Delay of gratification in non-human animals:

A review of inter-specific variation in performance

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Abstract

The ability to regulate and withhold an immediate behaviour in pursuit of a more preferred or valuable, albeit delayed, outcome is regarded as an important cognitive ability enabling adaptive decision-making in both social and asocial contexts. Abilities to cope with a delay in gratification have been investigated in a range of species using a variety of experimental paradigms. The present study attempts a first systematic evaluation of available experimental data from non-human animals, which is an essential basis for quantifying biological and non-biological factors (*e.g.* socio-ecology *versus* experimental design) affecting performance in delay of gratification tasks. Data were sourced from 52 separate studies, and a comprehensive overview of the available literature on delay of gratification in non-human animals is presented. We present data from 21 species, spanning across eight taxonomic order, with 1–9 species tested per taxonomic group. We highlight variation in experimental paradigms used to study delay of gratification abilities in non-human animals, both with regard to reward type or experimental setup, and discuss the implications for comparative analyses. We conclude that, at present, cross-species comparisons of delay of gratification abilities are hindered by a lack of consistency in experimental designs and low number of species tested across taxonomic orders. We hope to stimulate research on a more diverse set of species, and that future studies consider potential social and ecological factors that cause intra-specific variation in test performances, that is repeatedly seen across species.

Key words: comparative psychology, delay of gratification, delay maintenance, delay choice, non-human animals, self-control

Introduction

Animals, including humans, are frequently faced with decisions that affect what options or rewards become available in the future ('intertemporal choice', Stevens et al., 2011). For example, in cooperative interactions, individuals often invest time and energy although no immediate benefits are derived from reciprocation. In a foraging context, individuals may refrain from eating fruits upon first encounter in order to have riper fruits available in the future (Rosati 2017). In competitive contexts, if aggression is to be avoided, subordinate individuals must often wait in order to obtain access to resources monopolised by higher-ranking conspecifics (Bräuer et al. 2007). Intertemporal choices are also applicable to mate choice scenarios, wherein a female must decide whether to mate with an immediately available partner or whether to wait for a higher-quality mate (Sozou and Seymour 2003; Fawcett et al. 2012). Waiting, however, bears risks, as resources might become depleted, or an individual may not survive long enough for the reward to be harvested (Stevens and Stephens 2010; Hayden 2019).

The ability to delay gratification is one of the most challenging forms of behavioural inhibition, and enables adaptive decision-making in both social and asocial contexts (Beran 2015, 2018). Performance in delay of gratification tests is assumed to vary across individuals and to be linked to traits regulating motivational and control processes (Casey et al. 2011). In humans, such abilities are correlated with healthy dietary habits and financial wellbeing (Mischel 2014). Delay of gratification abilities during childhood have been suggested to predict positive outcomes later in life, *e.g.* in the context of social and academic competence (Mischel et al. 1988), resilience (Shoda et al. 1990), mental health (Tangney et al. 2004), and physical health, financial wealth, and low criminal activity (Moffitt et al. 2011). However, a recent replication of the famous Stanford

marshmallow test - during which a child was offered a choice between one small but immediate reward or two small 'future' rewards if they waited for a set period of time - challenged the direct link between delay of gratification performance as a child and achievements later in life. While an association was found between the two components, effects were sensitive to the inclusion of control variables describing (i) family and (ii) parental-educational and economic background (Watts et al. 2018); but see Michaelson and Munakata, 2019).

Since the second half of the 20th century, the ability to delay gratification has attracted considerable scientific interest from an array of disciplines, ranging from human economics (Frederick et al. 2002), psychology (Mischel et al. 1989), pharmacology (Evenden and Ryan 1996), and neuroscience (Casey et al. 2011), to animal cognition and behavioural ecology (Kacelnik and Bateson 1997; Miller et al. 2019). Measures of delay of gratification for non-human animals are often interpreted in a comparative context, *i.e.* some species are considered more or less able than others to delay gratification, *e.g.* (Miller et al. 2019). In non-human animals, the ability to delay gratification is typically assessed using established experimental paradigms: accumulation of rewards, exchange of rewards, hybrid delay task, and an intertemporal choice task that offers an immediate and a delayed option (for a detailed overview of tasks see Stevens 2017; Beran 2018; Miller et al. 2019). Successful experimental trials typically require two components: the selection of a delayed reward over an immediate option, *i.e.* 'delay choice', and the ability to sustain the decision even when the alternative, immediate reward is maintained within reach throughout the delay, *i.e.* 'delay maintenance' (Stevens and Stephens 2010). The ability to delay gratification is commonly evaluated as a measure of maximum delay endured, *e.g.* (Pelé et al. 2010; Dufour et al. 2012; Auersperg et al. 2013; Hillemann et al. 2014). In this particular experimental paradigm, namely the exchange task, only those focal subjects that successfully wait at least once in a given

condition are further tested, while subjects that fail to wait are removed from the experiment. Given such a design, the results of these studies reflect only the behaviour of a limited number of individuals in a low number of trials, which may not be representative of larger populations or of the species in general (Dufour et al. 2012; Hillemann et. 2014). Another measure for the ability to delay gratification that is reported frequently in non-human animal studies is the mean number of trials during which an individual was successful (*i.e.* managed to wait the required time) within a given delay condition. However, other measures of waiting performance have been used.

A major concern associated with the comparison of inhibitory control abilities among studies or between species is that measures of such abilities are not always correlated when different experimental paradigms are used (Addessi et al. 2013; Brucks et al. 2017). A meta-analysis by Duckworth and Kern (2011) on inhibitory control in humans revealed that cognitive inhibition tasks and delay of gratification questionnaires yielded moderately correlated measures of self-control (Duckworth and Kern 2011). Potential challenges associated with the assessment of individual inhibitory control abilities and comparing performances across tasks remain relatively unexplored in the non-human animal literature (but see: Bray et al. 2014; Marshall-Pescini et al. 2015; Müller et al. 2016). Further, at present, no formal agreement exists with regard to which measures can be reliably used to quantify the ability to delay gratification – *e.g.* does a minimum delay have to be endured, how many individuals need to endure the delay, and in what percentage of trials? It is also unclear whether inter-individual variations in maximum delay tolerated reflects biologically meaningful differences in non-human animals. Considering the complexity of inhibitory control and its components, it remains questionable whether any single measure can be regarded as a comprehensive or reliable evaluation of an individual's inhibition capacities (Brucks et al. 2017).

The present paper offers a systematic review of the available literature on experimental studies reporting delay of gratification performances in non-human animals. We aim to synthesise the available empirical evidence and to investigate whether waiting performance, *i.e.* mean percentage of successful waiting trials, can be compared across different species from a range of taxonomic groups. We further aim to describe how different experimental paradigms can affect waiting performance in different species. We outline gaps in the literature, which include the observations that (i) only a few species from a narrow taxonomic range have been tested so far, and (ii) that there is little standardisation of both experimental paradigms and reporting of results. We hope that our review stimulates future studies that address and close the gaps in the literature we identified here, to eventually enable systematic explorative analyses of biological (*e.g.* socio-ecology) and non-biological (*e.g.* experimental paradigm) factors affecting delay of gratification abilities.

Methods

Search protocol and criteria for inclusion

Literature searches were performed through the Web of Science research platform on August 22, 2019. An initial search for 'delay of gratification', 'delayed gratification', 'self-control', 'impulse control', 'impulsivity', 'inhibitory control', or 'intertemporal choice' as keywords yielded 35,268 abstracts. A further search in Scopus for the keywords 'delay of gratification', 'delayed gratification', 'self-control', 'impulse control', 'impulsivity', 'inhibitory control', or 'intertemporal choice' in abstract, title, keywords limit to biological sciences yielded a further 1,095 abstracts. In addition to the 36,363 records found through database searching, 20 studies were identified through alternative sources, such as a recent review by Miller et al. (2019). Abstracts were screened for inclusion and more than 99 % of studies were discarded due to the inclusion of humans as study subjects (36,298 studies). A further 33 studies were excluded from analysis owing to the relevant data being unavailable; only studies that presented mean percentages of successful trials, *i.e.* number of trials in which the focal individual waited out of the total number of trials, and which specified duration of the delay were selected. Further, research with forced learning trials was excluded from this study. A total of 52 papers were included in the present systematic review. See Figure 1 for a diagram of the search results and study selection process.

From each included study, the mean percentage of successful trials of all tested individuals in a given delay condition was recorded. In the instance of focus animals being tested under multiple delay conditions, performances in each condition were recorded, resulting in multiple data entries per study. Experimental paradigm used (exchange, accumulation, go/no-go, intertemporal choice, rotating tray task) and reward type (qualitative, *i.e.* gain of a more preferred reward after a given delay; or quantitative, *i.e.* gain of more of the same rewards after a given delay) were also

recorded. Mean percentage of successful trials was recorded for each focal individual in a given delay condition. The dataset generated and analysed in the current study are available as electronic supplementary materials.

Descriptive Analysis

We describe the effect of a number of target factors on species' performance in self-control tasks. Target factors included biological order, context (qualitative *versus* quantitative), amount of reward, duration of delay (seconds), form of delay test (maintenance *versus* choice), and experimental paradigm (accumulation, exchange, go/no-go, inter temporal choice, rotating tray); indicators of species' performance included mean percentage of successful waiting trials and maximum endured delay. We refrained from a more formal explorative statistical analysis of the presented dataset due to the data being patchy and not balanced, as species were rarely tested in multiple different experimental paradigms.

Results

Responses to delay of gratification tasks were analysed for 21 species - spanning across different taxonomic groups - tested under five different experimental paradigms. Primates are the most studied biological group, with nine species tested in total, followed by Passeriformes and Rodentia (five species each) and Psittaciformes (three species; Table 1). No species was tested in all five experimental paradigms; on average (± standard deviation, SD), species were tested in 1.4 (± 0.8) paradigms. The brown capuchin monkey, *Cebus apella,* was tested in four paradigms, making it the most-studied species. Only three of all tested species (14 %) were tested in both delay maintenance and delay choice tasks, and nine species (43 %) were tested in both quantitative and qualitative contexts.

Mean percentage of successful waiting trials ranged from 19 % successful trials in Passeriformes (n = 5) to 82 % successful trials in Psittacidae, Psittaciformes (n = 1). Range of performances in different orders and qualitative as well as quantitative tasks are shown in Figure 2. For most orders in which multiple species were tested under different paradigms, performance in tasks is highly variable (*e.g.* Primates, Passeriformes, Rodentia). Mean percentage of successful waiting trials decreased with duration of delay (Figure 3). Waiting performance varied in different experimental paradigms and was higher in delay choice (mean ± SD: 54 ± 23) compared to delay maintenance tasks (mean ± SD: 41 ± 33; Figure 4). Here, performance showed pronounced variation across different studies.

Discussion

The present study provides a systematic review of experimental data on delay of gratification abilities across different non-human species. It has been suggested that species differ in their abilities, or willingness, to wait for a better reward in food-related contexts due to socio-ecological factors. Here, we show that, due to a low number of individuals and species tested per taxonomic group, comparisons of biological factors affecting delay of gratification abilities should be taken with a grain of salt - if they are at all possible at present.

Delay of gratification studies typically report data for a small set of individuals (*e.g.* Beran and Evans 2006; Dufour et al. 2007, 2012; Pelé et al. 2010, 2011; Leonardi et al. 2012; Auersperg et al. 2013; Hillemann et al. 2014; Koepke et al. 2015; Schwing et al. 2017), which can bias estimates for a species or higher order, and may reduce the probability to detect between-species differences. The biological significance of inter-species differences in waiting performance remains, however, unclear. For example, Tonkean macaques, *Macaca tonkeana,* have proved capable of enduring delays of up to 2,560 seconds (Pelé et al. 2011), whilst carrion crows, *Corvus corone,* endured delays of up to 640 seconds (Hillemann et al. 2014). Does this mean that Tonkean macaques are four times better at coping with a delay in gratification compared to carrion crows, or that Tonkean macaques are able to delay future rewards whilst carrion crows are not? We suggest that mean delay performance, might be a more reliable measure of delay of an individual's or a species' gratification abilities compared to maximum delay endured; however, we also suggest that the development of more carefully standardised tests is necessary, and that these standardised tests should be conducted across a wider range of species. Our review of the available data suggests that previous conclusions about the evolution of cognitive skills under certain socio-ecological conditions are at best speculative, and that more comprehensive and systematic

comparative studies are certainly desirable, as current results are drawn from a limited number of studies with a potential bias towards a small number of commonly tested species.

Our review reveals that the mean percentage of successful trials varies substantially across studies, depending on experimental design and on whether the design was a delay maintenance or delay choice task. The percentage of successful trials was higher in delay choice tasks than in delay maintenance tasks, suggesting that choosing to wait for a better reward is easier when the reward is removed after the focal individual has made its choice, compared to maintaining the wait while having access to a food item. Delay maintenance tasks often involve some sort of training procedure and are generally more time consuming, hence many researchers rely on delay choice tasks. However, delay maintenance represents a very interesting aspect of delay of gratification that includes many unaddressed questions. For example, do individuals tend to fail at the beginning or the end of the delay period, *i.e.* can they anticipate how long they will have to wait for, and can individuals develop distraction strategies that improve their test performance (Dufour et al. 2012).

A standardisation of experimental paradigms across taxa is challenging, as tasks differ in the degree of training and time required and are thus not universally applicable. For example, the exchange paradigms restricted to habituated and trained animals. Researchers have thus been calling for the development of new, automated procedures (Adriani et al. 2013; Miller et al. 2019). A further challenge associated with the implementation of standardised delay of gratification assessments is that artificial experimental designs often present alternative options simultaneously (*e.g.* smaller-sooner and larger-later), a setup which does not necessarily reflect food availability in natural foraging contexts and may encourage impulsivity (Pearson et al. 2010; Blanchard et al. 2013). Surprisingly, species which are viewed, generally, as likely to 'fail' to cope with delayed

gratification under experimental conditions are regularly observed engaging successfully in natural behaviours that require such refraining abilities, including food caching, prey stalking, and long-distance travelling to high-quality food patches (Pearson et al. 2010). This raises the question of whether existing paradigms provide a reliable assessment of an animal's delay of gratification abilities. Individuals' performances in standard foraging problems (Hayden et al. 2011; Blanchard and Hayden 2014) may provide a more accurate measure of both human and non-human animals' time preferences (Carter et al. 2015).

The present study provides a systematic overview of currently available data on delay of gratification performances in experimental studies and suggests that the data do not allow for conclusions to be formulated with regard to ecological and social factors driving the evolution of self-control. This is due to a lack of consistency in commonly utilised experimental paradigms, and a relatively small number of species tested. The implementation of experimental designs reflecting species-specific ecology is herein encouraged, in addition to the testing of more species that differ in their socio-ecological characteristics.

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Author contributions

Conceptualisation: IS and CAFW; Data curation: IS and CAFW; Formal analysis: FH and CAFW; Visualisation: FH; Writing: IS, AS, FH and CAFW.

References

Abeyesinghe SM, Nicol CJ, Hartnell SJ, Wathes CM (2005) Can domestic fowl, Gallus gallus domesticus, show self-control? Anim Behav 70:1–11. https://doi.org/10.1016/j.anbehav.2004.10.011

Addessi E, Bellagamba F, Delfino A, et al (2014) Waiting by mistake: Symbolic representation of rewards modulates intertemporal choice in capuchin monkeys, preschool children and adult humans. Cognition 130:428–441. https://doi.org/10.1016/j.cognition.2013.11.019

Addessi E, Paglieri F, Beran MJ, et al (2013) Delay choice versus delay maintenance: Different measures of delayed gratification in capuchin monkeys (Cebus apella). J Comp Psychol 127:392–398. https://doi.org/10.1037/a0031869

Adriani W, Romani C, Manciocco A, et al (2013) Individual differences in choice (in)flexibility but not impulsivity in the common marmoset: An automated, operant-behavior choice task. Behav Brain Res 256:554–563. https://doi.org/10.1016/j.bbr.2013.09.001

Amici F, Aureli F, Call J (2008) Fission-fusion dynamics, behavioral flexibility, and inhibitory control in primates. Curr Biol 18:1415–1419. https://doi.org/10.1016/j.cub.2008.08.020

Anderson JR, Kuroshima H, Fujita K (2010) Delay of gratification in capuchin monkeys (Cebus apella) and squirrel monkeys (Saimiri sciureus). J Comp Psychol 124:205–210. https://doi.org/10.1037/a0018240

Aparicio CF, Hennigan PJ, Mulligan LJ, Alonso-Alvarez B (2019) Spontaneously hypertensive (SHR) rats choose more impulsively than Wistar-Kyoto (WKY) rats on a delay discounting task. Behav Brain Res 364:480–493. https://doi.org/10.1016/j.bbr.2017.09.040

Auersperg AMI, Laumer IB, Bugnyar T (2013) Goffin cockatoos wait for qualitative and quantitative gains but prefer ‘better’ to ‘more.’ Biol Lett 9:20121092. https://doi.org/10.1098/rsbl.2012.1092

Auersperg AMI, von Bayern AMP (2019) Who’s a clever bird — now? A brief history of parrot cognition. Behaviour 156:391–407. https://doi.org/10.1163/1568539X-00003550

Barrett L (2003) Primate cognition: from “what now?” to “what if?” Trends Cogn Sci 7:494–497. https://doi.org/10.1016/j.tics.2003.09.005

Beran MJ (2015) The comparative science of “self-control”: what are we talking about? Front Psychol 6:51. https://doi.org/doi: 10.3389/fpsyg.2015.00051

Beran MJ (2018) Self-control in Animals and People. Academic Press, London

Beran MJ, Evans TA (2006) Maintenance of delay of gratification by four chimpanzees (Pan troglodytes): The effects of delayed reward visibility, experimenter presence, and extended delay intervals. Behav Processes 73:315–324. https://doi.org/10.1016/j.beproc.2006.07.005

Beran MJ, Evans TA (2012) Language-trained chimpanzees (Pan troglodytes) delay gratification by choosing token exchange over immediate reward consumption: Tokens and delay of gratification. Am J Primatol 74:864–870. https://doi.org/10.1002/ajp.22042

Beran MJ, James BT, Whitham W, Parrish AE (2016a) Chimpanzees can point to smaller amounts of food to accumulate larger amounts but they still fail the reverse-reward contingency task. J Exp Psychol Anim Learn Cogn 42:347–358. https://doi.org/10.1037/xan0000115

Beran MJ, Perdue BM, Rossettie MS, et al (2016b) Self-control assessments of capuchin monkeys with the rotating tray task and the accumulation task. Behav Processes 129:68–79. https://doi.org/10.1016/j.beproc.2016.06.007

Beran MJ, Rossettie MS, Parrish AE (2016c) Trading up: chimpanzees (Pan troglodytes) show self-control through their exchange behavior. Anim Cogn 19:109–121. https://doi.org/10.1007/s10071-015-0916-7

Blanchard TC, Hayden BY (2014) Neurons in dorsal anterior cingulate cortex signal postdecisional variables in a foraging task. J Neurosci 34:646–655. https://doi.org/10.1523/JNEUROSCI.3151-13.2014

Blanchard TC, Pearson JM, Hayden BY (2013) Postreward delays and systematic biases in measures of animal temporal discounting. Proc Natl Acad Sci 110:15491–15496. https://doi.org/10.1073/pnas.1310446110

Boogert NJ, Madden JR, Morand-Ferron J, Thornton A (2018) Measuring and understanding individual differences in cognition. Philos Trans R Soc B Biol Sci 373:20170280. https://doi.org/10.1098/rstb.2017.0280

Bramlett JL, Perdue BM, Evans TA, Beran MJ (2012) Capuchin monkeys (Cebus apella) let lesser rewards pass them by to get better rewards. Anim Cogn 15:963–969. https://doi.org/10.1007/s10071-012-0522-x

Bräuer J, Call J, Tomasello M (2007) Chimpanzees really know what others can see in a competitive situation. Anim Cogn 10:439–448. https://doi.org/10.1007/s10071-007-0088-1

Bray EE, MacLean EL, Hare BA (2014) Context specificity of inhibitory control in dogs. Anim Cogn 17:15–31. https://doi.org/10.1007/s10071-013-0633-z

Brucks D, Marshall-Pescini S, Wallis LJ, et al (2017) Measures of dogs' inhibitory control abilities do not correlate across tasks. Front Psychol 8:849. https://doi.org/10.3389/fpsyg.2017.00849

Bunford N, Csibra B, Peták C, et al (2019) Associations among behavioral inhibition and owner-rated attention, hyperactivity/impulsivity, and personality in the domestic dog (Canis familiaris). J Comp Psychol 133:233–243. https://doi.org/10.1037/com0000151

Cano AM, Murphy ES, Lupfer G (2016) Delay discounting predicts binge-eating in Wistar rats. Behav Processes 132:1–4. https://doi.org/10.1016/j.beproc.2016.08.011

Carter EC, Pedersen EJ, McCullough ME (2015) Reassessing intertemporal choice: human decision-making is more optimal in a foraging task than in a self-control task. Front Psychol 6:. https://doi.org/10.3389/fpsyg.2015.00095

Casey BJ, Somerville LH, Gotlib IH, et al (2011) Behavioral and neural correlates of delay of gratification 40 years later. Proc Natl Acad Sci 108:14998–15003. https://doi.org/10.1073/pnas.1108561108

Cook PF, Spivak M, Berns G (2016) Neurobehavioral evidence for individual differences in canine cognitive control: an awake fMRI study. Anim Cogn 19:867–878. https://doi.org/10.1007/s10071-016-0983-4

De Petrillo F, Gori E, Micucci A, et al (2015) When is it worth waiting for? Food quantity, but not food quality, affects delay tolerance in tufted capuchin monkeys. Anim Cogn 18:1019–1029. https://doi.org/10.1007/s10071-015-0869-x

Drapier M, Chauvin C, Dufour V, et al (2005) Food-exchange with humans in brown capuchin monkeys. Primates 46:241–248. https://doi.org/10.1007/s10329-005-0132-1

Duckworth AL, Kern ML (2011) A meta-analysis of the convergent validity of self-control measures. J Res Personal 45:259–268. https://doi.org/10.1016/j.jrp.2011.02.004

Dufour V, Pelé M, Sterck EHM, Thierry B (2007) Chimpanzee (Pan troglodytes) anticipation of food return: Coping with waiting time in an exchange task. J Comp Psychol 121:145–155. https://doi.org/10.1037/0735-7036.121.2.145

Dufour V, Wascher CAF, Braun A, et al (2012) Corvids can decide if a future exchange is worth waiting for. Biol Lett 8:201–204. https://doi.org/10.1098/rsbl.2011.0726

Dunn J, Andrews C, Nettle D, Bateson M (2019) Developmental history, energetic state and choice impulsivity in European starlings, Sturnus vulgaris. Anim Cogn 22:413–421. https://doi.org/10.1007/s10071-019-01254-5

Evans TA, Beran MJ (2007) Delay of gratification and delay maintenance by rhesus macaques (Macaca Mulatta). J Gen Psychol 134:199–216. https://doi.org/10.3200/GENP.134.2.199-216

Evans TA, Beran MJ, Paglieri F, Addessi E (2012) Delaying gratification for food and tokens in capuchin monkeys (Cebus apella) and chimpanzees (Pan troglodytes): when quantity is salient, symbolic stimuli do not improve performance. Anim Cogn 15:539–548. https://doi.org/10.1007/s10071-012-0482-1

Evenden JL, Ryan CN (1996) The pharmacology of impulsive behaviour in rats: the effects of drugs on response choice with varying delays of reinforcement. Psychopharmacology (Berl) 128:161–170. https://doi.org/10.1007/s002130050121

Farrar AM, Kieres AK, Hausknecht KA, et al (2003) Effects of reinforcer magnitude on an animal model of impulsive behavior. Behav Processes 64:261–271. https://doi.org/10.1016/S0376-6357(03)00139-6

Fawcett TW, McNamara JM, Houston AI (2012) When is it adaptive to be patient? A general framework for evaluating delayed rewards. Behav Processes 89:128–136. https://doi.org/10.1016/j.beproc.2011.08.015

Frederick S, Loewenstein G, O'Donoghue T (2002) Time discounting and time preference: A critical review. J Econ Lit 40:351–401

Genty E, Karpel H, Silberberg A (2012) Time preferences in long-tailed macaques (Macaca fascicularis) and humans (Homo sapiens). Anim Cogn 15:1161–1172. https://doi.org/10.1007/s10071-012-0540-8

Green L, Estle SJ (2003) Preference reversals with food and water reinforcers in rats. J Exp Anal Behav 79:233–242. https://doi.org/10.1901/jeab.2003.79-233

Grosch J, Neuringer A (1981) Self control in pigeons under the mischel paradigm. J Exp Anal Behav 35:3–21

Hayden BY (2019) Why has evolution not selected for perfect self-control? Philos Trans R Soc B Biol Sci 374:20180139. https://doi.org/10.1098/rstb.2018.0139

Hayden BY, Pearson JM, Platt ML (2011) Neuronal basis of sequential foraging decisions in a patchy environment. Nat Neurosci 14:933–939. https://doi.org/10.1038/nn.2856

Hillemann F, Bugnyar T, Kotrschal K, Wascher CAF (2014) Waiting for better, not for more: corvids respond to quality in two delay maintenance tasks. Anim Behav 90:1–10. https://doi.org/10.1016/j.anbehav.2014.01.007

Hwang J (2009) Temporal discounting and inter-temporal choice in rhesus monkeys. Front Behav Neurosci. https://doi.org/10.3389/neuro.08.009.2009

Kacelnik A, Bateson M (1997) Risk-sensitivity: crossroads for theories of decision-making. Trends Cogn Sci 1:304–309

Koepke AE, Gray SL, Pepperberg IM (2015) Delayed gratification: A grey parrot (Psittacus erithacus) will wait for a better reward. J Comp Psychol 129:339–346. https://doi.org/10.1037/a0039553

Krebs CA, Reilly WJ, Anderson KG (2016) Reinforcer magnitude affects delay discounting and influences effects of d-amphetamine in rats. Behav Processes 130:39–45. https://doi.org/10.1016/j.beproc.2016.07.004

Leonardi RJ, Vick S-J, Dufour V (2012) Waiting for more: the performance of domestic dogs (Canis familiaris) on exchange tasks. Anim Cogn 15:107–120. https://doi.org/10.1007/s10071-011-0437-y

Logue AW, Chavarro A, Rachlin H, Reeder RW (1988) Impulsiveness in pigeons living in the experimental chamber. Anim Learn Behav 16:31–39. https://doi.org/10.3758/BF03209040

Madden GJ, Bickel WK, Jacobs EA (1999) Discounting of delayed rewards in opioid-dependent outpatients: Exponential or hyperbolic discounting functions? Exp Clin Psychopharmacol 7:284–293. https://doi.org/10.1037/1064-1297.7.3.284

Madden GJ, Smith NG, Brewer AT, et al (2008) Steady-state assessment of impulsive choice in lewis and fischer 344 rats: Between-condition delay manipulations. J Exp Anal Behav 90:333–344. https://doi.org/10.1901/jeab.2008.90-333

Malinen LM (2016) Motor self-regulation and self-control: a comparison of male and female impulsivity in Gallus gallus domesticus. Linköping University

Marshall-Pescini S, Virányi Z, Range F (2015) The effect of domestication on inhibitory control: Wolves and dogs compared. PLOS ONE 10:e0118469. https://doi.org/10.1371/journal.pone.0118469

Michaelson LE, Munakata Y (2019) Same dataset, different conclusions: Preschool delay of gratification predicts later behavioral outcomes in a preregistered study. PsyArXiv

Miller R, Boeckle M, Jelbert SA, et al (2019) Self control in crows, parrots and nonhuman primates. Wiley Interdiscip Rev Cogn Sci 10:. https://doi.org/10.1002/wcs.1504

Miller R, Frohnwieser A, Schiestl M, et al (2020) Delayed gratification in New Caledonian crows and young children: influence of reward type and visibility. Anim Cogn 23:71–85. https://doi.org/10.1007/s10071-019-01317-7

Mischel W (2014) The Marshmallow Test. Random House

Mischel W, Shoda Y, Peake PK (1988) The nature of adolescent competencies predicted by preschool delay of gratification. J Pers Soc Psychol 54:687–696

Mischel W, Shoda Y, Rodriguez M (1989) Delay of gratification in children. Science 244:933–938. https://doi.org/10.1126/science.2658056

Moffitt TE, Arseneault L, Belsky D, et al (2011) A gradient of childhood self-control predicts health, wealth, and public safety. Proc Natl Acad Sci 108:2693–2698. https://doi.org/10.1073/pnas.1010076108

Müller CA, Riemer S, Virányi Z, et al (2016) Inhibitory control, but not prolonged object-related experience appears to affect physical problem-solving performance of pet dogs. PLOS ONE 11:e0147753. https://doi.org/10.1371/journal.pone.0147753

Paglieri F, Focaroli V, Bramlett J, et al (2013) The hybrid delay task: Can capuchin monkeys (Cebus apella) sustain a delay after an initial choice to do so? Behav Processes 94:45–54. https://doi.org/10.1016/j.beproc.2012.12.002

Parrish A, Emerson I, Rossettie M, Beran M (2016) Testing the glucose hypothesis among capuchin monkeys: Does glucose boost self-control? Behav Sci 6:16. https://doi.org/10.3390/bs6030016

Pearson JM, Hayden BY, Platt ML (2010) Explicit information reduces discounting behavior in monkeys. Front Psychol 1:. https://doi.org/10.3389/fpsyg.2010.00237

Pelé M, Dufour V, Micheletta J, Thierry B (2010) Long-tailed macaques display unexpected waiting abilities in exchange tasks. Anim Cogn 13:263–271. https://doi.org/10.1007/s10071-009-0264-6

Pelé M, Micheletta J, Uhlrich P, et al (2011) Delay maintenance in tonkean macaques (Macaca tonkeana) and brown capuchin monkeys (Cebus apella). Int J Primatol 32:149–166. https://doi.org/10.1007/s10764-010-9446-y

Ramseyer A, Pelé M, Dufour V, et al (2006) Accepting loss: the temporal limits of reciprocity in brown capuchin monkeys. Proc R Soc B Biol Sci 273:179–184. https://doi.org/10.1098/rspb.2005.3300

Reynolds B, de Wit H, Richards JB (2002) Delay of gratification and delay discounting in rats. Behav Processes 59:157–168. https://doi.org/10.1016/S0376-6357(02)00088-8

Roesch MR, Takahashi Y, Gugsa N, et al (2007) Previous cocaine exposure makes rats hypersensitive to both delay and reward magnitude. J Neurosci 27:245–250. https://doi.org/10.1523/JNEUROSCI.4080-06.2007

Rosati AG (2017) Foraging cognition: Reviving the ecological intelligence hypothesis. Trends Cogn Sci 21:691–702. https://doi.org/10.1016/j.tics.2017.05.011

Schwing R, Weber S, Bugnyar T (2017) Kea (Nestor notabilis) decide early when to wait in food exchange task. J Comp Psychol 131:269–276. https://doi.org/10.1037/com0000086

Shoda Y, Mischel W, Peake PK (1990) Predicting adolescent cognitive and self-regulatory competencies from preschool delay of gratification: identifying diagnostic conditions. Dev Psychol 26:978

Sozou PD, Seymour RM (2003) Augmented discounting: interaction between ageing and time–preference behaviour. Proc R Soc Lond B Biol Sci 270:1047–1053. https://doi.org/10.1098/rspb.2003.2344

Steele CC, Pirkle JRA, Kirkpatrick K (2017) Diet-induced impulsivity: Effects of a high-fat and a high-sugar diet on impulsive choice in rats. PLOS ONE 12:e0180510. https://doi.org/10.1371/journal.pone.0180510

Stephens DW, McLinn CM, Stevens JR (2006) Effects of temporal clumping and payoff accumulation on impulsiveness and cooperation. Behav Processes 71:29–40. https://doi.org/10.1016/j.beproc.2005.09.003

Stevens JR (2017) Intertemporal choice and delayed gratification. In: APA Handbook of Comparative Psychology: Perception, Learning, and Cognition, In J. Call, G. M. Burghardt, I. M. Pepperberg, C. T. Snowdon, T. Zentall (Eds.). American Psychological Association

Stevens JR, Kennedy BA, Morales D, Burks M (2016) The domain specificity of intertemporal choice in pinyon jays. Psychon Bull Rev 23:915–921. https://doi.org/10.3758/s13423-015-0973-6

Stevens JR, Rosati AG, Heilbronner SR, Mühlhoff N (2011) Waiting for grapes: Expectancy and delayed gratification in bonobos. Int J Comp Psychol 24:99–111

Stevens JR, Stephens DW (2010) The adaptive nature of impulsivity. In: Madden GJ, Bickel WK (eds) Impulsivity: The behavioral and neurological science of discounting. American Psychological Association, Washington, pp 361–387

Szalda-Petree AD, Craft BB, Martin LM, Deditius-Island HK (2004) Self-control in rhesus macaques (Macaca mulatta): Controlling for differential stimulus exposure. Percept Mot Skills 98:141–146. https://doi.org/10.2466/pms.98.1.141-146

Tangney JP, Baumeister RF, Boone AL (2004) High self-control predicts good adjustment, less pathology, better grades, and interpersonal success. J Pers 72:271–324. https://doi.org/10.1111/j.0022-3506.2004.00263.x

Taylor AH (2014) Corvid cognition: Corvid cognition. Wiley Interdiscip Rev Cogn Sci 5:361–372. https://doi.org/10.1002/wcs.1286

Vick S-J, Bovet D, Anderson JR (2010) How do African grey parrots (Psittacus erithacus) perform on a delay of gratification task? Anim Cogn 13:351–358. https://doi.org/10.1007/s10071-009-0284-2

Watts TW, Duncan GJ, Quan H (2018) Revisiting the marshmallow test: a conceptual replication investigating links between early delay of gratification and later outcomes. Psychol Sci 29:1159–1177. https://doi.org/10.1177/0956797618761661

Tables and Figures

Table 1: Different taxonomic orders and species tested in different experimental paradigms. X indicates a species has been tested in a specific paradigm, when the column is empty, the respective species has not been tested. Accumulation, exchange, go-no go and rotating tray tasks are delay maintenance tasks, and intertemporal choice tasks are delay choice.

Order	Species	Accumulation	Exchange	Go-No Go	Inter-Temporal Choice	Rotating Tray Task	References
Carnivora	Domestic dog		x □	x			(Leonardi et al. 2012; Bunford et al. 2019)
Columbiformes	White Carneau Pigeon				x		(Logue et al. 1988)
	White King pigeon			x			(Grosch and Neuringe
Galliformes	ISA Brown layer hen				x		(Abeyesinghe et al. 20
	White leghorn chick				x		(Malinen 2016)
Passeriformes	Blue jay				x		(Stephens et al. 2006; 2016)
	Carrion crow	x □	x □				(Dufour et al. 2012; H 2014)
	Common raven	x □	x □				(Dufour et al. 2012; H 2014)
	European starling				x		(Dunn et al. 2019)
	New Caledonian crow					x □	(Miller et al. 2020)
Primates	Brown capuchin monkey	x	x □		x □	x □	(Drapier et al. 2005; R 2006; Amici et al. 200 2010; Pelé et al. 2011 Bramlett et al. 2012; A 2013; Paglieri et al. 20 2014; De Petrillo et al. 2016b; Parrish et al. 2
	Chimpanzee	x	x □				(Beran and Evans 200 al. 2007; Beran et al. 2
	Common marmoset				x		(Adriani et al. 2013; R
	Cottontop tamarin				x		(Rosati 2017)
	Long-tailed macaque	x	x		x		(Amici et al. 2008; Pel Genty et al. 2012)
	Rhesus macaque	x		x □	x		(Szalda-Petree et al. 2 Beran 2007; Hwang 2
	Spider monkey				x		(Amici et al. 2008)
	Squirrel monkey	x					(Anderson et al. 2010

	Tonkean macaque		x		(Pelé et al. 2011)
Psittaciformes	Grey parrot	x □			(Vick et al. 2010; Koep
	Goffin cockatoo		x □		(Auersperg et al. 2013
	Kea		x □		(Schwing et al. 2017)
Rodentia	F344 rat			x	(Madden et al. 2008)
	Lewis rat			x	(Madden et al. 2008)
	Long–evans rats			x	(Roesch et al. 2007)
	Sprague dawley rats			x	(Reynolds et al. 2002; 2003; Farrar et al. 200 2016; Steele et al. 201
	Wistar kyoto rats			x	(Cano et al. 2016; Apa

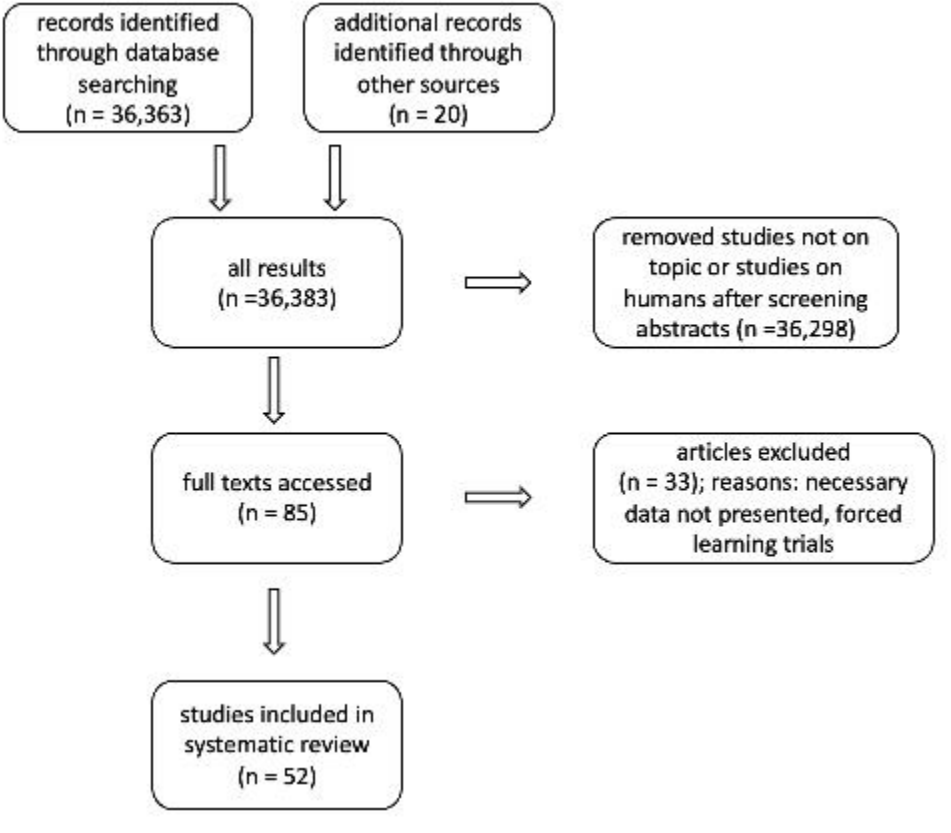
□ qualitative context
x quantitative context

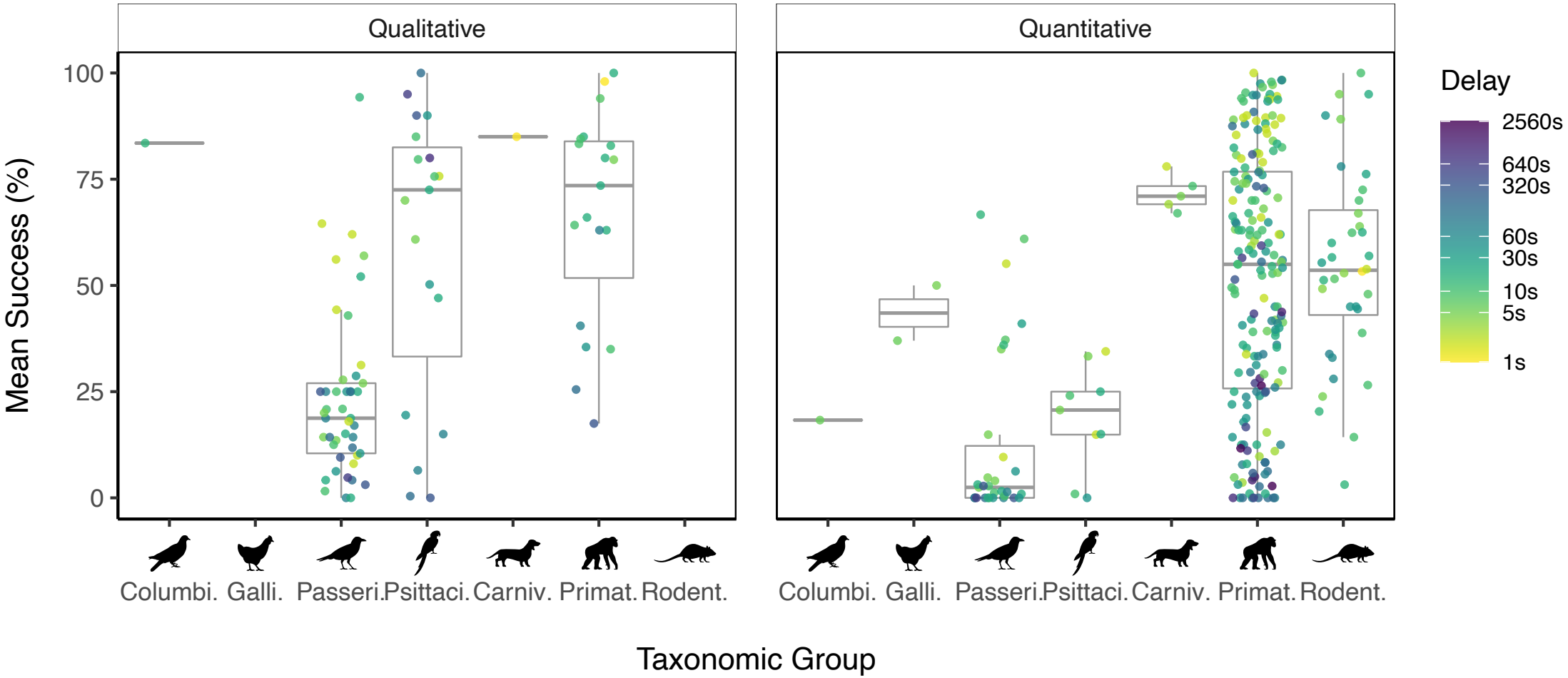
Figure 1. PRISMA diagram of the systematic literature and data search process.

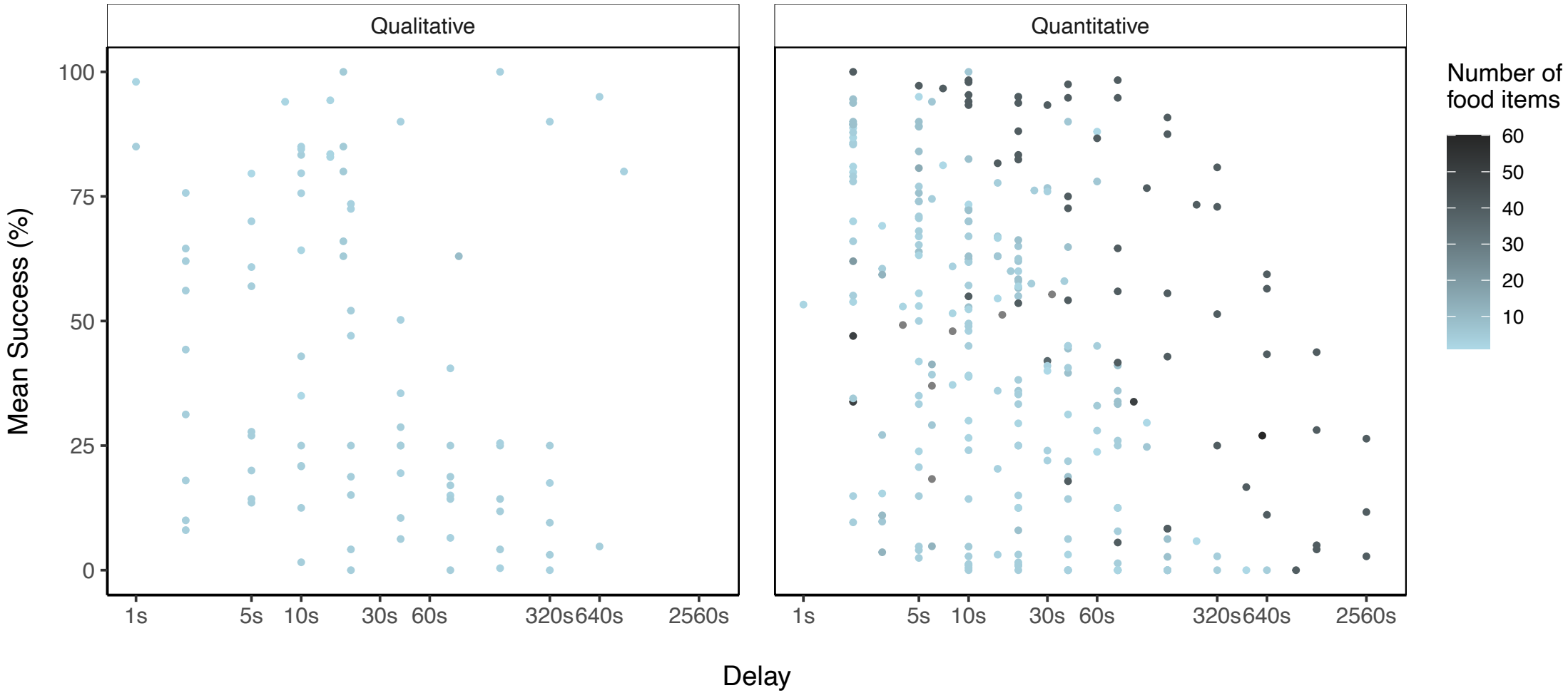
Figure 2: Mean percentage of trials in which individuals successfully waited in different biological orders. Box plots show the median of all individuals' performances and the interquartile range from the 25th to the 75th percentiles, each data point represents the mean waiting performance per species per study in each delay condition. The colour of each data point codes the delay condition; note that the colour legend is not on a linear, but on a log scale. Across all species tested, individuals had higher rates of successful waiting in trials of shorter delays and performances dropped in longer delay conditions.

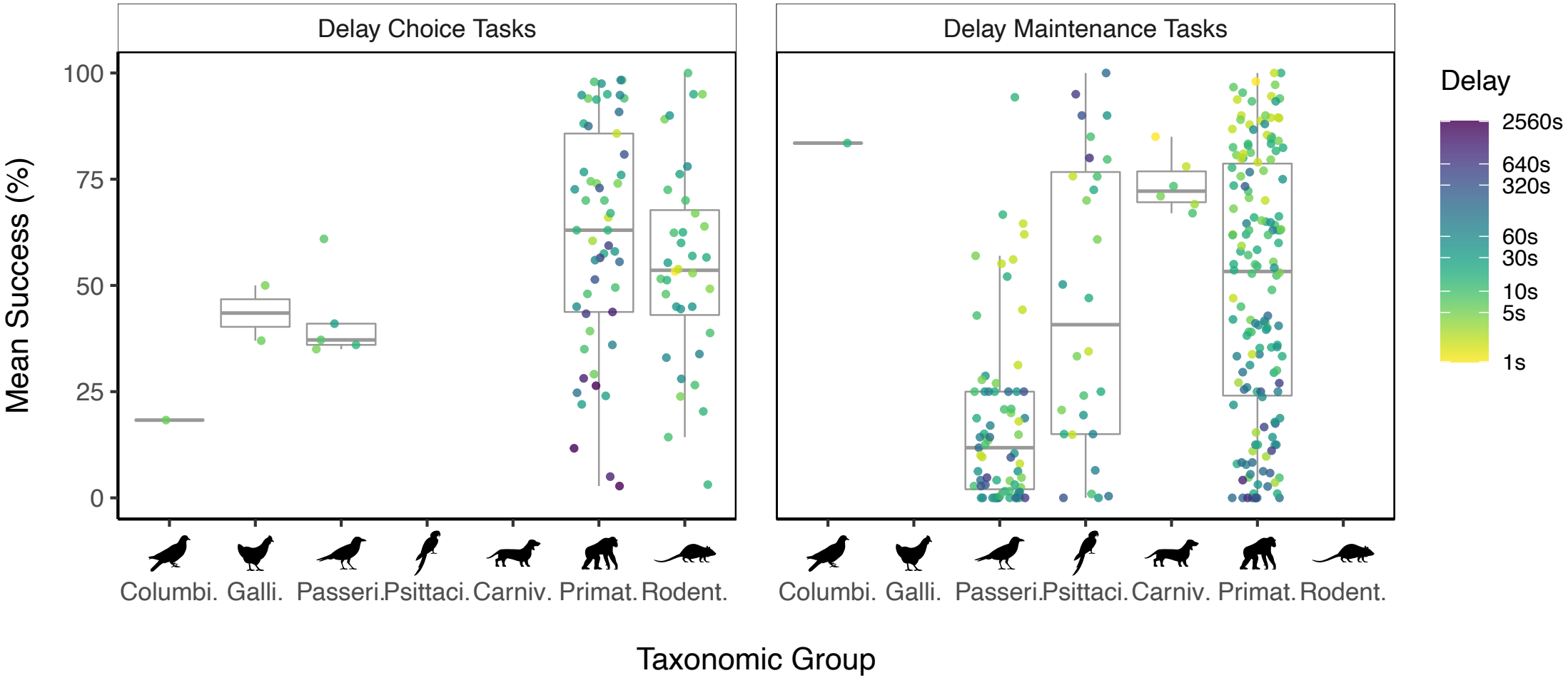
Figure 3: Mean percentage of trials successfully waited in a given delay condition. Data includes all species tested and individual dots present mean values per species per study. The shade of the dots represents the number of individual food items a subject gained in that experimental session. Note that the X-axis is on a log scale. With increasing delays, successful waiting performance decreases across all species, both when waiting for a qualitatively or quantitatively more preferred reward.

Figure 4: Mean percentage of trials successfully waited in different experimental paradigms. Box plots show the median and the interquartile range from the 25th to the 75th percentiles for each order (Columbiformes, Galliformes, Passeriformes, Psittaciformes, Carnivora, Primates, and Rodentia). The colour of each data point refers to the session's delay condition; note that the colour legend is on a log scale.


records identified through database searching (n = 36,363)
additional records identified through other sources (n = 20)
all results (n =36,383)
removed studies not on topic or studies on humans after screening abstracts (n =36,298)
full texts accessed (n = 85)
articles excluded (n = 33); reasons: necessary data not presented, forced learning trials
studies included in systematic review (n = 52)


Qualitative
Quantitative
Mean Success (%)
100
75
50
25
0
Columbi.
Galli.
Passeri.
Psittaci.
Carniv.
Primat.
Rodent.
Taxonomic Group
Delay
2560s
640s
320s
60s
30s
10s
5s
1s


Qualitative
Quantitative
Mean Success (%)
100
75
50
25
0
1s
5s
10s
30s
60s
320s
640s
2560s
Delay
Number of food items
60
50
40
30
20
10


Delay Choice Tasks
Delay Maintenance Tasks
Mean Success (%)
100
75
50
25
0
Columbi.
Galli.
Passeri.
Psittaci.
Carniv.
Primat.
Rodent.
Taxonomic Group
Delay
2560s
640s
320s
60s
30s
10s
5s
1s