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A parasitoid wasp has deposited half of her eggs in a host. She now faces the choice between depositing her remaining eggs in the same host or searching for another. Continuing to deposit in the current host provides the immediate payoff of completing her reproductive duties, allowing her to move on to other activities such as foraging or searching for another mate. Searching for another host, in contrast, delays the payoffs of reproducing until a suitable host is found.

This wasp faces an *intertemporal choice*—that is, a choice between options that involve payoffs available at different times (Read, 2004; Stevens, 2010). These choices typically involve a smaller option available sooner and a larger option available later. In the wasp example, depositing all eggs in one host provides the smaller, sooner option because, though curtailing search sooner, increased offspring competition and risk of total failure reduces the overall benefit of this option. The larger, later option of continuing to search involves a time delay but yields a higher payoff with reduced competition and probability of total brood failure.

In addition to reproductive decisions, animals make these choices on a daily basis when foraging, searching for a mate, seeking shelter, avoiding predators, and interacting with social partners (Stevens, 2010). Many aspects of life history theory provide examples of intertemporal choices. For instance, allocating energy toward reproduction or growth is a classic life history tradeoff that pits the smaller, sooner payoffs of reproducing now vs. the larger, later payoffs for growing and delaying reproduction. At this level of analysis, organisms without a central nervous system, such as plants and bacteria, make intertemporal choices (Kacelnik, 2003). Though not well researched outside of the animal kingdom, researchers have explored intertemporal choices in a wide range of animal species, including insects, fish, birds, rodents, dogs, and primates (Table 1). Comparative psychologists have investigated both why individuals should choose either the smaller, sooner or larger, later option via modeling approaches and how different psychological mechanisms regulate intertemporal choice.

[*Insert Table 1 about here*]

Approaches and theory

The study of intertemporal choice originated fairly independently in economics, psychology, and behavioral ecology, each starting from a particular perspective with different goals and methods. In each of these fields, a different normative theory predicts what individuals *should* choose. Critically, all theories have situations in which choosing the smaller, sooner option is the optimal choice. So, opting for immediate payoffs is not necessarily impulsive. The fields have developed different modeling approaches to investigate whether choices are reasonable or impulsive.

Economic approaches

The notion of intertemporal choice originated with economists modeling how people choose between different streams of future payoffs, for example annual salaries. Samuelson (1937) developed the discounted utility model of intertemporal choice. The temporal discounting approach assumes that individuals generate a present value for an option discounted based on the time delay to receiving it: \$100 available in a year is not as valuable as \$100 available now. The specific form of discounting developed by Samuelson is called *exponential discounting*, which calculates the value of a future benefit as $V = Ae^{-\delta t}$, where V represents the present value, A represents the amount of the benefit, δ represents a discount factor related to the rate of discounting, and t represents the time delay to receiving the benefit. A key prediction of exponential discounting is that the rate of discounting (the proportion of value lost over a given time) remains constant across time (Figure 1). Economists typically test this model by offering human participants real choices between smaller, sooner and larger, later monetary rewards, such as \$100 today vs. \$105 in one month. The empirical data, however, do not support exponential discounting. Instead, they show a decreasing rate of discounting with time delay: value drops sharply at short delays, but the rate of discounting slows with time (Thaler, 1981).

[*Insert Figure 1 about here*]

Psychological approaches

Psychologists interested in the effect of delays to reinforcement on choice behavior developed an independent series of models of intertemporal choice based on the matching law (Herrnstein, 1961), in which individuals should prefer the option with the greatest reinforcement rate, or ratio of reward amount to delay to reinforcement A/t (Chung & Herrnstein, 1967). McDiarmid and Rilling (1965) modified this model by including a free parameter to adjust for bias observed in experimental data: $V = kA/t$, where k represents the free parameter. This *simple reciprocal model* of choice has the inconvenient mathematical property that the value goes to infinity as the time delay approaches zero (Figure 1). Mazur (1987) proposed a modification of this model $V = A/(1+kt)$ that assigns the full amount value (rather than infinite value) when the delay is zero (Figure 1). Though all of these models generate hyperbolic value functions (meaning the proportional decrease in value is steep at short delays and drops as delay increases), Mazur's model has become the standard *hyperbolic discounting model* in the human and animal literatures (Table 2).

[*Insert Table 2 about here*]

In animals, researchers test these models with a number of different intertemporal choice tasks (Table 3). To precisely control aspects of the task needed to estimate model parameters, behavioral psychologists typically use a concurrent-chain procedure or a delay choice task in an operant box. The *concurrent-chain procedure* offers animals (usually pigeons, *Columba livia*) two phases of schedules of reinforcement. In the initial choice phase, subjects choose between two keys that typically lead to a variable interval schedule (a time delay that varies in length around a mean value). After responding to the key again following the expiration of the variable interval, the subject begins the second phase in which it must complete a second schedule of reinforcement. For studies of intertemporal choice, the second phase is often a fixed interval schedule (a fixed time delay) followed by reinforcement (e.g., Grace, Sargisson, & White, 2012). The *delay choice task* (sometimes called self-control or intertemporal choice task) offers animals repeated choices between two simultaneously presented options, one smaller, sooner and one larger, later (McDiarmid & Rilling, 1965). This can involve either arbitrary signals of the options (e.g., colored lights) or visually presenting the actual quantity of food rewards for each option. Once they choose the option, they wait the required time delay to receive the reward amount. These techniques often involve many trials to collect the data needed to create discounting functions (Figure 1).

The repeated nature of the choices for animals differs from the typical one-off choices used in human data. Further, the human experiments usually use time delays of days, weeks, months, or years, whereas animal experiments use seconds or minutes. Despite these methodological differences, the hyperbolic discounting model fits both human and animal data well and better than the exponential discounting model (Green & Myerson, 2004). Hyperbolic discounting outperforms exponential discounting because it captures the decreasing rate of discounting with time delay, which contradicts the exponential model’s requirement of constant discounting. Further, animals show preference reversals not predicted by exponential discounting. For instance, Green et al. (1981) offered pigeons a choice between a smaller, sooner and larger, later reward in which the two reward amounts were held constant and the difference between time delays was always 4 s. As the delay to the smaller reward increased, the pigeons reversed their preferences from the smaller, sooner to the larger, later option, thereby violating the predictions of exponential discounting. Though still the standard model of intertemporal choice in the psychology literature, the hyperbolic discounting model has come under fire in the human and animal literatures for two reasons. First, hyperbolic discounting fails to account for some aspects of behavioral data. Namely, (1) choice data show effects of reward magnitude, sign (gain or loss), and temporal sequences not predicted by hyperbolic discounting (Read, 2004), (2) preference reversals in humans do not fit predictions of hyperbolic discounting (Luhmann, 2013), and (3) hyperbolic discounting models fit to animal data to not generalize to foraging tasks (Blanchard & Hayden, 2015; Luhmann, 2013). Second, hyperbolic discounting fails to provide a clear process model of the mechanisms of intertemporal choice (Rubinstein, 2003; Stevens, 2015).

Behavioral ecological approaches

Behavioral ecologists have also investigated intertemporal choice as a key component of foraging behavior. Foraging requires repeatedly acquiring food as energy is depleted to maintain homeostasis, enhance growth, and invest in reproduction. Foraging choices are embedded in a stream of decisions that influence an organism's energy intake rate. Behavioral ecologists, therefore, frame these choices in terms of maximizing intake rates (Stephens & Krebs, 1986). Models of intake rate share the hyperbolic property of the psychologist's reinforcement models (Figure 1). However, behavioral ecologists started with the assumption that all time components should be included in the models because they influence the long-term intake rate, the critical currency for optimal foraging. Thus, in addition to the time delay between choice and receiving rewards, the delay between consuming food and receiving another choice (travel time, intertrial interval, or post-trial delay) and the time between receiving and completely consuming the reward (handling time) should be included, generating the *long-term rate maximization model*: $R = A/(t + T + h)$, where T represents travel time and h represents handling time. Across a range of natural and artificial foraging tasks, the long-term rate maximization model fits actual choices. In the delay choice task, however, subjects prefer the smaller, sooner option more often than expected by the long-term rate maximization model (McDiarmid & Rilling, 1965). Further, pigeons and blue jays (*Cyanocitta cristata*) neglect changes in the travel time for delay choice tasks (Stephens & Anderson, 2001), which contradicts long-term rate predictions. In rhesus macaques (*Macaca mulatta*), however, enhancing the salience of the travel time can bias choices in ways consistent with long-term rate maximization (Pearson, Hayden, & Platt, 2010).

Bateson and Kacelnik (1996) demonstrated that, though European starling (*Sturnus vulgaris*) choices in a delay choice task did not match long-term rate-maximizing predictions, they did match a short-term rate maximization models that omit the travel time. The birds maximized based only on delay time $R = A/t$ or delay and handling time $R = A/(t + h)$. Cotton-top tamarins (*Saguinus oedipus*) also matched the model that included handling time (Stevens, Hallinan, & Hauser, 2005).

Stephens and Anderson (2001) suggested that the short-term rate model works well because it is equivalent to a long-term rate model in a more naturalistic foraging task. In the *patch use task*, rather than facing a simultaneous choice between two options, individuals receive the small food amount after the short time delay (Table 3). Afterward, individuals must chose to continue to “stay in the patch” for longer to receive more food or leave the patch to initiate the travel time and then another instance of the smaller, sooner option. Stephens and Anderson argued that this stay-or-go choice more closely resembles a natural foraging decision that animals typically face. Since the short-term rate results in the same choices as the long-term rate, and the short-term rate requires tracking less information (travel time), natural selection might favor this simpler rule for foraging decisions (Stephens, 2002). When applied to an artificial foraging task with simultaneously presented options, the rule fails to maximize intake.

Shapiro, Siller, & Kacelnik (2008) also argued that animals rarely face simultaneously available options in their natural foraging environments. They proposed a *sequential choice model* in which the choices between simultaneously presented options result from sampling from the distributions of latencies to choose the individual options. The logic underlying this model is that (1) animals experience options in their environment sequentially and must decide to accept or reject them and (2) the latency to accept an item indicates strength of preference, with highly preferred items having shorter latencies. When two options are presented simultaneously, the animal effectively samples from each option's distribution of latencies and chooses the option with the shortest latency. This model, therefore, provides a window into the process of choice that rate maximization models do not offer. Shapiro et al. found that the sequential choice model outperformed exponential discounting, hyperbolic discounting, and several rate maximization models, with the exception of a short-term rate model that includes choice delay and choice latency, which performed equally well.

Another alternative to the rate-based approach taken by behavioral ecologists is to potentially provide an adaptive account for discounting. Devaluing the future may be beneficial when the future is uncertain (Stephens, 2002). The longer one must wait for a reward, the more likely something will prevent the acquisition of the reward. The parasitoid wasp *Leptopilina heterotoma*, for example, dumps more eggs in a single host as the barometric pressure drops, presumably signaling the possibility of a storm and uncertainty about the wasp's future opportunities to find an additional host (Roitberg, Sircom, Roitberg, van Alphen, & Mangel, 1993). Henly et al. (2008) introduced uncertainty into a delay choice task with blue jays by varying the rate at which the reward was interrupted and not delivered. Though modeling efforts predicted that the interruptions influence intake rates, empirical work suggested that they jays did not attend to the interruptions in the predicted manner. In a different task, however, bonobos (*Pan paniscus*) did reduce waiting times when the reward became more uncertain (Stevens, Rosati, Heilbronner, & Schmücking, 2011). Therefore, under some circumstances, the uncertainty associated with the future can shape intertemporal choices.

Delayed gratification

Much of the intertemporal choice work in economics and behavioral ecology has focused on binary choice, such as the delay choice task. Some psychologists, however, have explored other ways to study intertemporal choice. Notably, Mischel and colleagues (Mischel & Ebbesen, 1970; Mischel, Ebbesen, & Zeiss, 1972) investigated the notion of *delayed gratification*—that is, choosing to defer immediate gratification for higher long-term gain. Though clearly a subset of intertemporal choices, researchers assess delayed gratification using different measures than the delay choice task (Table 3). Mischel and colleagues measured delayed gratification in human children by placing a small reward in front of them (often a cookie or marshmallow) and telling the children that they could have the small reward in front of them or wait until the experimenter returned to receive a larger reward (e.g., two marshmallows). The experimenters then measured how long the children waited.

A key difference between these methods and the delay choice task is that delayed gratification requires the ability to both make a choice for a delayed option and maintain that choice in the presence of a constant temptation for immediate gratification (Beran, 2002; Mischel

& Ebbesen, 1970). In an operant version of a *delay maintenance task*, pigeons could peck a key and receive a low-quality reward or inhibit pecking during a delay to receive a high-quality reward (Grosch & Neuringer, 1981). At any time during the delay, the pigeon could peck the key for the low-quality reward. In a related delayed gratification paradigm called the *exchange task*, subjects receive a small or low-quality reward and must hold onto this reward during the delay and exchange it for a large or high-quality reward (Ramseyer, Pelé, Dufour, Chauvin, & Thierry, 2008). Therefore, subjects must avoid consuming the food in a similar way as the children do but potentially with the food actually in their hands or beaks. Finally, in an *accumulation task*, experimenters provide a stream of rewards at a constant rate, say, one food item every five seconds, and, once the subject reaches for or begins consuming the rewards, the experimenter stops delivering them (Beran, 2002). Though the delay choice task has been tested on more species, recently researchers have begun testing a number of species (particularly primates) in the delayed gratification tasks (Table 1, Figures 2-4).

[*Insert Figures 2-4 about here*]

Understanding measures of intertemporal choice

Having a variety of intertemporal choice measures raises questions about the reliability of choices both within and between tasks. Do individuals have consistent preferences? Do preferences carry over across tasks? Humans show fairly high levels of test-retest reliability for intertemporal choices within the same task, with correlation coefficients around 0.70 after a year (Kirby, 2009). Rats (*Rattus norvegicus*) showed comparable levels of test-retest reliability in a delay choice task over the course of days or weeks (Peterson, Hill, & Kirkpatrick, 2015), and dogs (*Canis familiaris*) showed high correlations within individuals (correlation coefficient =

0.80) in a delay choice tasks after six years (Riemer, Mills, & Wright, 2013). Intertemporal choices appear to be quite stable within individuals across time when using the same task.

Some tasks have different procedures to evaluate intertemporal choices. In the delay choice task, for example, multiple procedures can measure indifference points. Peterson et al. (2015) compared how rats performed in three different indifference point elicitation procedures in which the small amount, short delay, and large amount were constant and the long delay either varied systematically or adaptively. Systematic procedures consistently increased the delay by a fixed unit either after a fixed block of trials or after a fixed number of sessions, regardless of choice. Adaptive procedures adjusted the delay based on the subject's recent choices, increasing the delay when the subject preferred the later option and decreasing the interval when it preferred the sooner option. Though the two systematic procedures (block- and session-based increases) showed high correlations (r = 0.61-0.90), comparisons across systematic and adaptive procedures showed lower correlations (r = 0.08-0.51). This suggests that even within a general type of task, different procedures can result in different patterns of choice, as has also been demonstrated in humans (Hardisty, Thompson, Krantz, & Weber, 2013).

Though researchers use delay choice, exchange, and accumulation tasks to measure intertemporal choice, it is not clear that the different tasks measure the same construct. For example, Addessi et al. (2013) found mixed results when offering the same capuchin monkeys both a delay choice and an accumulation task: one population of monkeys showed a positive relationship across the two tasks, whereas another did not. This matches findings in human children in which neither boys nor girls showed significant correlations between delay choice and delay maintenance (Toner, Holstein, & Hetherington, 1977). The fact that these tasks differ in the presence or absence of a delay maintenance component may explain this difference. The more closely related exchange and accumulation tasks have been tested in the same individuals, but the within individual correlations were not reported (Pelé, Dufour, Micheletta, & Thierry, 2010; Pelé, Micheletta, Uhlrich, Thierry, & Dufour, 2011). Therefore, we do not have clear evidence that the different tasks measure the same components of intertemporal choice.

Psychological mechanisms

With the exception of the sequential choice model (Shapiro et al., 2008), most theoretical approaches to animal intertemporal choice neglect psychological mechanisms that are used to make these choices. Nevertheless, empirical research has begun to uncover the cognitive, motivational, and emotional processes involved in intertemporal choice.

Reward amount and time delay discrimination

Intertemporal choices involve assessing reward amounts and time delays. Though these core abilities are well studied in isolation from intertemporal choices (reviewed in Brannon, 2005; Meck, 2003), surprisingly little is known about how they relate to these choices. Multiple studies have shown that, when time delays are held constant, choices for the larger, later option increase with the magnitude of the large amount, demonstrating sensitivity to reward magnitude (Freeman, Green, Myerson, & Woolverton, 2009; Marshall, Smith, & Kirkpatrick, 2014). Individual differences in sensitivity to magnitude, however, do not correlate with choice in delay choice tasks (Marshall et al., 2014). Humans show an additional effect of reward amount on intertemporal choice (the magnitude effect), in which the discounting rate declines as the magnitude of the rewards increases (Thaler, 1981). Rats show this magnitude effect in concurrent chain tasks (Grace et al., 2012; Orduña, Valencia-Torres, Cruz, & Bouzas, 2013; Yuki & Okanoya, 2014); however, it has not yet been demonstrated in delay choice tasks (Freeman et al., 2009; Green, Myerson, Holt, Slevin, & Estle, 2004).

Time perception is clearly relevant to intertemporal choices as well. Recent work has found that individual differences in the variance in precision for time perception correlate with intertemporal choices, with rats showing poor precision in time estimates choosing smaller, sooner options more than those with more precise time estimates (Marshall et al., 2014; McClure, Podos, & Richardson, 2014). Behavioral interventions that improve the precision of time estimation also increases choices for larger, later options in delay choice tasks, further supporting the notion that timing estimates play a critical role in intertemporal choice (Smith, Marshall, & Kirkpatrick, 2015).

Inhibitory control

Animals have a rather difficult time inhibiting strong prepotent responses to selecting higher magnitude rewards over lower magnitude rewards. This difficulty in inhibitory control is evidenced by the reverse contingency task in which subjects can see both a high and low magnitude reward and must point at the low magnitude reward to receive the high magnitude reward and vice versa (Boysen & Berntson, 1995). Subjects across a wide range of species have a difficult time inhibiting their prepotent responses to choose the high magnitude reward (Shifferman, 2009). Some researchers suggest that this inhibitory control problem is more difficult for amounts than delays and may result in more choice for a larger, later option in delay choice tasks in which the rewards are visible during choice (Addessi et al., 2014; Genty, Karpel, & Silberberg, 2012).

Commitment

One key cognitive strategy that can help overcome the strong temptation to select immediate payoffs over larger but delayed payoffs is the use of commitment devices that rely on the external environment to solve this problem. An example of using commitment in a human intertemporal choice is placing an alarm clock well out of reach, so that when the alarm goes off, you have committed yourself to get up to turn it off. Rachlin and Green (1972) tested commitment in an operant delay choice task in which pigeons had a commitment option to remove the smaller, sooner option from the choice set. Pigeons faced a choice between two keys: one key resulted in a fixed interval before presenting the simultaneous choice between the smaller, sooner and larger, later options, whereas the other key resulted in the same fixed interval, but only the larger, later option was presented afterward. Rachlin and Green then varied the fixed interval to influence the overall reinforcement rate, which determines whether the smaller, sooner or larger, later option yields the higher reinforcement rate. Pigeons, in fact, used the commitment option more when the larger, later option offered the higher rate, suggesting that they could use this commitment device to prevent succumbing to the temptation for the smaller, sooner option when it yielded lower payoffs.

Attention and distraction

A related cognitive strategy used to avoid the temptation of immediate gratification is directing attention away from the smaller, sooner option. Mischel and Ebbeson (1970) measured whether attention to the rewards influenced delayed gratification in children by leaving the smaller reward, larger reward, both rewards, or neither reward in sight during the delay. They found that having any rewards in view prevented the children from waiting for the delayed reward. Grosch and Neuringer (1981) conducted a similar study in pigeons by varying whether both small and large rewards were visible during the waiting period of an operant delayed gratification task. Matching the findings with children, the pigeons waited longer when the food was not visible. In contrast, Genty et al., (2012) found that long-tailed macaques (*Macaca fascicularis*) chose the larger, later option more in a delay choice task when both food rewards were visible compared to hidden. Though the pigeon and children's data imply that attention to any rewards triggers choice for the smaller, sooner option, Genty et al. argued that the visibility of rewards focuses attention exclusively on the large reward, triggering the prepotent response for larger over smaller.

In addition to manipulating the visibility of food rewards, Mischel et al. (1972) manipulated the overall salience of the rewards by comparing a condition in which experimenters instructed children to think about the rewards during the delay to a condition with no instructions to think about rewards. Children waited less for rewards when instructed to think about them. Grosch and Neuringer (1981) mimicked this scenario in pigeons by comparing a condition with an illuminated food bin during the delay to a condition with a darkened food bin. The pigeons waited less with an illuminated food bin, matching the finding in children that enhancing attention to the reward reduces delayed gratification.

Though visibility can draw attention to the reward, individuals may be able to use distraction to break this attention. Mischel et al. (1972) not only enhanced children's attention to the reward but also provided potential distractions by offering toys for children to play with during the delay. Children who had toys to play with waited longer than children without toys. Similarly, Grosch and Neuringer (1981) found that pigeons waited longer when given an additional key to peck in the rear of the operant box compared to when the key was not present. Evans and Beran (2007a) took the study of distraction a step further by assessing whether chimpanzees (*Pan troglodytes*) can self-distract in an accumulation task. Like Michel et al., the chimpanzees experienced the accumulation task with and without toys provided in the room. In a third condition, toys were provided in the room, but the subject could not access the rewards from the accumulation task. Three out of four chimpanzees received more rewards (a proxy for length of time waited) when toys were present than when absent, suggesting that toys distracted the chimpanzees. Moreover, three out of four chimpanzees also manipulated the toys more when the accumulation of rewards was accessible compared to when not accessible, indicating that the subjects may have actively self-distracted to earn more rewards. Thus, distraction is not only passive but can be an active strategy specifically aimed at delaying gratification.

Working memory

Some psychological approaches to intertemporal choice attribute impulsivity and self-control to executive function, or the "control mechanisms that modulate the operation of various cognitive subprocesses" (Miyake et al., 2000, p. 50). Working memory is often touted as a key exemplar of executive function that has demonstrated connections to intertemporal choice in humans. Namely, individual differences in working memory correlate with differences in intertemporal choice (Shamosh et al., 2008), and explicit training in working memory performance reduce impulsive choice (Bickel, Yi, Landes, Hill, & Baxter, 2011). Experiments with rats replicate the correlational work, with subjects who chose larger, later options in a delay choice intertemporal choice task also performing well on an operant delayed matching-to-sample working memory task (Renda, Stein, & Madden, 2014). A study using a radial arm maze task to test working memory in rats, however, did not show a relationship between intertemporal choice and working memory (Dellu-Hagedorn, 2006). Further, intertemporal choice in rats did not respond to trained improvement in working memory performance (Renda, Stein, & Madden, 2015). The role of working memory in animal intertemporal choice, therefore, remains unresolved.

Prospective cognition

Intertemporal choices involve dealing with future rewards. But do these choices require animals have prospective cognition in which they represent the future and plan based on this representation (Stevens, 2011; Thom & Clayton, 2014)? Prospective cognition has been explored across a range of species in a variety of contexts (Raby & Clayton, 2009). For instance, Western scrub jays (*Aphelocoma californica*) have demonstrated elements of prospective cognition in a number of caching tasks (Clayton & Dickinson, 1998; Raby, Alexis, Dickinson, & Clayton, 2007). These studies use rather short time delays to recovery (on the order of hours or days), so we do not know whether prospective cognition is tapped for the longer-term caching decisions that these corvids face in the wild. Nevertheless, given that caching decisions offer a natural example of intertemporal choices (Stevens, 2010; Thom & Clayton, 2014), the work on prospective cognition in caching situations connects this cognitive mechanism to animal intertemporal choice.

Another potential example of prospective cognition relevant to these choices is route planning. Both brown capuchin monkeys (*Sapajus apella*) and chacma baboons (*Papio ursinus*) travel from a sleeping site directly to more preferred food locations, bypassing less preferred food on the way (Janson, 2007; Noser & Byrne, 2007). The direct nature of the travel in the absence of visual access to the goal implies that the primates prospectively planned their routes. The fact that they bypassed nearby food indicates that they opted for a larger, later (more distant) reward over a smaller, sooner (less distant reward), a key characteristic of intertemporal choice. Therefore, we have hints that animals may use elements of prospective cognition to make intertemporal choices. More research is needed, however, to investigate how and whether animals use representations about the future in intertemporal choices (Stevens, 2011; Thom & Clayton, 2014).

Motivational mechanisms and emotional responses

In addition to cognitive mechanisms, intertemporal choices involve motivational and emotional mechanisms. Hunger levels are a key motivational factor influencing choice. But should hungry individuals place greater emphasis on getting food sooner or on getting more food? The empirical data reflect this ambiguity. In some studies, for example, pigeons' deprivation level did not influence choice in the delayed choice task (Logue, Chavarro, Rachlin, & Reeder, 1988; Logue & Peña-Correal, 1985). In other studies, increasing deprivation in pigeons increased choice for the smaller, sooner option (Eisenberger, Masterson, & Lowman, 1982; Snyderman, 1983), and honeybees (*Apis mellifera*) showed similar effects (Mayack & Naug, 2015). In contrast, rats demonstrate the opposite finding for liquid rewards (Bradshaw & Szabadi, 1992; Christensen-Szalanski, Goldberg, Anderson, & Mitchell, 1980). Thus, hunger plays a central motivational role for intertemporal choice, but we have yet to unravel the complexity of its motivational effects.

Waiting for the delayed rewards can prove difficult for animals. Rosati and Hare (2013) measured behaviors associated with stress and affect (negative vocalizations, scratching, and banging) in chimpanzees and bonobos during the delay of a delayed choice task. Both chimpanzees and bonobos exhibited all three of these measures more following choice for the larger, later option than following choice for the smaller, sooner option. Yet, individual measures of negative affect did not correlate with individual measures of choice. The species did differ, however, in negative affect, with chimpanzees showing more negative vocalizations than bonobos. This maps onto a species difference in choice where chimpanzees waited longer than bonobos. So, though chimpanzees show more negative reactions to waiting, they wait longer than bonobos. More work is need to disentangle how motivational influences and emotional responses interact with intertemporal choice.

Conclusion

Research on animal intertemporal choice has come a long way in the last 50 years, since McDiarmid and Rilling's (1965) work on the effect of reinforcement rate on pigeon choices. Theorists have developed a rich set of models that capture the behavioral dynamics of these choices. Importantly, this theory is moving beyond 'as-if' models that purely predict behavior (Berg & Gigerenzer, 2010) to develop models of the cognitive process (e.g., Shapiro, Siller, & Kacelnik, 2008; Stevens, 2015). The empirical work on intertemporal choice has greatly expanded recently to test a variety of species across a range of taxa, including invertebrates and fish, as well as birds and mammals (Table 1). Moreover, comparative psychologists are developing and testing multiple methods to examine different components of intertemporal choice (Table 3). Research on humans clearly demonstrates different subcomponents of impulsivity, where performance correlates across some tasks but not others. Animal intertemporal choice shows a similar mix of relationships across tasks. Delay choice and delay maintenance tasks do not seem to result in similar behavior patterns (Addessi et al., 2013). More work is needed in this area, however, especially comparing performance on the more similar exchange task and accumulation task.

From basic timing, quantification, inhibitory control, and attention processes to more cognitively demanding effects of distraction and prospective cognition, research on psychological mechanisms associated with intertemporal choice has increased rapidly in recent years. Further, new developments in motivational and emotional processes shed light on novel mechanisms of animal intertemporal choice. A mature research program to fully understand intertemporal choice, however, requires integration across a number of levels of analysis. Research in the genetic (Mitchell, 2011), neural (Kalenscher et al., 2005), and hormonal

(Bayless, Darling, & Daniel, 2013) underpinnings of choice begin to complete our understanding of the proximate mechanisms of intertemporal choice. Yet, these proximate mechanisms need to be connected to and informed by the ultimate, adaptive explanations for intertemporal choice (Fawcett, McNamara, & Houston, 2012; Stevens & Stephens, 2009). Current work indicates that feeding ecology (Rosati, Stevens, Hare, & Hauser, 2007; Stevens et al., 2005), social system (Amici, Aureli, & Call, 2008), and allometric scaling (Stevens, 2014) predict intertemporal choice. But researchers have not properly integrated evolutionary factors with the mechanistic approach to these choices. A complete understanding of how and why humans and other species make intertemporal choices requires further integration of proximate and ultimate approaches, leveraging models and methods from a range of disciplines.

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Table 1

First references for various species tested in different intertemporal choice tasks

Species	Delay choice task	Exchange task	Delayed gratification task
Honey bee (*Apis mellifera*)	(Cheng, Penea, Porter, & Irwin, 2002)		
Guppy (*Poecilia reticulata*)	(Mühlhoff, Stevens, & Reader, 2011)		
Pigeon (*Columba livia*)	(McDiarmid & Rilling, 1965)		(Grosch & Neuringer, 1981)
Chicken (*Gallus gallus domesticus*)	(Abeyesinghe, Nicol, Hartnell, & Wathes, 2005)		
European starling (*Sturnus vulgaris*)	(Bateson & Kacelnik, 1995)		
Blue jay (*Cyanocitta cristata*)	(Stephens & Anderson, 2001)		
Pinyon jay (*Gymnorhinus cyanocephalus*)	(Stevens, Kennedy, Morales, & Burks, 2015)		
Western scrub jay (*Aphelocoma californica*)	(Thom & Clayton, 2014)		
Carrion crow (*Corvus corone*)		(Dufour, Wascher, Braun, Miller, & Bugnyar, 2012;	(Hillemann, Bugnyar, Kotrschal, & Wascher, 2014)

		Wascher, Dufour, & Bugnyar, 2012)	
Common raven (*Corvus corax*)		(Dufour et al., 2012)	(Hillemann et al., 2014)
Goffin's cockatoo (*Cacatua goffini*)		(Auersperg, Laumer, & Bugnyar, 2013)	
African grey parrot (*Psittacus erithacus*)			(Vick, Bovet, & Anderson, 2010)
Mouse (*Mus musculus*)	(Mitchell, 2014)		
Rat (*Rattus norvegicus*)	(van Haaren, van Hest, & van de Poll, 1988)		(Reynolds, de Wit, & Richards, 2002)
Domestic dog (*Canis familiaris*)	(Wright, Mills, & Pollux, 2012)	(Leonardi, Vick, & Dufour, 2012)	
Black-and-white ruffed lemur (*Varecia variegata*)	(Stevens & Mühlhoff, 2012)		
Red ruffed lemur (*Varecia rubra*)	(Stevens & Mühlhoff, 2012)		
Black lemur (*Eulemur macaco*)	(Stevens & Mühlhoff, 2012)		
Cotton-top tamarin (*Saguinus oedipus*)	(Stevens et al., 2005)		
Common marmoset (*Callithrix jacchus*)	(Stevens et al., 2005)		
Squirrel monkey (*Saimiri sciureus*)			(Anderson, Kuroshima, & Fujita,

			2010)
Brown capuchin (*Sapajus apella*)	(Amici et al., 2008)	(Ramseyer et al., 2008)	(Anderson et al., 2010)
Black-handed spider monkey (*Ateles geoffroyi*)	(Amici et al., 2008)		
Rhesus macaque (*Macaca mulatta*)	(Szalda-Petree, Craft, Martin, & Deditius-Island, 2004)		(Evans & Beran, 2007b)
Long-tailed macaque (*Macaca fascicularis*)	(Tobin, Logue, Chelonis, & Ackerman, 1996)	(Pelé et al., 2010)	(Pelé et al., 2010)
Tonkean macaque (*Macaca tonkeana*)		(Pelé et al., 2011)	(Pelé et al., 2011)
Lowland gorilla (*Gorilla gorilla*)	(Amici et al., 2008)		
Orangutan (*Pongo pygmaeus*)	(Amici et al., 2008)		(Beran, 2002)
Bonobo (*Pan paniscus*)	(Rosati et al., 2007)		(Stevens et al., 2011)
Chimpanzee (*Pan troglodytes*)	(Rosati et al., 2007)	(Dufour, Pelé, M, & Thierry, 2007)	(Beran, Savage-Rumbaugh, Pate, & Rumbaugh, 1999)
Human (*Homo sapiens*)	(Rodriguez & Logue, 1988)	(Steelandt, Thierry, Broihanne, & Dufour, 2012)	(Mischel & Ebbesen, 1970)
Total number of	24	9	14

species

Table 2

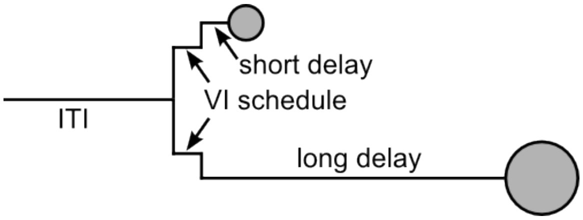
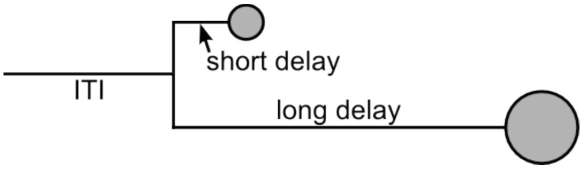
Models of intertemporal choice

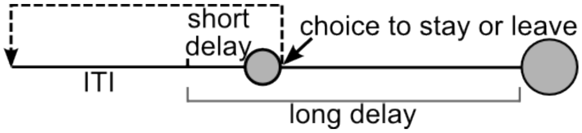
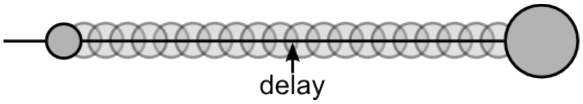
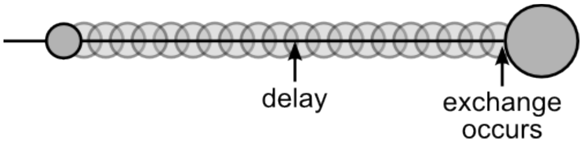
Functional form	Model	Reference
$V = Ae^{-\delta t}$	Exponential discounting	(Samuelson, 1937)
$V = A/t$	Matching	(Chung & Herrnstein, 1967)
$V = kA/t$	Simple reciprocal	(McDiarmid & Rilling, 1965)
$V = A/(1+kt)$	Hyperbolic discounting	(Mazur, 1987)
$R = A/(T + t + h)$	Long-term rate maximization	(Stephens & Krebs, 1986)
$R = A/t$ or $R = A/(t + h)$	Short-term rate maximization	(Bateson & Kacelnik, 1996; Stephens & Anderson, 2001)

Notes: V = value of option, R = intake rate, A = reward amount, t = time delay between choice and onset of reward availability, T = time delay between consumption of reward and choice (intertrial interval), h = time between onset of reward availability and final consumption (handling time), δ and k = free parameters associated with discounting rates and amount and time sensitivity.

Table 3

Intertemporal choice and delayed gratification tasks

Task	Description	Representative reference
Concurrent chain	In an operant task, subject chooses between a variable interval followed by a smaller, sooner reward and a variable interval followed by a larger, later reward. 	(Herrnstein, 1964)
Delay choice	Subjects choose between a smaller reward available sooner and larger reward available later. This can be an operant task in which symbols represent the two options or a physical task in which the subjects can see the actual rewards when choosing between them. 	(McDiarmid & Rilling, 1965)
Patch use	In an operant task, subject initiates trial and waits for short delay before smaller reward is delivered. Then it chooses between continuing on to receive	(Stephens & Anderson, 2001)

	more reward (with total time equaling long delay and total reward equally larger reward) or starting a new trial. 	
Delay maintenance	In an operant or physical task, subjects can select an option at any time that immediately delivers a smaller reward or wait until a delay expires to receive a larger reward. 	(Grosch & Neuringer, 1981)
Exchange	Subject receives smaller or lower-quality reward and must wait time delay and exchange it with experimenter to receive larger or higher-quality reward. 	(Dufour et al., 2007)
Accumulation	Experimenter or machine delivers rewards at fixed rate (e.g., 1 reward per second). Once subject reaches for reward or puts reward in its mouth, rewards stop accumulating.	(Beran et al., 1999)

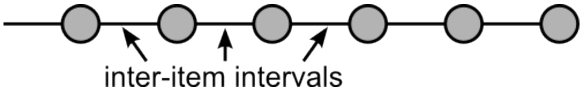

inter-item intervals

Figure 1

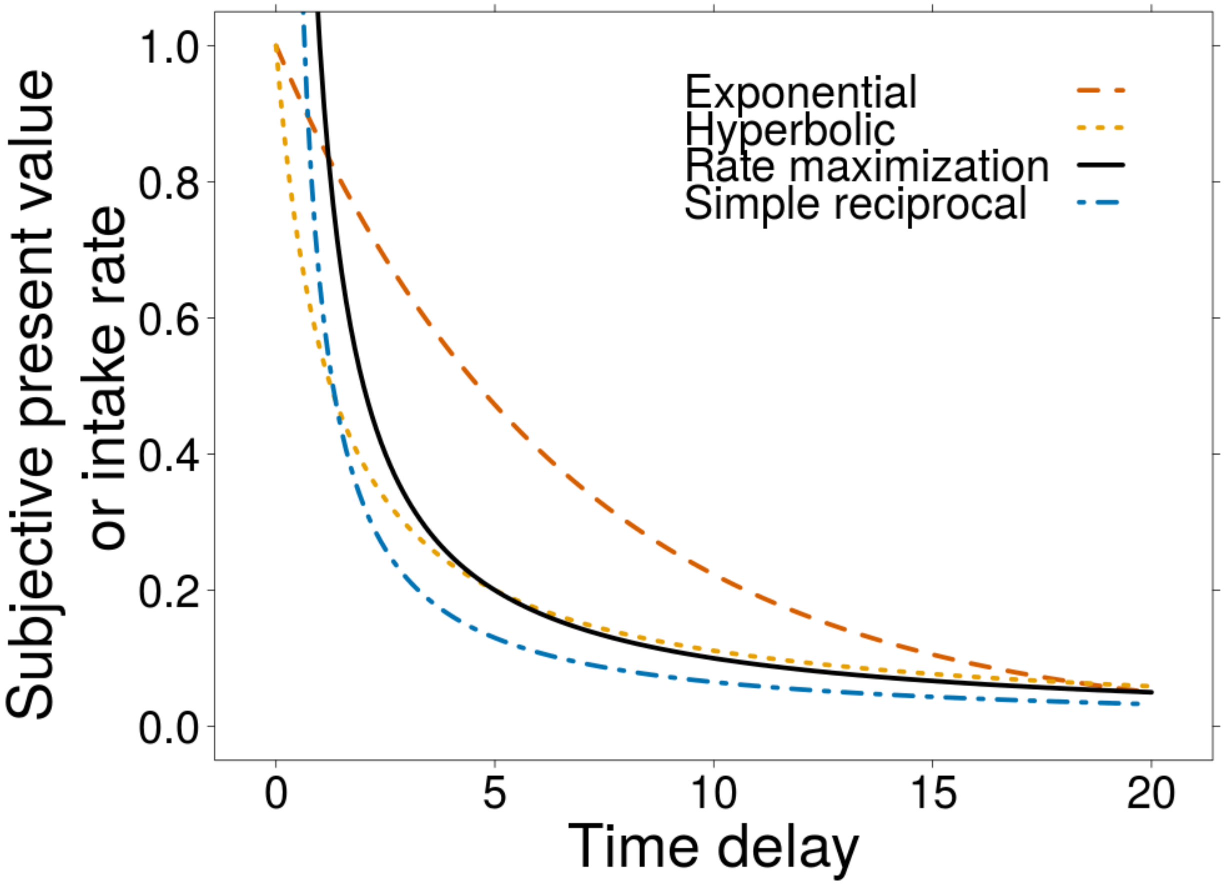


Figure 1: Intertemporal choice model predictions. Different models of intertemporal choice illustrate how the subjective present value of a delay reward or the reward intake rate decreases with time delay. Exponential discounting predicts a constant rate of discounting, whereas hyperbolic, simple reciprocal, and rate maximization predicts a decreasing rate of discounting. Rate maximization is a special case of simple reciprocal.

Figure 2

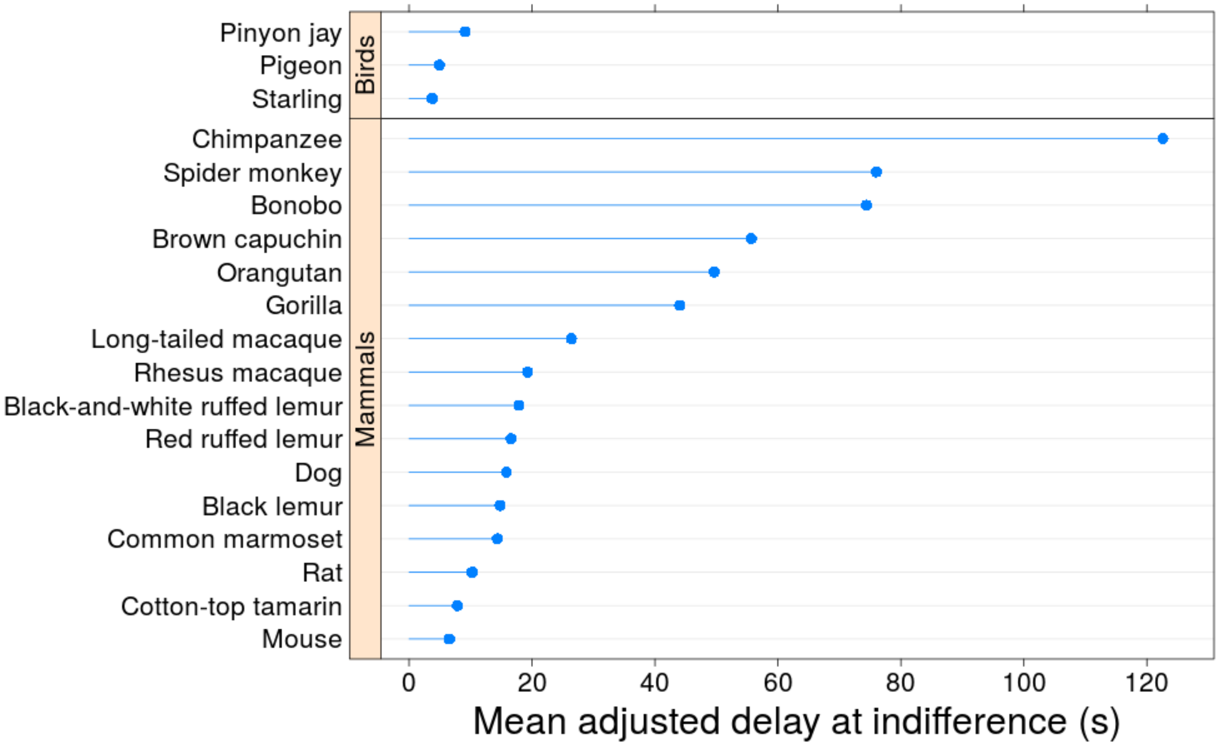


Figure 2: Delay choice titration task data. In the titration task, the experimenter adjusts the amount or delay to find a point at which the subject is indifferent between a smaller amount available immediately and a larger amount available later. Though not all data here use the same methods, here they are converted into comparable data that provide the mean delay at which subjects are indifferent between one food item available immediately and three food items available after a delay. Date taken from: pinyon jays (Stevens et al., 2015), pigeons (Green, Myerson, Shah, Estle, & Holt, 2007), European starlings (Bateson, Brilot, Gillespie, Monaghan, & Nettle, 2015), chimpanzees (Rosati et al., 2007), black-handed spider monkeys (Amici et al., 2008), bonobos (Rosati et al., 2007), brown capuchins (Addessi, Paglieri, & Focaroli, 2011; Amici et al., 2008), orangutans (Amici et al., 2008), lowland gorillas (Amici et al., 2008), long-tailed macaques (Amici et al., 2008; Tobin et al., 1996), rhesus macaques (Louie & Glimcher,

2010; Pearson et al., 2010), black-and-white ruffed lemurs (Stevens & Mühlhoff, 2012), red ruffed lemurs (Stevens & Mühlhoff, 2012), domestic dogs (Wright et al., 2012), black lemurs (Stevens & Mühlhoff, 2012), common marmosets (Stevens et al., 2005), Wistar rats (Perry, Larson, German, Madden, & Carroll, 2004), cotton-top tamarins (Stevens et al., 2005), and mice (Mitchell, 2014).

Figure 3

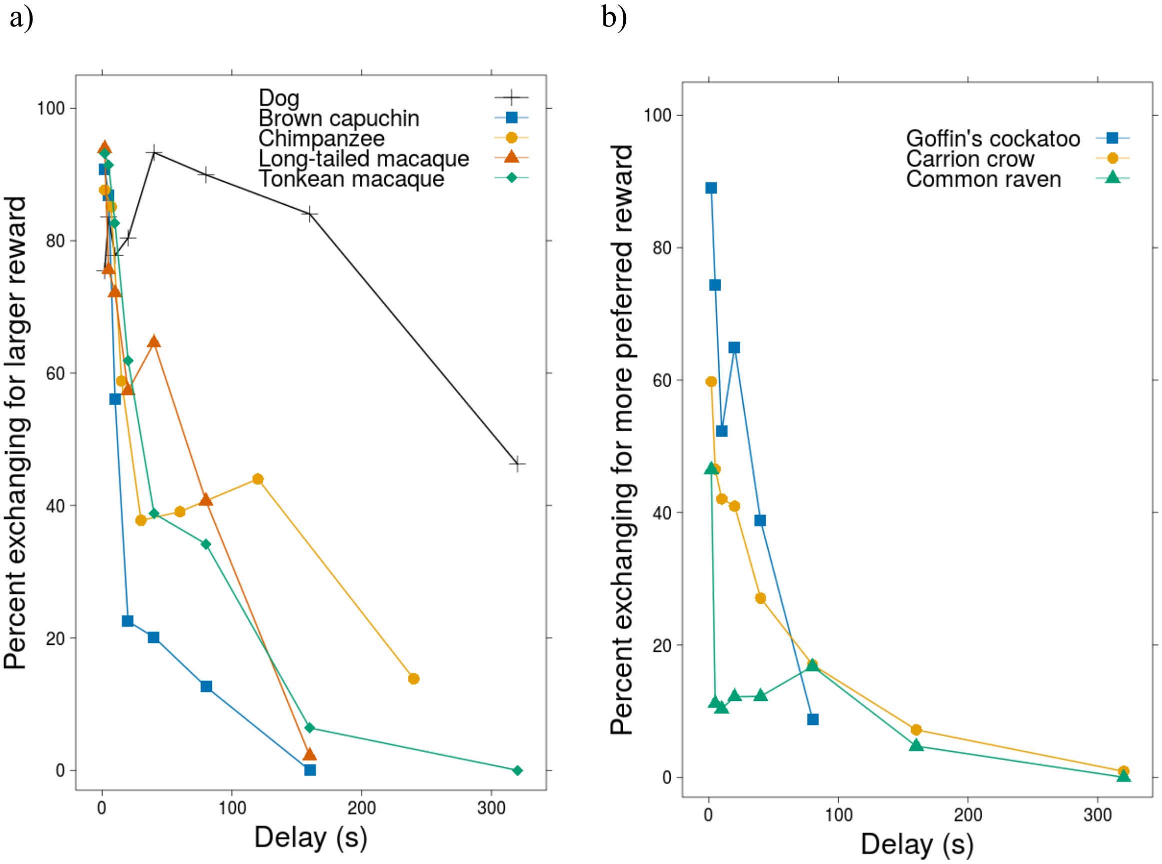


Figure 3: Exchange task data. Different experiments require exchanging (a) a smaller reward for a larger reward or (b) a less preferred reward for a more preferred reward. For the quantitative exchange task (a), subjects exchanged for a larger reward eight times the size of the smaller reward. Exchanges tend to decrease with the delay to exchange. Date taken from: domestic dogs (Leonardi et al., 2012), brown capuchins (Pelé et al., 2011), chimpanzees (Dufour et al., 2007), long-tailed macaques (Pelé et al., 2010), Tonkean macaques (Pelé et al., 2011), Goffin's cockatoos (Auersperg et al., 2013), carrion crows (Wascher et al., 2012), common ravens (Wascher et al., 2012).

Figure 4

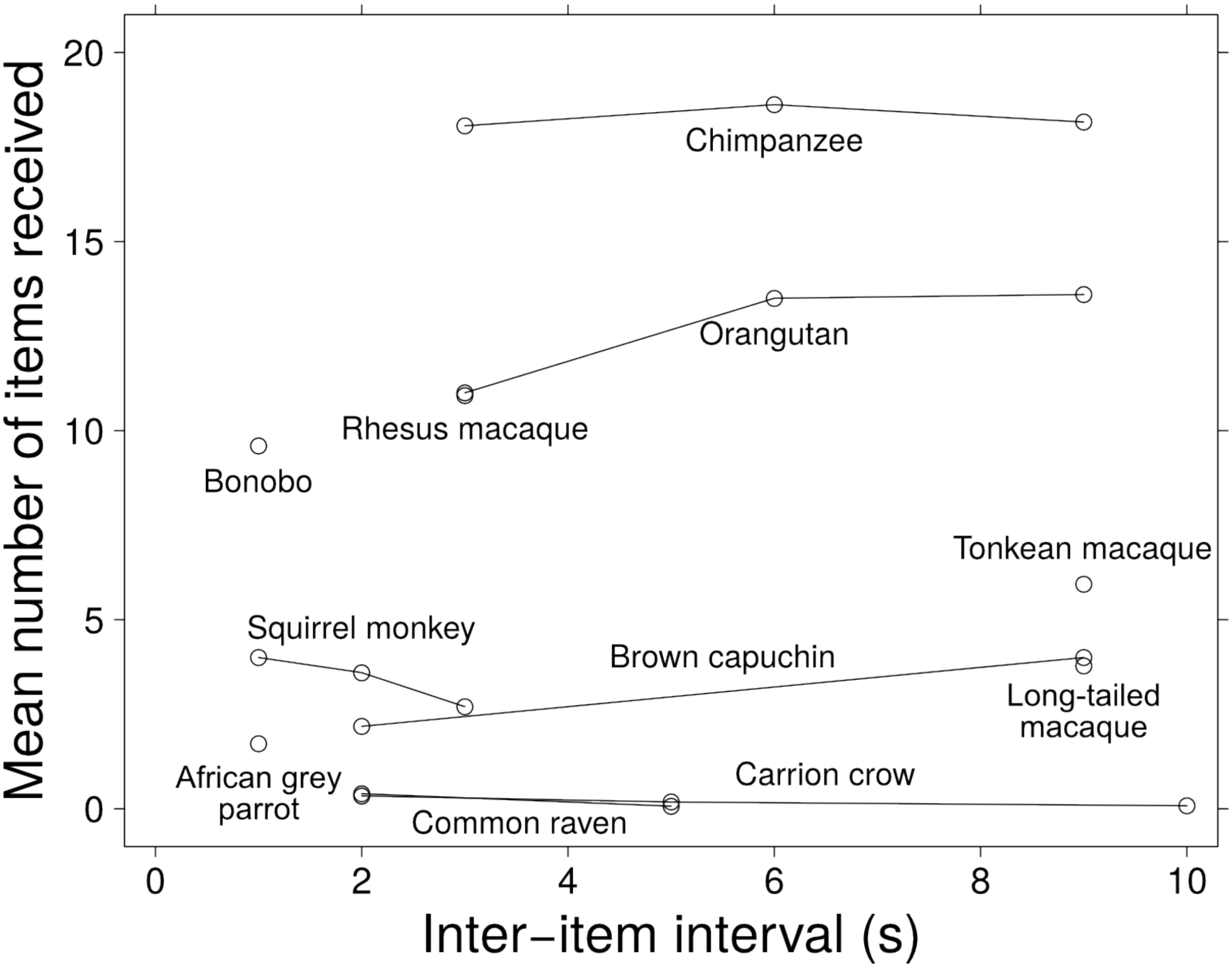


Figure 4: Accumulation task data. In the accumulation task, rewards accumulate as a machine or experimenter releases food rewards at a fixed inter-item interval. Species vary in the number of items that they receive. Date taken from: African grey parrots (Vick et al., 2010), carrion crows (Hillemann et al., 2014), common ravens (Hillemann et al., 2014), squirrel monkeys (Anderson et al., 2010), brown capuchins (Addessi et al., 2013), long-tailed macaques (Pelé et al., 2010), rhesus macaques (Evans & Beran, 2007b), Tonkean macaques (Pelé et al., 2011), orangutans (Beran, 2002), bonobos (Stevens et al., 2011), and chimpanzees (Beran, 2002).