; Houston et al., 2007). Thus, this evolutionary approach highlights the importance of considering both the cognitive rules that individuals use when making decisions, but also the environments in which such decisions are typically made. Importantly, decision strategies that appear irrational in simplified experimental settings can seem much more rational when examined in naturalistic contexts.

2.3. Ecological rationality

A different approach to explain observed deviations from economic axioms of rationality involves using evolutionary theory to build new normative models of behavior. While bounded rationality perspectives incorporate more realistic expectations about what computations decision-makers can actually make, and how their decisions play out in real world environments, biological or ecological rationality challenge the foundational principles of normative economic models: that decision-makers seek to maximize utility. The idea that individuals seek to optimize some metric of value is a crucial tenant of both economic and biological theory—but whereas economists approach this problem by assuming that individuals maximize their utility, biologists assume animals want to maximize their *biological fitness* (Kacelnik, 2006; Krebs and Davies, 1978; Stephens and Krebs, 1986). Biological models of optimal foraging decisions are therefore in many ways similar to normative economic models in that they are derived from 'first principles', but they aim to predict the best strategies for maximizing fitness, for example by using long-term rate of energy intake as a fitness proxy (Bateson, 2002; Stephens and Krebs, 1986). Crucially, biological theories inherently assume that the context of the decision shapes its fitness consequences (Houston and McNamara, 1999; Houston et al., 2007; Modeling Animal Decision Group et al., 2014). Thus, animals may show preference inconsistencies and still maximize their fitness (Kacelnik and Marsh, 2002; Rosati and Stevens, 2009; Schuck-Paim et al., 2004).

For example, *risk sensitivity theory* proposes that the relationship between foraging gains and fitness depends on the energetic state of animals when they make their choice in a variable environment (Caraco et al., 1980; Stephens, 1981). An important empirical demonstration of this idea comes from the foraging behavior of yellow-eyed juncos (*Junco phaeonotus*), a small bird species. Caraco and colleagues (1980) gave these birds choices between two feeding stations: one containing a constant amount of millet seeds, and the other a variable amount of seeds. The twist was that birds made choices while in different energetic states: they were either food-restricted for a short period (1 h), or for a longer period (4 h). In fact, birds preferred the safe option while in the more positive energetic state, whereas their preference flipped when in a negative energetic state. The adaptive logic for this shift is that pursuing a more constant reward is advantageous for a small animal in a positive energetic state because the payoff from the safe option 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. Only by selecting the risky option might they obtain enough of an energy boost 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 individual decision-maker (Kacelnik and El

Mouden, 2013; Kacelnik and Marsh, 2002). Thus, animals in a positive energy budget may show risk aversion following a concave function, whereas those in a negative budge show risk-seeking behavior following a convex function (Kacelnik and Bateson, 1996; Kacelnik and El Mouden, 2013; Kalenscher and Van Wingerden, 2011). Similar to prospect theory for human risky choice (Kahneman and Tversky, 1979), risk sensitivity theory therefore predicts risk aversion when 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 (Mishra et al., 2012; Stephens, 1981; Stephens and Krebs, 1986).

Importantly, the exact relationship between rewards and fitness can vary across species, so the form of risk sensitivity predicted for a species like juncos is not a hard-and-fast rule governing risky choices across all species. For example, risk sensitivity theory is more successful at predicting the preferences of some species, mostly small-bodied animals (Kacelnik and El Mouden, 2013). However, as body size increases, short-term energetic requirements do not represent a significant threat to survival—small species are at higher short-term risk of starvation than larger species, and thus may be more prone to modify their preferences as their energy budget changes (Kacelnik and Bateson, 1996, see also Kacelnik and El Mouden, 2013). Larger animals may therefore show different patterns of risk sensitivity. For example, wild chimpanzees are more likely to hunt colobus monkeys—an economically risky strategy with uncertain outcomes—during seasons when high-quality fruits are abundant (Gilby and Wrangham, 2007). This suggests that risk-seeking behaviors in larger animals may emerge more often when they are in a positive energetic state. Similarly, several large-bodied primate species in captive contexts show marked preferences for risk in several contexts (De Petrillo et al., 2015; Heilbronner et al., 2008; Haun et al., 2011; Rosati and Hare, 2012, 2013). 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 in their specific ecological context.

3. Evolutionary variation in decision strategies

While humans and animals often violate axioms of economic rationality, experimental work also shows that species can vary in the particular preferences they exhibit. For example, when making intertemporal choices between a smaller sooner option and a larger option available in the future, species vary radically in how long they are willing to wait for larger payoffs. While some species wait only few seconds, others can wait minutes or—in the case of humans—much longer (Addessi et al., 2011; Mazur, 1987; Myerson et al., 2003; Richards et al., 1997a, 1997b; Rosati et al., 2007; Stevens, 2014; Stevens et al., 2005; Tobin and Logue, 1994). Similarly, when deciding between a certain payoff and a payoff with variable return, species vary in their willingness to accept these risks, with some commonly exhibiting risk aversion but others showing risk-seeking behaviors (Caraco et al., 1980; Hayden and Platt, 2007; Heilbronner et al., 2008; Haun et al., 2011; Kacelnik and Bateson, 1996; McCoy and Platt, 2005; Rosati and Hare, 2012, 2013; Stephens, 1981; Stevens, 2010). Theoretical approaches from biology suggest that to evaluate whether these different strategies are rational, it is necessary to account for the environment in which decisions are being made. Here we examine empirical studies of primates' patterns of decision-making to understand the origin of this variation. We argue that current evidence supports the view that a species' wild ecology is a strong force shaping patterns of primate decision-making.

3.1. Comparative approaches to decision-making

A powerful tool to address the evolution of different traits is the comparative method. The comparative method examines how traits of different species varies with their socio-ecological environment (Clutton-Brock and Harvey, 1979; Mayr, 1982). In doing so, this method can be used to reconstruct the evolutionary history of a particular trait, and to identify which selective pressures have shaped it. For example, a comparative approach can be used to understand what kinds of ecological or social environments promote the evolution of a specific trait, by relating variation in that trait to variation in a different species' or population's natural history.

This technique has been widely used to understand the evolution of physical traits and behavior in animals. For example, Darwin already extensively used the comparative method to understand and explain natural phenomena (Harvey and Pagel, 1991). During the voyage of the H.M.S Beagle, Darwin observed the great variation in beak morphology across finch species living in the Galapagos Islands. He documented that finches in this archipelago possess beaks of differing length and breadth, allowing different species to feed on different types of food (Darwin, 1854). In modern applications, comparative methods involve statistical techniques to relate differences in a trait of interest to differences in evolutionary characteristics while also accounting for phylogeny (Nunn, 2011; Nunn and Barton, 2001). This is important because closely related species may exhibit similar traits due to shared evolutionary history, a phenomenon called phylogenetic signal. Accounting for phylogeny is therefore important to be able to tease apart whether animals show similar traits only because they are closely related, or more specifically because they face similar ecological or social problems in their environment.

More recently, the comparative method has been increasingly applied to the study of cognitive evolution (MacLean et al., 2012), especially to the evolution of traits like spatial memory (Clayton and Krebs, 1994; Healy et al., 2009; Rosati, 2017a, 2017b, 2017c, 2017d; Sherry, 2006; Shettleworth, 2010). For example, bird species that depend on caching large quantities of food to survive winter seasons seem to have more robust spatial memory capacities (Healy et al., 2005; Pravosudov and Roth, 2013; Sherry, 2006). Studies of brain evolution also highlight the potential role of feeding ecology on cognition, as species that are frugivorous or extractive foragers tend to have larger brains than folivorous species that depend more on leaves (Clutton-Brock and Harvey, 1980; DeCasien et al., 2017; Gibson, 1986; MacLean et al., 2009; Milton, 1981; Parker and Gibson, 1977). This supports the idea that species living in more complex environments may need more sophisticated cognitive abilities. However, it is important to note that much of this work involves metrics of brain size as a proxy for cognition, and generally involves very broad neuroanatomical areas, so it is difficult to apply these findings to specific cognitive functions. Thus, one important question is how more specific cognitive traits relate to ecological niche. The next section focuses on controlled comparisons of decision-making across species to address this.

3.2. Decision-making across species

One line of evidence that species' decision-making strategies are tailored to their environments comes from experimental comparisons of pairs of species that differ in evolutionarily-relevant characteristics. By comparing species who are largely similar, but diverge in some key way, it is possible to then isolate how that feature may affect their patterns of decision-making. Crucially, this line of work compares species on the same matched task under similar conditions—an important consideration because animals are unlikely to have static decision strategies, but rather will flexibly adapt their choices to the context at hand. For example, the same individuals might modulate their preferences to relatively more risk-seeking or more risk-averse depending the exact payoffs they face (De Petrillo et al., 2015; Rosati, 2017a). As such, even subtle variation in the task design, such as reward amount or learning schedule, is likely to affect their preferences (see Heilbronner and Hayden, 2013 for an example). Yet some species

nonetheless may show clear differences in how they respond to a given type of decision, even when tested in largely identical contexts and with similar energy budgets.

One example comes from comparisons of cotton-top tamarins (*Saguinus oedipus*) and common marmosets (*Callithrix jacchus*) Although these species of New World monkeys are closely related, with similar body sizes and social group structures, they show a major difference in the diets they eat in the wild. Whereas marmoset are obligate gummivores, who consume sap using specialized dental adaptations to gouge holes in trees, tamarins rely more on ephemeral and widely-distributed fruit and insects, and only feed on gums in an opportunistic fashion (Garber, 1993; Rylands and de Faria, 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 (Rosati et al., 2006; Stevens et al., 2005a, 2005b). In particular, in temporal discounting tasks, marmosets waited almost twice as long as tamarins for obtaining a larger quantity of food—lining up with their willingness to wait for sap to exude from trees. In contrast, 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 et al., 1996). Thus, differences in these species' patterns of decision-making seem to map onto their wild foraging ecology.

Another example of this approach comes from comparisons of decision-making in chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*). These species are our closest living relatives, and diverged from one other less than 1 mya (Prüfer et al., 2012). Although they share many morphological and behavioral similarities, they show a few important differences in their wild socioecology. Compared to bonobos, chimpanzees exploit more seasonally variable fruit resources, exhibit high rates of hunting, and use tools to access foods (Malenky and Wrangham, 1994; Rosati, 2017a, 2017b, 2017c, 2017d; Stanford, 1999). Bonobos, in contrast, depend more on homogenously-distributed terrestrial herbs, rarely hunt, and have not been observed to use tools in the wild (Furuichi et al., 2015; Surbeck and Hohmann, 2008). This means that chimpanzees frequently face delays in food consumption and invest energy in pursuing risky outcomes, whereas bonobos spend less time and effort to find food in their natural environment. Following these ecological differences, these species exhibit key differences in their decision strategies that map onto these differences in their natural history (Rosati, 2017b). For example, chimpanzees wait longer to obtain a larger reward in intertemporal choice tasks (Rosati and Hare, 2013; Rosati et al., 2007), and are also more risk seeking than bonobos (Heilbronner et al., 2008; Haun et al., 2011; Rosati and Hare, 2012, 2013, 2016; Rosati et al., 2007).

Additional support for the relationship between ecology and decision-making comes from comparisons of a broader range of species. For example, some work has examined risk preferences across all four great apes: chimpanzees, bonobos, gorillas (*Gorilla gorilla*), and orangutans (*Pongo abelii*). Orangutans show a feeding ecology somewhat similar to that of chimpanzees (Knott, 1999), as they feed on highly seasonally variable fruits that are superabundant in some periods but not others, and furthermore engage in extractive foraging and tool use (Fox et al., 1999; Van Schaik and Knott, 2001). Gorillas, in contrast, rely more on leaves and roots that are always available in their environment, and do not use tools or hunt in foraging contexts (Rogers et al., 2004). In a comparison of risk preferences across these four species, chimpanzees and orangutans were both more risk-seeking, whereas bonobos and gorillas were relatively risk-averse. Wolves and dogs show a similar pattern in terms of the relationship between risky hunting and decision preferences. Wolves—who depend on hunting —are more risk-prone, whereas dogs—who rely mostly on human provisioning—are relatively risk averse (Marshall-Pescini et al., 2016). However, not all work has found cognitive differences in species with different ecologies. For example, comparisons of different lemur species varying in aspects of socioecology have not found major differences in their intertemporal

and risk preferences (MacLean et al., 2012; Stevens and Mühlhoff, 2012). However, in these cases the sample size of each species was small and may not have been sufficient to detect a difference.

More recently, several studies have taken a broader comparative approach to directly compare the relative importance of ecological and social characteristics in predicting decision-making traits while also accounting for phylogeny. This can disentangle the contributions of social characteristics (such as a species' typical group size or social structure) versus ecological characteristics (such as diet or home range size)—while also controlling for different species' relatedness. For example, Stevens (2014) investigated different primates' willingness to delay gratification in inter-temporal choice tasks. A comparison of discounting preferences in 13 primate species showed that ecological factors (such as larger home-ranges) were better predictors of delay of gratification than were social factors (like group size). This indicates that species who tend to face longer times spent searching for food in the wild, are more willing to wait to get a larger reward in experimental tasks, highlighting the special role of ecology in shaping decision preferences. Similarly, work comparing aspects of motor inhibitory control across 23 species of lemurs, monkeys and apes found that feeding ecology was the main evolutionary predictor of self-regulation abilities, not social complexity (MacLean et al., 2014). Overall, this line of work highlights that patterns of decision-making vary in a systematic way that are tailored to a species' wild environment, even when accounting for phylogenetic history.

4. Evolutionary convergence and decision-making

Comparative approaches can provide crucial insights into the processes of natural selection shaping decision-making, and evolutionary convergence provides an important example of this approach. Convergent evolution occurs when different species respond to similar evolutionary pressures by independently developing analogous traits (Keeton and Gould, 1986)—that is, the same trait evolves multiple times in response to the same evolutionary context. A classic example of convergence is the evolution of flight in vertebrates. Several distantly-related taxa including pterosaurs, birds, bats all independently evolved wings from more typical forelimb structures, acquiring a similar physical trait to access a similar 'aerial' niche. Convergent evolution can also be used to understand the history of behavioral and cognitive traits. For example, both chimpanzees and New Caledonian crows have independently evolved extractive foraging techniques involving tool use to access similar food resources in their environment (Hunt and Gray, 2004; Lefebvre et al., 2002). Indeed, some corvids possess remarkable cognitive abilities that are similar to those found in apes, but are not present in other animals' groups (Emery and Clayton, 2004). Thus, convergence is a chance to 'replay' evolution and see if the same traits pop up again in distantly related animals who experience the same evolutionary pressures. Here we argue that instances of evolutionary convergence provide a new important test case for our understanding of rational decision-making making (see Fig. 1).

4.1. Convergence in the natural history of capuchins and chimpanzees

Within primates, capuchin monkeys (*Sapajus apella*) and chimpanzees are a noteworthy example of evolutionary convergence in ecology and behavior (McGrew and Marchant, 1997; Visalberghi and McGrew, 1997). Although these species diverged 40–45 million years ago (Perelman et al., 2011), they exhibit several striking similarities (Visalberghi, 1993; Visalberghi and McGrew, 1997). Both species live in primary and secondary forest, exploiting a similar environmental niche. Both have a wide geographical distribution suggesting a need for flexibility in behavior to account for local circumstances: chimpanzees are widespread across equatorial Africa and can live in diverse habitats including tropical rainforest and dry savannahs (Pruetz, 2006, 2007), and capuchins are widespread in both the Amazonian humid tropical
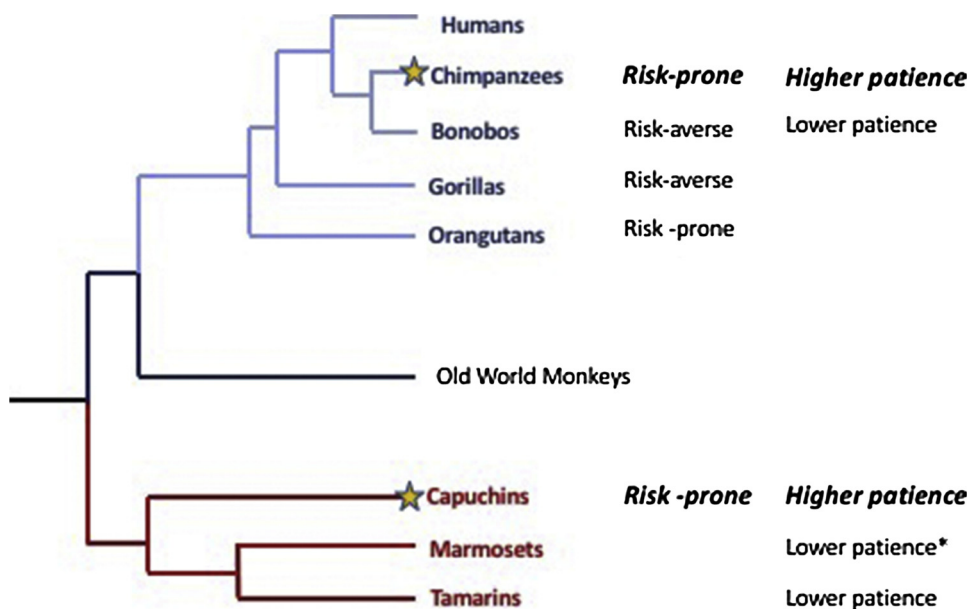
Fig. 1. Decision-making strategies across focus species. Both chimpanzees and capuchins (indicated by stars) have evolved a risk-prone, patient strategy that is dissimilar from more closely related species within the great ape clade (in blue) and New World monkey clade (in red), respectively. *Note that marmosets show greater patience for temporal delays than tamarins, but both are much less patient than capuchins or apes.

forests and in the semi-arid habitats in north-eastern Brazil (Fragaszy et al., 2004; Prüfer et al., 2012). Importantly, these features are not necessarily seen in species that are more closely related to either, such as other New World monkeys or other apes.

These similarities in wild environments go hand-in-hand with several key examples of convergence in chimpanzees' and capuchins' life history and behavior. Both species have long life spans, long infancy and juvenile periods, and large brains relative to their body size (Fragaszy and Bard, 1997; Stephan et al., 1988). In terms of foraging, both chimpanzees and capuchins exhibit an omnivorous diet and exhibit dietary breadth where they exploit many different kinds foods. Although they rely on fruits, both are also able to obtain food from sources that other species in the same locations do not, including hardshell nuts; invertebrates like ants; honey; and even meat by hunting vertebrates (Boesch and Boesch, 1990; Brewer and McGrew, 1990; Fragaszy et al., 2004; Stanford and Wrangham, 1998; Wrangham et al., 1991, 1993). For example, chimpanzees hunt a wide range of prey species, with a special preference for red colobus monkeys (*Procolobus* spp.) (Gilby et al., 2017; Mitani and Watts, 2001; Stanford and Wrangham, 1998). Capuchins also occasionally hunt small vertebrate prey species, including snakes (Falótico et al., 2018; Perry and Rose, 1994; Spagnoletti et al., 2012). As with their ecological niche, species more closely related to chimpanzees or capuchins do not show frequently show these behaviors, if they do at all. For example, bonobos, the sister species of chimpanzees, sometimes hunt in the wild—but much more rarely than do chimpanzees (Stanford, 1999; Surbeck and Hohmann, 2008). Similarly, hunting behavior has been only sporadically reported in other species of New World monkeys, such as tamarins and marmosets (Digby and Barreto, 1998; Heymann et al., 2000). This pattern of data suggests that chimpanzees and capuchins have independently evolved similar behaviors like hunting in response to a similar foraging niche.

Both chimpanzees and capuchins also are specialized in their use of complex extractive foraging behaviors involving manipulative tool use (Fragaszy et al., 2004; Goodall, 1986;). Extensive natural observations have demonstrated that chimpanzees possess a complex tool kit, and are able to use and even combine different materials in order to exploit food sources (McGrew, 2010). For example, many chimpanzees' populations use stick probes to engage in termite or ant fishing (Sanz et al., 2004, 2009), and some use tools to extract honey from beehives (Sanz and Morgan, 2009), or even use stones to crack nuts (Boesch and Boesch, 1990; Boesch and Boesch-Achermann, 2000; Brewer and

McGrew, 1990; Whiten et al., 2005). Indeed, some chimpanzee populations actively create tools by extensively modifying natural materials (Sanz and Morgan, 2009; Sanz et al., 2004, 2009). Capuchins also exhibit a complex toolkit, using sticks as probes, and employ stone tools for a variety of purposes (Mannu and Ottoni, 2009; Visalberghi and Fragaszy, 2013). Capuchins may prefer to engage in tool use even when alternative and usually safer resources are available in their environment (Spagnoletti et al., 2012; Visalberghi and Fragaszy, 2013). Remarkably, this kind of tool use, and stone tool use in particular, occurs in a very limited number of primates: only chimpanzees, bearded capuchin monkeys and, to a lesser extent, long-tailed macaques (Boesch and Boesch-Achermann, 2000; Gumert and Malaivijitnond, 2013; Matsuzawa, 2011; Visalberghi and Fragaszy, 2013). Thus, wild observations show that both chimpanzees and capuchins are specialized in exploiting food resources that are unpredictable and not immediately available, and they frequently invest energy to obtain costly or uncertain outcomes, as in the case of tool use and hunting.

4.2. Convergence in capuchin and chimpanzee decision strategies

Drawing on these similarities in these species' natural environments, and observed convergences in their wild behaviors, we predicted that chimpanzees and capuchins will also show *convergent rationality* in their decision-making preferences. In particular, an evolutionary view predicts that the preferred decision-making strategies of capuchins and chimpanzees will be highly similar since they face similar ecological problems. Indeed, some work already suggests convergent cognitive skills in other domains. For example, capuchins and chimpanzees exhibit similar abilities for object manipulation, which is proposed to be an adaptation for the extraction of embedded food sources (Parker and Gibson, 1977). Along these lines, there are also important similarities in the neuroanatomy of chimpanzee and capuchin motor systems that might ultimately stem from similarities in tool use (Visalberghi et al., 2015), as both species have well-developed cortical areas associated with motor planning, grasping and manipulation (Padberg et al., 2007). Are there similar patterns of convergence in these species' decision preferences as well?

Several studies have compared capuchin decision-making to that of apes in matched contexts to address this question. For example, one series of studies examine patience across apes and capuchins (see Fig. 2). Chimpanzees and bonobos were presented with a series of choices between a smaller reward immediately available and a larger
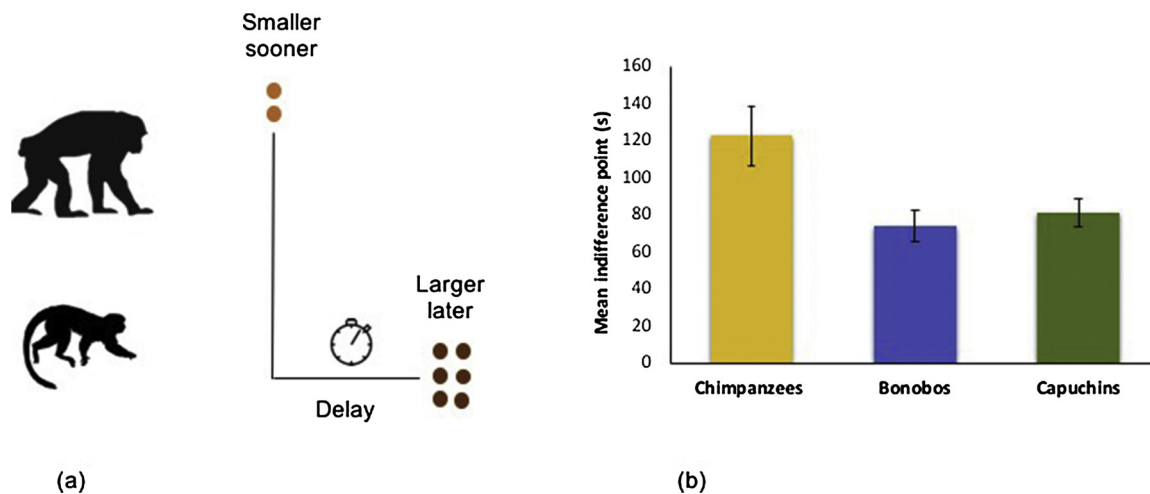
Fig. 2. Comparison of delay tolerance in apes and capuchin monkeys. (a) In a temporal discounting task, apes and capuchin monkeys made choices between two pieces of food immediately available and six pieces of food available after a delay. The delay to receive the larger reward was systematically adjusted to determine their delay indifference point where they valued both options equally. (b) Indifference points (in seconds) exhibited by apes from Rosati et al. (2007), and capuchins from Addessi et al. (2011).

reward available after a delay (Rosati et al., 2007). The time that apes had to wait in order to receive the larger reward was systematically adjusted across sessions to determine the delay at which each individual was indifferent between the smaller and the larger option, for example switching from preferring the larger delayed reward to preferring the immediate reward. Whereas chimpanzees on average waited 2 min before switching to the immediate reward, bonobos waited only 74 s—long compared to many other primates, but significantly shorter than chimpanzees. In a subsequent study, capuchin monkeys were tested using the same experimental procedure, and were found to wait an average of 80 s (Addessi et al., 2011). Comparisons across these species showed that chimpanzees exhibit longer 'indifference points' than other apes, and capuchins similarly showed a high degrees of delay tolerance exceeding that of other closely-related New World monkeys tested in a similar paradigm (see also Amici et al., 2008; Stevens, 2014). For example, marmosets and tamarins—two species of New World monkeys that are more closely related to capuchins than are chimpanzees—both wait less than 15 s on average in this context (Rosati et al., 2006; Stevens et al., 2005a). These results provide the first evidence for convergent rationality in capuchin and chimpanzee decision-making, suggesting that species that face higher temporal costs to obtain food in their wild environments evolve a greater tolerance to reward delays.

Other work has compared chimpanzee and capuchin preferences when making decisions under risk, following the same logic (see Fig. 3). In one experiment, chimpanzees and bonobos chose between a safe option that provided a constant four pieces of food, and a risky option that provided either one or seven pieces of food with equal probability. Thus, these options provided the same average payoff across trials, but the risky option showed probabilistic variation in rewards. When faced with this choice, chimpanzees were risk-seeking and actively preferred the variable option, whereas bonobos were risk-averse (Heilbronner et al., 2008). According to the convergent rationality hypothesis, capuchin monkeys—who, like chimpanzees, rely upon hazardous and unpredictable resources—should also exhibit a similar preference for risky options. Indeed, a subsequent study investigating capuchins risk preference in the same risky choice task showed that they consistently preferred the risky option (De Petrillo et al., 2015).

Overall, these studies suggest that both capuchins and chimpanzees exhibit high degrees of patience and risk-seeking compared to other more closely-related taxa. This supports the claim that they show convergent rationality, as both species live in wild ecological niches centered in the exploitation of temporal costly and risky foods, with

extensive use of both hunting and extractive tool use to support this foraging niche. Indeed, an evolutionary perspective generally suggests that high levels of patience should be linked with high levels of risk tolerance, as rewards that are delayed are inherently uncertain in natural contexts because they might not materialize (Kacelnik, 2003). In that sense, organisms that tolerate long delays in obtain rewards while foraging—for example, by traveling longer distances to seek them out—constantly face the possibility that they might not actually find those resources. As such, risk-seeking and temporal patience should go hand-in-hand according to ecological rationality, in contrast to many dominant views from psychology that risk-seeking and temporal *impulsivity* are linked (e.g. Rachlin, 2000).

4.3. Convergence in psychological mechanisms for decision-making

Taken together, these findings indicate that key decision-making strategies for dealing with risk and time show convergence in chimpanzees and capuchins. But one crucial question is whether primates show convergence not just in their strategies, but also in the underlying psychological mechanisms that support these choice processes. Chimpanzees and capuchins might show the same kinds of *behavioral* preferences, but these patterns might emerge due to different underlying *psychological* reasons. How exactly do chimpanzees and capuchins make value-based decisions from a proximate perspective, and do the same kinds of psychological processes promote similar patterns of decision-making across these species?

One possibility is that the cognitive abilities in dealing with probabilities or numerical quantities differ across species and can account for some of the variability in decision-making observed across primates. For example, animals might show different decision-making preferences if they vary in their ability to distinguish different quantities of reward, or vary in their ability to infer the probability of winning a gamble. However, the comparative decision-making studies described previously also demonstrated that these species could discriminate the reward quantities used, and capuchins and apes more generally show similarly accurate abilities to discriminate numerical quantities across many different contexts (Addessi et al., 2008; Beran et al., 2011; Evans et al., 2009; Hanus and Call, 2007; vanMarle et al., 2006). Moreover, recent studies examined primates' abilities to make inferences about probability found that apes and capuchin monkeys are quite accurate at using information about probability to select options that are most likely to provide a high-value reward (Eckert et al., 2017, 2018a, 2018b; Rakoczy et al., 2014; Tecwyn et al., 2017). Along the same lines,
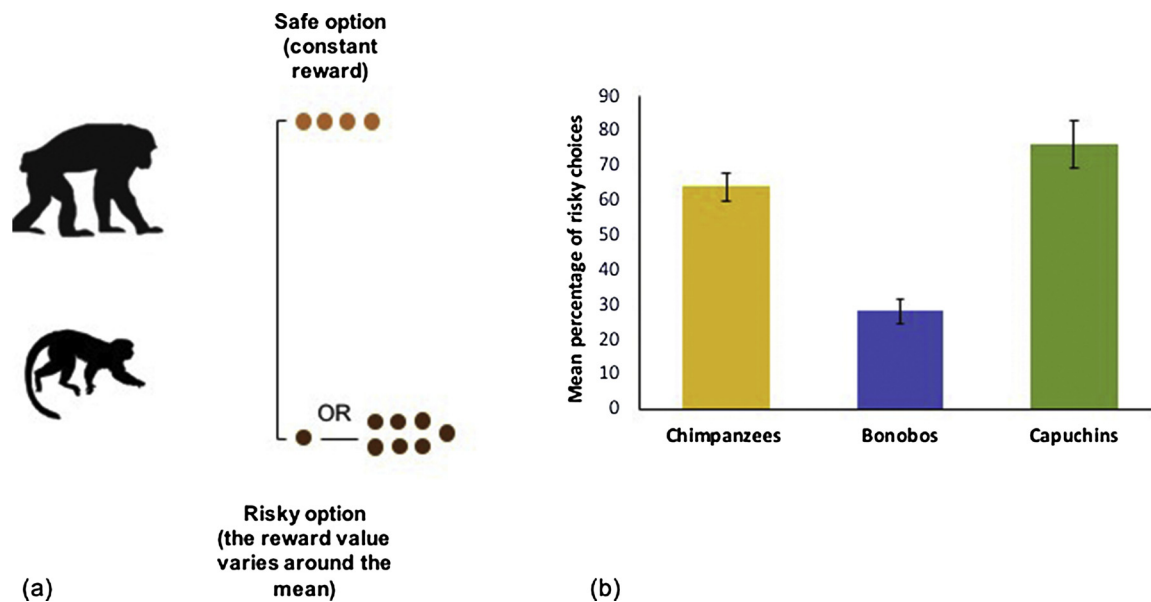
Fig. 3. Comparison of risk preferences in apes and capuchin monkeys. (a) In a risky choice task, apes and capuchin monkeys chose between a safe option that always provided four pieces of food and a risky option, that provided either one or seven pieces of food with a 50% chance. (b) Risk preferences exhibited by apes from Heilbronner et al. (2008), and capuchins from De Petrillo et al. (2015).

chimpanzees and bonobos show a similar ability to flexibly modulate their choices in response to different levels of known risk (e.g., a 0%, 50%, or 100% chance of winning a high value reward) once their overall risk preference in equated (Rosati and Hare, 2011). Thus, it seems that abilities for tracking reward quantities and probabilistic payoffs are largely similar among these species, and therefore cannot account for the different decision-making preferences they exhibit.

Another possibility is that these species' preferences stem from underlying emotional or motivational processes. Emotions are a fundamental component of decision-making in humans, and differences in emotional reactions to decision outcomes can shape preferences in several ways. For example, when making decisions under risk, both the emotions experienced at the time of a decision and the more general emotional state of the decision-maker can influence people's evaluation of alternative options (Lerner and Keltner, 2001; Raghunathan and Pham, 1999; see also Lerner et al., 2015 for a review). Whereas people tend to be more risk-prone when experiencing positive or angry emotional states, those in a sad state tend to be more risk-averse. These emotional processes play a causal role in decision-making as people actively shift their preferences when they experience negative states, such as regret or disappointment, as a consequence of unfavorable outcomes (Camille et al., 2004; Coricelli et al., 2007). Furthermore, people can even anticipate that they will experience such emotions and take this possibility into account when making decisions (Bell, 1982; Coricelli et al., 2007; Loomes and Sugden, 1982; Zeelenberg, 1999; Zeelenberg et al., 1996, 1998). As decisions have emotional consequences that can, in turn, impact subsequent decisions (Bechara et al., 1997; Crone et al., 2004; Schwarz, 2000), emotions are a key proximate mechanism underlying decision strategies in humans.

Is the same true for animals? Although there has been little work on nonhuman's emotional states during decision-making, recent work suggests that apes and capuchins show similar kinds of affective reactions to decision outcomes (see Fig. 4). In a risky decision-making task (Rosati and Hare, 2013), chimpanzees and bonobos were scored for indicators of negative emotional states, such as negative vocalizations, scratching and throwing a tantrum after the choice outcome was revealed. In fact, both chimpanzees and bonobos showed more indicators of negative emotional states after choosing to gamble and then receiving a low-value outcome, versus after choosing to gamble and then receiving high-value outcome or choosing the safe alternative. This

suggests that these species, like humans, experience negative emotional states in response to losing a risky gamble. In addition, chimpanzees and bonobos often spontaneously attempted to switch their initial choices after gambling and receiving a low-value outcome—that is, they would then attempt to revise their choice and select the alternative, a response they rarely showed if they gambled and won or chose to play it safe. In this way, choice switching might be a behavioral indicator of 'regret'. Yet while both species showed these kinds of responses at similar rates, they seemed to have a bigger impact on the choice preferences of bonobos. For example, the individual bonobos that made the most attempts to switch their choices in response to bad outcomes were also the most risk-averse; while chimpanzees also showed choice-switching responses, but there was no relationship between this response and their risk preferences. Moreover, bonobos, but not chimpanzees, modulated their choices based on the outcome of their previous decisions—choosing the risky option more often following a win than a loss—whereas chimpanzees showed a high preference for the risky option regardless of the outcomes they had previously experienced.

In a subsequent study, De Petrillo and colleagues (2017) used the same methodology to examine how capuchin monkeys react to different risk outcomes. Like chimpanzees and bonobos, capuchins showed negative emotional responses more often after gambling and receiving the low-value outcome than after gambling and receiving the preferred outcome or after choosing the safe alternative. Similar to chimpanzees but unlike bonobos, capuchins nonetheless did not modulate their choices according to the outcome of their previous choices. Thus, for capuchins and chimpanzees the outcome of their choices elicited an emotional response, but did not deter their overall preferences for risk-seeking. One possibility is that these emotional responses have a coping function for these species (e.g. Maestripieri et al., 1992), and that they represent a convergent proximate mechanism that supports risk proneness. In fact, if the decision-making strategies observed in chimpanzees, bonobos and capuchins are an adaptive response to their natural ecologies, we could expect that such strategies arise as the result of a joint selection on emotional and cognitive systems (Rosati and Hare, 2013).

This work suggests several important similarities in the emotional mechanisms supporting ape and capuchin decision-making. Another related mechanism shaping patterns of decision-making is social
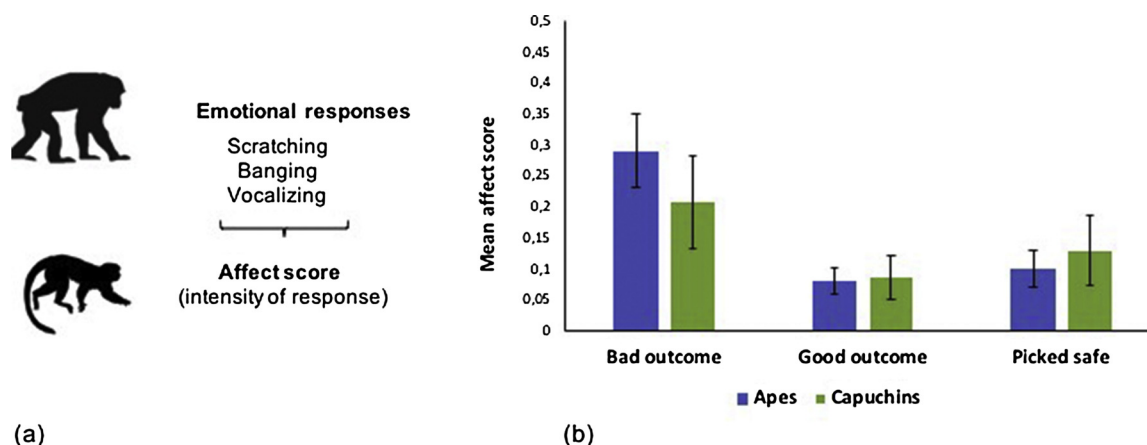
Fig. 4. Comparison of emotional responses in apes and capuchin monkeys. (a) Primates' emotional responses to decision outcomes in a risky choice task. The affect score is a composite measure of the intensity of emotions responses, integrating scratching, banging, and negative vocalizing; more negative responses are indexed by a higher mean affect score. (b) Both apes (collapsing across chimpanzees and bonobos) and capuchin monkeys exhibit more negative responses after gambling and receiving a bad outcome than after gambling and receiving a good outcome, or after choosing the safe options. Emotional responses in apes from Rosati and Hare (2012), and capuchins from De Petrillo et al. (2017).

context, which can also shift decision-makers' emotional and motivational states. For example, people tend to be more risk-seeking when choosing among lotteries when in the presence of other people than when alone (Bault et al., 2008), and are also more risk-prone in competitive contexts where a high-value payoff would allow them to relatively outperform a social competitor (Hill and Buss, 2010). Most primates live in social groups, which means that they must account for the behavior of other group members when making decisions. Since competition in particular is a pervasive aspect of group-living primates, social context may represent another important proximate mechanism underlying decision strategies in nonhumans as well.

Some preliminary evidence indicates that social context can play a powerful role in the (non-social) risk preferences of chimpanzees, bonobos and capuchin monkeys. For example, both chimpanzees and bonobos are more risk-seeking following a competitive interaction with a human, compared to a neutral or a playful one (Rosati and Hare, 2012). Conversely, capuchin monkeys actually become less risk-seeking when they make choices in the presence of a conspecific than when tested alone (Zoratto et al., 2018). In this case, however, it is tricky to directly compare the performance of capuchins and apes because of important differences in experimental design: whereas apes were tested in a competitive interaction with a human exhibiting a pre-programmed behavioral pattern, capuchins were tested in the presence of a naturally-acting conspecific. Apes may in fact show different reactions to a conspecific competitor. While both chimpanzees and bonobos showed similar responses to the competitive social interaction with a human (Rosati and Hare, 2012), bonobos are more able to share food and tolerantly co-feed with a conspecific than are chimpanzees (Hare et al., 2007; Wobber et al., 2010a, 2010b). Broadly taken, however, these studies indicate that social context can influence economic decisions in primates possibly because accounting for the behavior of others has important implications for foraging success.

5. Implications for human decision-making

We have argued that decision-making strategies across species are shaped by ecology. While we have focused on convergence in chimpanzees and capuchins as a specific test-case for this proposal, the idea that patterns of rational decision-making may depend on ecology has important implications for understanding the origins of human economic behavior as well. For example, modern human hunter-gatherers, who are our best model the lifestyle of humans throughout most of our species' existence, inhabit an ecological niche that shares several special characteristics with the foraging patterns of chimpanzees and

capuchins Human foragers tend to focus on especially high-value foods, such as meat, nuts and honey that are costly to obtain in terms of time and energy—and can further require hunting, tool use, or extensive forms of processing to utilize (Kaplan et al., 2000; Marlowe et al., 2014). Humans also exhibit the largest day range of any ape species (Marlowe, 2005), traveling extensive distances in order to locate food and bring it back to a central camp location. Some theories propose that this shift toward high quality, but difficult to acquire, foods dispersed in more open habitats were a key evolutionary transition in divergence of hominins from *Pan* (Kaplan et al., 2000). As a consequence, humans might have evolved specific cognitive abilities, such as future planning and patience, in order to deal with the new foraging problems posed by this environment (Rosati, 2017b, c). Indeed, humans are unique in their ability to think and plan for the future, and show abilities to delay gratification that far exceed other primates (Stevens and Stephens, 2008; Suddendorf and Corballis, 2007).

These ecological pressures may have also shaped human decision-making strategies for risk. In fact, the highly cooperative nature of hunter-gatherer foraging is thought to have evolved as a mechanism to buffer the risks associated with humans' dietary specialization on high-reward but high-risk foods. Hunter-gatherer groups engage in several economically risky activities, such as hunting, which requires a high investment of effort in a venture with a low rate of success. Indeed, the majority of hunters are successful at most only half of time (Hawkes et al., 2001; Rosati, 2017c, d). In order to reduce the variability associated with hunting, humans engage in extensive food-sharing with group-mates, exhibiting food transfers at much higher rates than other primates—and especially compared with chimpanzees, who rarely transfer food between adults (Jaeggi and Gurven, 2013; Kaplan et al., 2012; Rosati, 2017c, d). More generally, the high levels of resource variability seen in forager diets suggests that humans, similar to chimpanzees and capuchin monkeys, may have evolved a higher tolerance to risk. Along these lines, people can be quite risk-seeking when making decisions in some contexts (Hertwig and Erev, 2009), even though they are generally risk averse for monetary gains.

In terms of the ecological perspective on decision-making we have used here, humans also seem to be relatively risk-seeking when faced with choices about food that emulate foraging decisions (Hayden and Platt, 2009; Rosati and Hare, 2016). For example, when people are presented with identical experimental procedures involving choices between food rewards as used previously with apes (Rosati and Hare, 2013), they exhibit a preference for the risky option comparable to that shown by chimpanzees (Rosati and Hare, 2016) and capuchin monkeys (De Petrillo et al., unpublished data). This supports the convergent

rationality proposal that species with shared foraging ecologies seem to exhibit similar decision strategies. However, it is important to note that to date little work has examined human decision-making in these experience-based foraging contexts similar to animal studies, so further tests of the ecological hypothesis will require direct comparisons of decision-making between humans and other primates. More generally, this suggests that it is crucial to test people in more naturalistic contexts, not only in simplified laboratory situations, in order to evaluate human rationality from an evolutionary perspective.

6. Conclusions

We have argued that decisions about time and risk depend on ecological context. Species that exploit high-value, costly, and variable food resources seem to show strategies that integrate a high level of temporal patience with risk-seeking preferences. We specifically propose that chimpanzees and capuchin monkeys have independently evolved these strategies because they inhabit similar ecological niches—a case of convergent evolution. In particular, species that inhabit similar ecological conditions may have evolved similar abilities in response to challenges posed by their environment. In the case of chimpanzees and capuchins, both species feed primarily on variable and unpredictable food sources, exhibit extracting foraging behaviors by using tools, and frequently invest energy to obtain uncertain outcomes while hunting. In line with these ecological similarities, these species show high levels of delay tolerance and similar risk-seeking strategies, traits that differentiate them from their closer phylogenetic relatives. Interestingly, capuchins and chimpanzees also seem to show convergence in some of the specific psychological mechanisms supporting their decision strategies, as both exhibit emotional responses to decision outcomes, and these emotions seem to have a similar functional role in both species.

Taken together, these findings support the proposal that cognitive capacities, including decision-making, can be shaped by ecology. 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 with classical notions of economic rationality. These findings highlight the value of a comparative approach for probing the adaptive nature of traits, including different metrics of rationality, and show how comparisons of decision-making across diverse species that vary in their ecological characteristics are critical to understand the evolutionary implications of different choice strategies in the real world. Extending this approach to also include humans, by comparing our own preferences with those of other species, can further provide a new framework for understand human economic behavior. In sum, an evolutionary approach to the study of decision-making is a crucial tool for identifying the ultimate causations of decision-making behaviors.

Declarations of interest

None.

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