Delay of gratification in non-human animals:

A review of inter- and intra-specific variation in performance

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Abstract

The ability to regulate and withhold an immediate behaviour in pursuit of a more advantageous or valuable, albeit delayed, outcome is generally termed 'self-control' and is regarded 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 analysis of available experimental data from non-human animals, to evaluate the effects of experimental design and taxonomic group on performance in delay of gratification tasks. Data were sourced from 52 separate studies and a comprehensive overview of available literature on delay of gratification in non-human animals is presented, identifying a significant lack of socio-ecological diversity across investigated taxa. Both mean percentage of successful waiting trials and maximum endured delay were found to be significantly affected by experimental design, and both measures of waiting performance were independent of taxonomic order. An analysis of data from 25 studies, for which additional individual-level waiting performances were available, identified substantial intra-specific variation in performance. Overall, cross-species comparisons of delay of gratification abilities are hindered by a lack of consistency in experimental designs, and inferences about evolutionary origins of such capacities are unsuitable at present due to the low number of species tested across different orders. Future research on a larger pool of taxa belonging to separate taxonomic groups is encouraged. Research on social and ecological factors causing intra-specific, individual variation in performance should also be considered.

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

Introduction

Animals, including humans, are frequently faced with decisions that affect what options or rewards become available in the future ('intertemporal choice') [1]. In cooperative interactions, individuals often invest time and energy despite an immediate benefit not being 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 [2]. 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 [3]. Intertemporal choices are also applicable to mate choice scenarios, wherein a female must decide whether to mate with the immediately available partner or whether to wait for a higher-quality mate [4,5]. Waiting, however, bears risks, as resources might become depleted or an individual may not survive long enough for the reward to be harvested [6,7]. The rate of temporal discounting is predicted by several theoretical models. Among these, exponential discounting maintains that a delayed reward is discounted at a constant rate, while hyperbolic discounting predicts the discounting rate to decrease over time [8].

The ability to withhold or delay an immediate behaviour in pursuit of a more advantageous or valuable, albeit delayed, outcome is generally subsumed under the term 'self-control'. Self-control is one of the most challenging forms of behavioural inhibition, and enables adaptive decision-making in both social and asocial contexts [9]. Levels of self-control are assumed to vary between individuals and to be linked to traits regulating motivational and control processes [10]. In humans, high levels of self-control have been shown to be correlated with healthy dietary habits and financial wellbeing [11]. Moreover, high childhood self-control has been suggested to predict positive outcomes later in life, *e.g.* in the context of social and academic competence [12],

resilience [13], mental health [14], and physical health, financial wealth, and criminal activity [15]. A recent replication of the famous marshmallow test, however, 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 family and parental-educational and economic background [16]; but see [17].

Since the second half of the 20th century, self-control has attracted considerable scientific interest from an array of disciplines, ranging from human economics [18], psychology [19], pharmacology [20], and neuroscience [10], to animal cognition and behavioural ecology [21,22]. Measures of self-control 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.* [22]. Self-control is thought to find its origins in sociality, and cognitive prerequisites of self-control are believed to have evolved together with cooperative social interactions [23]. Alternatively, it is argued that future planning in a foraging context and food-storing behaviour may have led to the evolution of improved abilities to delay immediate gratification, *e.g.* [24,25].

In non-human animals, the ability to delay gratification is typically assessed using established experimental paradigms, *e.g.* accumulation paradigm, exchange paradigm, hybrid delay, and intertemporal choice task (for an overview see [22,26]). 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' [6]. The ability to delay gratification is successively evaluated most commonly as a measure of maximum endured delay, *e.g.* [27–30]. Results from such experimental studies tend to reflect, however, the performance of a

few individuals waiting in a low number of trials, hence representing the behaviour of single subjects rather than populations or species [28,30].

A major concern associated with the comparison of inhibitory control abilities, *e.g.* self-control, among studies or between species is that measures of such abilities are not always consistent across individuals when different experimental paradigms are used [31,32]. 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 [33]. Potentially similar difficulties associated with the assessment of inhibitory control remain relatively unexplored in the non-human animal literature (but see [34–36]). Further, at present, no formal agreement exists with regard to which measures prove presence of the ability to delay gratification in a given species – *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 endured delay reflect biologically meaningful differences in non-human animals. Considering the complexity of inhibitory control and its components, and the consequent inconsistencies across tasks, it remains questionable whether any single measure can be regarded as a comprehensive or reliable evaluation of an individual's inhibition capacities [32].

The present paper offers a systematic review of the available literature on experimental studies reporting delay of gratification performances in non-human animals in an attempt to draw conclusions about ecological and social drivers in the evolution of delay of gratification abilities. Waiting performance, *i.e.* mean percentage of successful waiting trials and maximum endured delay, of species from a range of taxonomic groups was compared across different delay of gratification tasks to test the hypothesis that large-brained, social species (Primates, Psittaciformes,

and corvids) perform better in delay of gratification tasks compared to species believed to require non-elaborate cognitive skills for cooperative social interactions (*e.g.* Columbiformes and Galliformes). Individual variation in waiting performances and effects of experimental paradigm used are described, and resulting findings discussed with regard to drawing inferences about the evolutionary origin of self-control.

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 percentage 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. A total of 52 studies 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, 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. Additionally, data on individual performance of focal individuals was available for 25

studies on 14 species. Mean percentage of successful trials was recorded for each focal individual in a given delay condition.

Statistical Analyses

To analyse the effect of a small number of target factors (*e.g.* experimental paradigm) on species' performance in self-control tasks, while accounting for repeated measures of species, generalised linear mixed models (GLMM) were generated. Model GLMM1 included mean percentage of successful waiting trials as response variable, with the following factors as fixed effects: biological order, context (qualitative, quantitative), duration of delay (seconds), form of delay test (maintenance, choice), and experimental paradigm (accumulation, exchange, go/no-go, inter temporal choice, rotating tray). Model GLMM2 included maximum endured delay as response variable, while using the same fixed factors as GLMM1: biological order, condition, form of delay test, and experimental paradigm. For each model, species was fitted as a random term. GLMMs were run with Gaussian error distributions, using the 'glmer' function in the 'lm4' R package (version 1.1-19; [37]). *P*-values for fixed factors were obtained from Wald chi-square tests using the Anova function from the 'car' R package. Prior to fitting the regression models, model validity was confirmed through visual inspection of (i) residual distribution, (ii) Q-Q-plots, and (iii) plotting of residuals against fitted values, to test common model assumptions (*e.g.* slopes and intercepts of random effects are normally distributed). Potential multicollinearity between fixed factors was tested for through calculation of variance inflation factors (VIFs) using the 'vif' function in the package 'car' [38]. VIFs were below 2.7 for all fixed factors, suggesting no collinearity [39]. Marginal and conditional R^2 values are provided for model variance description. R^2 values describe the proportion of variance explained by (i) fixed and (ii) fixed and random effects combined,

respectively [40]. Marginal and conditional R^2 values were calculated using the 'r.squaredGLMM' function in 'MuMIn'. All statistical analyses were performed using R version 3.5.3 [41].

Results

Responses to delay of gratification tasks were analysed for 21 species, spanning across different taxonomic groups and five different experimental paradigms. Data on individual performance were analysed for 14 species. The most studied biological order was primates, with nine species tested, 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*) represents the most-studied species, being tested in four out of five paradigms. 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.

GLMM1 – Mean percentage of successive trials

Mean percentage of successful waiting trials was not significantly affected by biological order (Table 2, Figure 2), but whether subjects were tested in a qualitative or quantity context. Individuals waited in a significantly larger proportion of trials in the quantity context, *i.e.* when offered a larger amount of the same food, compared to the quality context, *i.e.* when offered a more preferred type of food reward (estimate ± SE = -17.918 ± 4.851, t-value = -3.754, $p < 0.001$). Mean percentage of successful waiting trials significantly decreased with duration of delay (estimate ± SE = -0.04 ± 0.004, t-value = -8.477, $p < 0.001$; Figure 3), and was significantly higher in delay choice compared to delay maintenance tasks (estimate ± SE = -41.743 ± 5.475, t-value = -7.623, $p<0.001$). Further, waiting performance was significantly affected by experimental paradigm (Table 2, Figure 4). Overall, 29 % of the variation in mean waiting performance in GLMM1 was explained by all fixed factors together (R^2 marginal), and an additional 23 % of the variation was explained by the random factor (species, R^2 conditional).

GLMM2 – Maximum endured delay

Individuals reached longer delay durations in delay maintenance compared to delay choice tasks (estimate ± SE = 607.06 ± 244.908, t-value = 2.478, p = 0.013). Neither of the investigated factors, *i.e.* biological order, experimental paradigm, and reward type (quality/quantity), exerted a significant effect on maximum endured delay (Table 3). Overall, 25% of variation in maximum endured delay duration in GLMM2 was explained by fixed factors (R^2 marginal), and the random factor 'species' explained an additional 31% of variation (R^2 conditional).

Individual performance

All species showed moderate-to-high intraspecific variation in waiting performance in a range of delay of gratification experiments. Mean percentage of successful trials was compared across all short delay conditions (≤ 15 s) for species for which data on individual waiting performance were available (n=14). Within-species standard deviations were found to be high for all species, indicating individual variation in the ability to cope with delaying a food reward, even for short time periods. Maximum delay endured also showed strong intraspecific variation; while some individuals endured only very short delays (*e.g.* 2 s), other individuals of the same species were willing to wait up to several minutes for a more desired food reward (Table 4).

Discussion

The present study provides a systematic review of experimental data on delay of gratification abilities across different non-human species, while investigating cross-taxa variability of separate measures of delay of gratification performance (mean percentage of successful trials and maximum endured delay). It had 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; however, our study finds that both proxies of self-control were independent of biological order. Delay of gratification studies typically report data for a small set of individuals, representing a specific taxon (*e.g.,* [27–30,42–47]), which may affect the probability to detect between-species differences. Pronounced intra-specific variation in experimental waiting performance is presented for all species tested, suggesting that factors causing individual variation (*e.g.* body condition or social status) may provide rich opportunities to investigate the evolution of self-control abilities [48].

The biological significance of inter-individual or potential 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 [44], whilst carrion crows, *Corvus corone,* endured delays of up to 640 seconds [30]. 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? Looking at the performance of different groups, Carnivora were the best performing biological Order, followed by Rodentia, Columbiformes, and Primates. On the other hand, Psittaciformes, Galliformes, and Passeriformes (including corvids and starlings) were identified as the worst performing groups. This is surprising as Primates, Psittaciformes, and possibly Passeriformes - which include multiple tested corvid species -

would be expected to represent the best performing groups [49–51]. The present results indicate that any conclusion about the evolution of cognitive skills under certain socio-ecological circumstances must be treated with extreme caution 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 systematic review revealed both mean percentage of successful trials and maximum endured delay to be significantly influenced by details of experimental design and whether the design was a delay maintenance or delay choice task. The percentage of successful trials was higher in delay choice than maintenance tasks, indicating that choosing to wait for a better reward seems easier for individuals when is removed after the focal individual has made its choice, compared to actually maintaining the wait while having access to a food item. However, despite being less successful, subjects endured longer delays in the latter paradigm. The characteristics of the experimental design may have yet again shaped such results: while the entire sample is tested in short delay durations, those who fail these first conditions are not tested in longer delay conditions. These paradigms inevitably result in biasing performance in longer delay conditions towards better performing individuals.

A standardisation of experimental paradigms across taxa, however, is challenging, as tasks differ in the degree of training and time required and are thus not universally applicable. This is exemplified, *inter alia*, by exchange paradigms, these being restricted to habituated, trained animals. Researchers have thus been calling for the development of new, automated procedures [22]. 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 [52][53]. In fact, species which '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 [52]. This raises the question of whether existing delay of gratification tasks provide a reliable assessment of an animal's self-control abilities. It has been suggested that individuals' performances in standard foraging problems [54,55] may provide a more accurate measure of both human and non-human animals' time preferences [56].

The present study provides first systematic evidence that currently available data on delay of gratification abilities 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. 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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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 inter temporal choice tasks are delay choice, except one exchange study, which was conducted as delay maintenance and delay choice.

Order	Species	Accumulation	Exchange	Go-No Go	Inter-Temporal Choice	Rotating Tray Task	References
Carnivora	Domestic dog		x •	x			[45,57,58]
Columbiformes	White Carneau Pigeon				x		[59]
	White King pigeon			x			[60]
Galliformes	ISA Brown layer hen				x		[61]
	White leghorn chick				x		[62]
Passeriformes	Blue jay				x		[63,64]
	Carrion crow	x •	x •				[28,30]
	Common raven	x •	x •				[28,30]
	European starling				x		[65]
	New Caledonian crow					x •	[66]
Primates	Brown capuchin monkey	x	x •		x •	x •	[31,44,67–77]
	Chimpanzee	x	x •				[42,43,78–80]
	Common marmoset				x		[2,81]
	Cottontop tamarin				x		[2]
	Long-tailed macaque	x	x		x		[27,69,82]
	Rhesus macaque	x		x •	x		[83–85]
	Spider monkey				x		[69]
	Squirrel monkey	x					[70]
	Tonkean macaque		x				[44]
Psittaciformes	Grey parrot	x •					[46,86]
	Goffin cockatoo		x •				[29]
	Kea		x •				[47]
Rodentia	F344 rat				x		[87]
	Lewis rat				x		[87]
	Long–evans rats				x		[88]
	Sprague dawley rats				x		[89–93]
	Wistar kyoto rats				x		[94,95]

• qualitative context

x quantitative context

Table 2: Results of the generalized mixed linear model (GLMM1) investigating factors affecting mean waiting performance, measures as mean percentage of successive trials per species. Significance levels were obtained from Wald chi-square tests, significant factors are highlighted in bold.

Parameters	Estimate ± SE	*t*	*P*
Intercept	**116.315 ± 20.424**	**5.694**	**<0.001**
Order (Columbiformes relative to Carnivora)	-34.685 ± 27.17	-1.276	0.159
Order (Galliformes relative to Carnivora)	-25.274 ± 27.727	-0.911	
Order (Passeriformes relative to Carnivora)	-40.418 ± 20.806	-1.942	
Order (Primates relative to Carnivora)	-11.926 ± 19.733	-0.604	
Order (Psittaciformes relative to Carnivora)	-20.149 ± 21.512	-0.936	
Order (Rodentia relative to Carnivora)	-14.876 ± 21.5	-0.691	
Context (quantity relative to quality)	**-17.918 ± 3.693**	**-4.851**	**<0.001**
Delay duration	**-0.04 ± 0.004**	**-8.477**	**<0.001**
Form (delay maintenance relative to delay choice)	**-41.743 ± 5.475**	**-7.623**	**<0.001**
Paradigm (exchange relative to accumulation)	**7.5 ± 4.058**	**1.848**	**<0.001**
Paradigm (go/no-go relative to accumulation)	**28.446 ± 13.385**	**2.125**	
Paradigm (inter temporal choice relative to accumulation)	**-29.401 ± 8.862**	**-3.317**	
Paradigm (rotating tray relative to accumulation)	**30.327 ± 8.379**	**3.619**	

Table 3: Results of the generalized mixed linear model (GLMM2) investigating factors affecting maximum endured delay.

Parameters	Estimate ± SE	*z*	*P*
Intercept	-458.114 ± 624.466	-0.733	0.463
Order (Columbiformes relative to Carnivora)	349.5 ± 657.58	0.531	0.575
Order (Galliformes relative to Carnivora)	503.746 ± 692.532	0.727	
Order (Passeriformes relative to Carnivora)	217.093 ± 587.718	0.369	
Order (Primates relative to Carnivora)	615.365 ± 551.455	1.115	
Order (Psittaciformes relative to Carnivora)	-20.882 ± 610.505	-0.034	
Order (Rodentia relative to Carnivora)	532.976 ± 616.36	0.864	
Context (quantity relative to quality)	-39.862 ± 191.495	-0.208	0.835
Form (maintenance relative to choice)	**607.06 ± 244.908**	**2.478**	**0.013**
Paradigm (exchange relative to accumulation)	130.802 ± 193.112	0.677	0.314
Paradigm (go/no-go relative to accumulation)	-328.968 ± 403.839	-0.814	
Paradigm (rotating to relative to accumulation)	-470.351 ± 384.966	-1.221	

Table 4: Variation in individual waiting performance in studies for which data on individual performance was available (14 studies). Percentage of successful trials per delay condition (mean and standard deviation, SD) across all individuals and all trials with short delay conditions (15 seconds and less), minimum to maximum delay condition endured by at least one individual are given for all studies were the maximum delay duration was not fixed, number of individuals succeeding in maximum delay condition and number of individuals tested (NrIndMax), and number of individuals tested (NrInd).

Species	Mean Success (% trials, short delays)	SD	Endured delay (seconds; min - max)	Nr Ind Max	Nr Ind
Domestic dog	70.43	19.45	fixed	13	42
Carrion crow	21.79	26.65	5 - 640	1	10
Common raven	21.75	26.15	5 - 320	1	6
European starling	37.18	17.63	fixed	29	29
New Caledonian crow	80.47	25.71	fixed	9	9
Brown capuchin monkey	67.4	33.60	2 - 2560	1	25
Chimpanzee	78.64	23.19	10 - 480	4	9
Long-tailed macaque	77.59	27.98	80 - 2560	1	15
Rhesus macaque	31.10	34.02	fixed	2	14
Squirrel monkey	9.75	16.3	fixed	4	4
Tonkean macaque	75.43	29.21	320 - 2560	4	10
Goffin cockatoo	22.67	21.71	10 - 320	1	14
Grey parrot	47.1	28.38	2 - 900	1	4
Rats	33.69	32.39	fixed	24	43

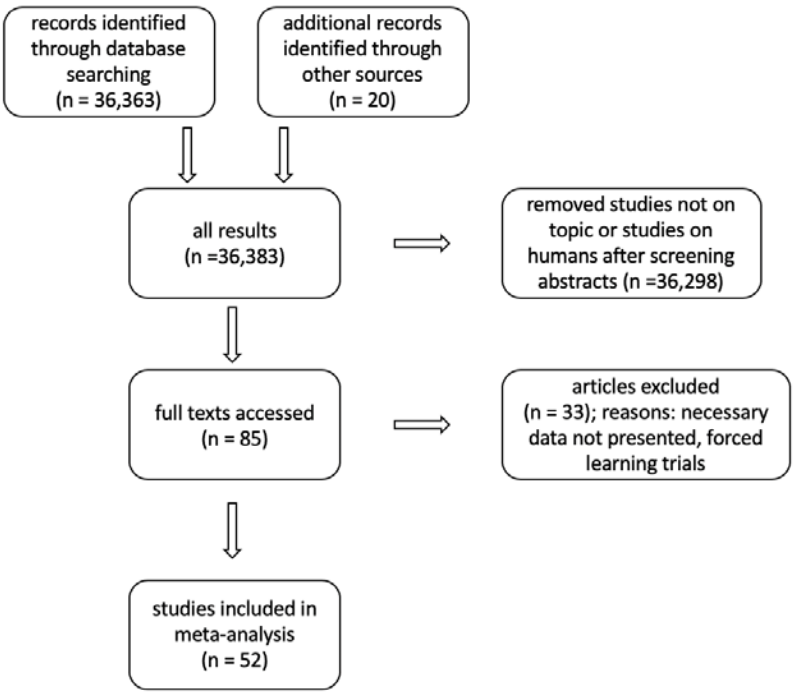

Figure 1. PRISMA diagram of the systematic literature and data search process.

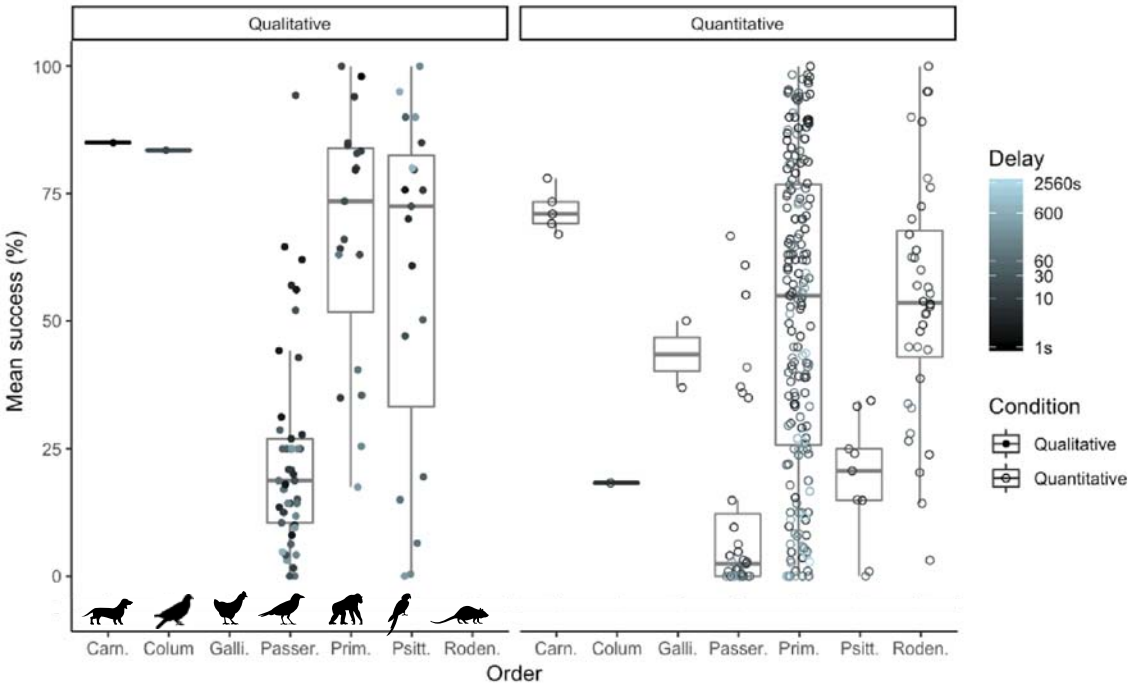

Figure 2: Mean percentage of trials successfully waited in different biological Orders. Box plots show the median and the interquartile range from the 25th to the 75th percentiles, each data point is an individual's waiting performance across all delay conditions in which it was tested.

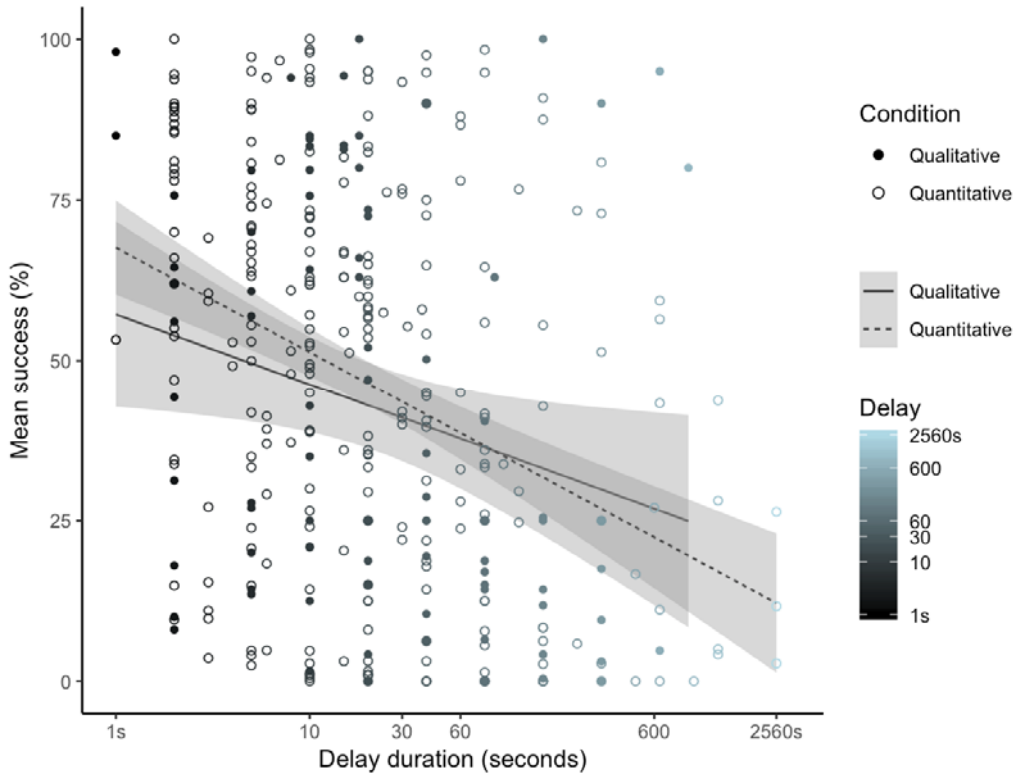

Figure 3: Mean percentage of trials successfully waited depending on delay duration. The predicted values are shown as solid line and 95% CI as shaded area. Black dots present mean values per species per study.

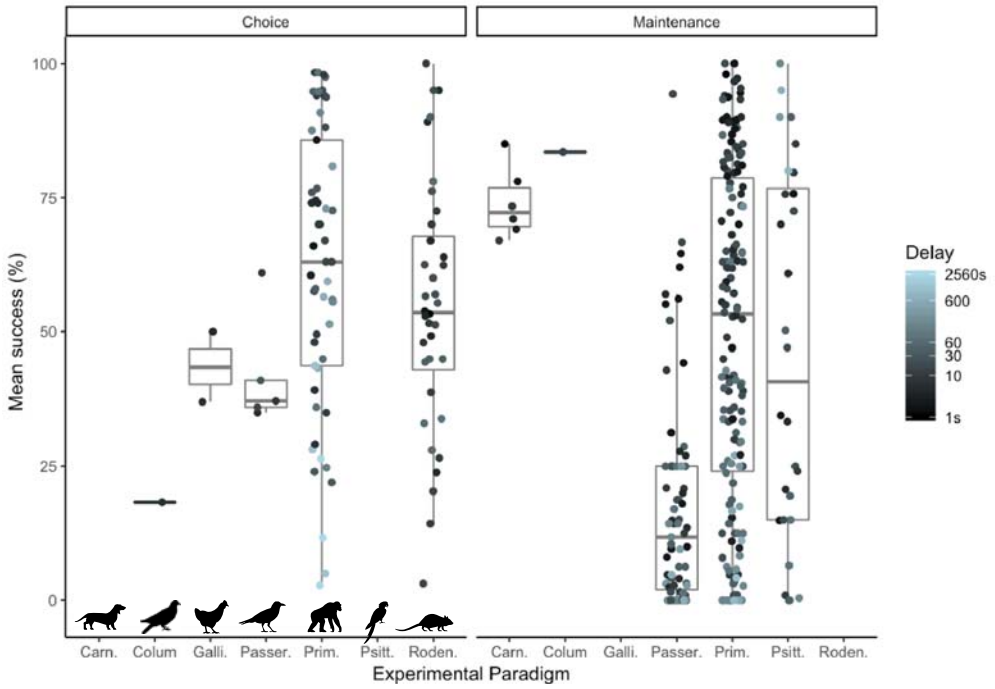

Figure 4: Mean percentage of trials successfully waited in different experimental paradigms. Box plots show the median and the interquartile range from the 25th to the 75th percentiles for each order (Carnivora, Columbiformes, Galliformes, Passeriformes, Primates, Psittaciformes, and Rodentia).