



## Waiting for better, not for more: corvids respond to quality in two delay maintenance tasks



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Self-control, that is, overcoming impulsivity towards immediate gratification in favour of a greater but delayed reward, is seen as a valuable skill when making future-oriented decisions. Experimental studies in nonhuman primates revealed that individuals of some species are willing to tolerate delays of up to several minutes in order to gain food of a higher quantity or quality. Recently, birds (carrion crows, *Corvus corone*, common ravens, *Corvus corax*, Goffin cockatoos, *Cacatua goffiniana*) performed comparably to primates in an exchange task, contradicting previous notions that birds may lack any impulse control. However, performance differed strikingly with the currency of exchange: individuals of all three species performed better when asked to wait for a higher food quality, rather than quantity. Here, we built on this work and tested whether the apparent difference in levels of self-control expressed in quality versus quantity tasks reflects cognitive constraints or is merely due to methodological limitations. In addition to the exchange paradigm, we applied another established delay maintenance methodology: the accumulation task. In this latter task, food items accumulated to a maximum of four pieces, whereas in the exchange task, an initial item could be exchanged for a reward item after a certain time delay elapsed. In both tasks, birds (seven crows, five ravens) were asked to wait in order to optimize either the quality or the quantity of food. We found that corvids were willing to delay gratification when it led to a food reward of higher quality, but not when waiting was rewarded with a higher quantity, independent of the experimental paradigm. This study is the first to test crows and ravens with two different paradigms, the accumulation and the exchange of food, within the same experiment, allowing for fair comparisons between methods and species.

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Animals regularly encounter choice situations in which the alternatives' values and consequences vary in time. Such intertemporal choice situations occur naturally in various contexts (Stevens & Stephens, 2010), ranging from foraging decisions (Kacelnik, 2003; reviewed in Stephens & Anderson, 2001) to social interactions, for example mate choice (Sozou & Seymour, 2003) or reciprocity in cooperative events (Stevens & Hauser, 2004). Going for the immediately available but less preferred option instead of postponing action in favour of an overall better but delayed reward is defined as impulsivity, whereas self-control refers to the opposite strategy (Ainslie, 1974; Kalenscher, Ohmann, & Güntürkün, 2006; Logue, Chavarro, Rachlin, & Reeder, 1988).

From an economical point of view, the preference for a maximum payoff should be selected for (Noë, Hooff, &

Hammerstein, 2001); still, some nonhuman animals tested in self-control set-ups commonly favour the immediate option, even when the delayed one results in a reward of higher value (e.g. pigeons, *Columba livia*: Ainslie, 1974; common marmosets, *Callithrix jacchus*, and cottontop tamarins, *Saguinus oedipus*: Stevens, Hallinan, & Hauser, 2005; domestic fowl, *Gallus gallus domesticus*: Abeyesinghe, Nicol, Hartnell, & Wathes, 2005). It has been commonly suggested that temporal discounting is a critical factor in intertemporal decisions (Kacelnik & Bateson, 1996; Kalenscher & Pennartz, 2008; Stevens & Stephens, 2010). Accordingly, future rewards are subjectively rated less valuable the longer the delay until they are received, because delay is associated with uncertainty for realization of the benefits and probability of loss. Alternatively, it has been argued that choosing an immediate option may be appropriate in relation to reproduction (Sozou & Seymour, 2003). Furthermore, impulsive foraging actually leads to maximized long-term rates of food intake (Kagel, Greent, & Caraco, 1986; Stephens, 2002; Stephens & Anderson, 2001; Stephens, Kerr, & Fernández-

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Juricic, 2004). It is difficult to ascertain whether impulsiveness is an adaptive strategy, or rather a cognitive constraint, since the optimal model of choice may depend on the particular situation (Fawcett, McNamara, & Houston, 2012; Stevens & Stephens, 2010).

From a cognitive point of view, the ability to delay gratification is seen as a critical skill for making future-oriented decisions in various contexts (e.g.: Kacelnik, 2003; Mischel, 1974). In humans, the degree of impulse control varies markedly between individuals (Mischel, Shoda, & Rodriguez, 1989; Steelandt, Thierry, Broihanne, & Dufour, 2012), particularly depending on the social conditions during early upbringing (Diamond & Lee, 2011). Impulse control is a core competence of 'executive functions' (Miyake et al., 2000), which strongly predicts individual academic success and involvement in society. In mammals, these 'executive functions' are associated with the prefrontal cortex (Miyake et al., 2000). The corresponding avian forebrain structure, the nidopallium caudolaterale, is highly similar in terms of anatomy, neurophysiology and cognitive characteristics (Güntürkün, 2005). In birds, food-storing behaviour offers an illustrative example of how future anticipation and the need to plan for the future may have reinforced the evolution of self-control (Feeney, Roberts, & Sherry, 2011; Raby, Alexis, Dickinson, & Clayton, 2007).

The operational level of self-control and the ability to delay gratification has been investigated by applying tasks in which subjects are given the choice either to take an immediately available but smaller or less-preferred food item, or to wait for a larger or more preferred food reward. In so-called delay choice tasks, subjects cannot modify their decision once a choice has been made, whereas in delay maintenance tasks, subjects are allowed to discontinue waiting at any point. A drawback of delay choice tasks is that the choice for the better, usually larger, delayed option is effected by an impulsive tendency to point to the larger food, and the task does not test whether the subject is able to sustain the chosen delay (for discussion see Bramlett, Perdue, Evans, & Beran, 2012; Paglieri et al., 2013). Common delay maintenance tasks make use of the exchange or the accumulation paradigm. In exchange tasks, subjects can return an initial item after a certain delay in order to obtain a reward of higher value (in terms of either quality or quantity), or consume the item at any time during the delay. In accumulation tasks, subjects can maximize the gain of sequentially delivered food items, or stop the accumulation by consuming the food.

Surprisingly few attempts have been made to reconcile different approaches and apply different experimental procedures within the same study, although recent studies on capuchin monkeys, *Cebus apella*, have compared performance in a delay choice and in a delay maintenance task (Addessi et al., 2013), and used a novel methodology, the hybrid delay task, to assess the ability to maintain a chosen delay (Paglieri et al., 2013). In fact, animals sustain varying delay times, depending on the experimental approach (outlined in Pelé, Micheletta, Uhlrich, Thierry, & Dufour, 2011). This may have various reasons; for example, some tasks require particular training, whereas others aim at an intuitive understanding of the task (Bramlett et al., 2012). Importantly, tasks also differ in respect to what happens during the waiting period. In the accumulation task, the reward constantly increases in value over time (e.g. Evans & Beran, 2007), whereas in the exchange task, the reward remains the same throughout the delay (e.g. Pelé, Dufour, Micheletta, & Thierry, 2010). Accordingly, the impulsive option may become a stronger temptation in the accumulation than in the exchange task. Yet, the exchange procedure appears to be more complex than the accumulation task, as subjects not only have to suppress impulses for immediate food consumption in favour of profitability but additional cognitive skills may also be required to judge and compare the trade values (Drapier, Chauvin, Dufour,

Uhlrich, & Thierry, 2005). Another critical aspect in applying the exchange task is that not all nonhuman animals have functional hands but, as is the case in birds or dogs, have to keep the initial item in their beak or mouth; having the food already in the oral cavity could potentially make it more difficult to control the impulse to eat the initial item (Leonardi, Vick, & Dufour, 2012; Wascher, Dufour, & Bugnyar, 2012).

Both paradigms have been applied to various primate species, revealing waiting performances from some seconds up to several minutes (e.g. exchange task: chimpanzees, *Pan troglodytes*: Dufour, Pelé, Sterck, & Thierry, 2007; capuchin monkeys: Drapier et al., 2005; accumulation task: bonobos, *Pan paniscus*: Stevens, Rosati, Heilbronner, & Mühlhoff, 2011; capuchin monkeys and squirrel monkeys, *Saimiri sciureus*: Anderson, Kuroshima, & Fujita, 2010; chimpanzees and orang-utan, *Pongo pygmaeus*: Beran, 2002; Beran & Evans, 2009; rhesus macaques, *Macaca mulatta*: Evans & Beran, 2007; both paradigms: longtailed macaques, *Macaca fascicularis*: Pelé et al., 2010; Tonkean macaques, *Macaca tonkeana*, and capuchin monkeys: Pelé et al., 2011). The exchange paradigm has recently been applied in two corvid species, the common raven, *Corvus corax*, and the carrion crow, *Corvus corone*, and one parrot species, the Goffin cockatoo, *Cacatua goffiniana*. The tested species performed well, in a manner comparable to primates, in overcoming impulsivity in order to optimize food quality, but were considerably worse than primates in the context of quantity (Auersperg, Laumer, & Bugnyar, 2013; Dufour, Wascher, Braun, Miller, & Bugnyar, 2012; Wascher et al., 2012). The only avian species that has been tested for self-control with the accumulation paradigm performed rather impulsively, waiting only a few seconds for larger rewards (African grey parrots, *Psittacus erithacus*: Vick, Bovet, & Anderson, 2010).

We investigated whether avian performances in previous experiments were predisposed by the methodological paradigm and, for the first time in birds, applied the accumulation and the exchange paradigm within the same experiment. We expected individuals to perform similarly in both tasks, suggesting that specific cognitive abilities may account for the high level of impulse control in crows and ravens, relative to other bird species. Alternatively, differing results between the tasks would point towards a methodological bias in previous studies on birds.

Additionally, we ran modifications of the original exchange task (Dufour et al., 2012; Wascher et al., 2012), which allowed us to explore the effects of differing relative attractiveness of the initial item and the potential reward. In exchange trials, we presented the subjects with various combinations of food items that differed in quality, whereas in previous studies, subjects were only asked to exchange food of low quality for higher, that is, the initial item was always a less-preferred food item. Birds were expected to be less likely to exchange when the initial item, the food to be returned, was of similar quality to the subsequent reward (as found in capuchin monkeys: Drapier et al., 2005), or when the possible reward was of relatively low value. Finally, we aimed to investigate whether self-control in crows and ravens is mediated by the 'value' of food. Specifically, we tested the assumption that the ability to maintain a delay in order to get a greater amount of food depends on the subjective preference of the food, with less-preferred food being easier to restrain from immediate consumption.

## METHODS

### *Ethical Note*

Individuals participating in the experiments were all hand-raised and either zoo-bred (three ravens), picked up by private people as apparently injured or abandoned young (all crows, one

raven), or collected from the wild with permission of the 'Ministerium für Landwirtschaft, Umweltschutz und Raumordnung des Landes Brandenburg' (one raven). The birds are kept in pairs, except one group of three crows, in the Cumberland game park or at the Konrad Lorenz research station, both in Grünau, Austria, accredited by the Austrian and local government (licence AT00009917). The animals are housed in large naturalistically designed outdoor enclosures (size ranging from 23.5 m<sup>2</sup> for crow enclosures to up to 110 m<sup>2</sup> for raven aviaries) containing perches, vegetation cover, shelter and natural soil. Their daily food consists of a mixed assortment of, for example, bread, fruits, meat and vegetables. The birds are never deprived of food, and water is available ad libitum for drinking and bathing. This study adheres the ASAB Guidelines for the Use of Animals in Research. After completion of the present study, all individuals remained in captivity.

### Study Subjects

We conducted the accumulation task with 12 birds: seven crows (two male, five female) and five ravens (three male, two female). In the exchange task, all crows and three ravens participated (two male, one female; two ravens were not trained to exchange an inedible token for a reward). In Table 1, we present information about subjects' species, sex, age and experimental experience.

### Training and Experiments

We conducted the experiments from May to August 2012, with a maximum of two sessions per day for each subject, and the test paradigm (exchange or accumulation) was presented in counter-balanced order. For testing, subjects participated voluntarily and the experimenter separated them from each other using positive reinforcement, for example highly preferred treats such as fried pork fat ('greaves').

### Food preference test

Prior to the study, we determined individual food preferences in preference trials, in which the experimenter presented two equally sized pieces of different food simultaneously. The item to which the bird pointed with its beak initially was given to the bird and rated as the preferred food item, whereas the experimenter removed the alternative food. For each subject we assessed a discrete hierarchy

of four different qualities (low, mid1, mid2, high) for seven food items (bean, bread, cheese, corn, grape, greaves, sausage), testing each possible combination three times, randomly spread over six sessions of 12 or 15 trials.

### Task 1: exchange task

We introduced the subjects to the exchange procedure using progressive behavioural shaping as described by Dufour et al. (2012). Some birds had participated in previous exchange experiments (see Table 1). Perched in front of the experimenter, the subject received an initial (food) item, which it could exchange for a reward which the experimenter presented in the other hand (left and right in random order) and which remained visible during the defined waiting period. Subjects could exchange their item for food that was either qualitatively different (task 1A) or of a higher quantity, that is, two, four or eight pieces (task 1B). All items were of equal size (0.5 × 0.5 × 0.5 cm).

In the first delay condition, subjects were asked to give back the initial item after 2 s. An exchange failed when the subject ate the initial food, dropped it, or did not give it back after three nonverbal requests by the human experimenter. Analogous to the methodology applied in previous primate studies (Drapier et al., 2005; Dufour et al., 2007; Pelé et al., 2010, 2011), a subject moved on to the next delay condition if it successfully exchanged at least once in either task 1A or 1B. We then tested the subject with a longer delay in both tasks; we tested the following delay conditions: 2 s, then 5, 10, 20, 40, 80, 160, 320, 640, 1280 s. As an exception, in the second delay condition (5 s), all subjects participated regardless of their performance in the first delay condition (2 s). We randomized the order of presentation of task 1A and task 1B among the subjects, but maintained the individual order during the entire experiment, that is, subjects starting with task 1A in the 2 s delay condition were tested first in the qualitative exchange in any following delay condition.

In task 1A, we gave the birds the chance to exchange food of different qualities. In extension to the original corvid study by Dufour et al. (2012), we confronted the birds with various possible combinations of food items that differed in their absolute quality, resulting in different relative gain and a reversed preference combination: low–mid1/mid2/high, mid1–mid2/high, mid2–high, mid2–mid1. In the 2 s delay condition, we tested every combination nine times in seven sessions of nine trials each. In the subsequent delay conditions we tested every combination three times by distributing them randomly over two sessions of 10 or 11 trials.

In task 1B, subjects could exchange an initial item of a given quality for a larger amount of the food. In previous experiments, both crows (Wascher et al., 2012) and ravens (A. Braun, unpublished data) appeared reluctant when required to control their impulsivity in order to increase the number of food items of a relatively high quality. Here, we systematically tested the subjects with different food qualities. In the 2 s delay condition, we tested the four different food qualities (low, mid1, mid2, high) four times in each quantity combination (1 versus 2, 1 versus 4, 1 versus 8), randomly spread over four sessions of 12 trials each. In the following delay conditions, we tested each combination three times, allocated in a random order in three sessions of 12 trials.

### Task 2: accumulation task

The set-up consisted of two plastic lids (9 cm diameter), one storing and one offering the reward. At the start of a trial, the experimenter showed the content of the storing lid to the subject and set it next to the serving lid so that all food items remained visible but out of reach for the bird. Per trial, the subject could gain up to four pieces, either of the same food type or of increasing quality.

**Table 1**

Species, sex, age at the time of the study and experimental experience of the birds participating in the present study

Subject	Sex	Year of birth (age years)
<b>Crows</b>		
Baerchen <sup>*,†,‡</sup>	Male	2008 (4)
Gabi <sup>*,†,‡</sup>	Female	2007 (5)
Gertrude <sup>§</sup>	Female	2011 (1)
Klaus <sup>†,‡</sup>	Male	2009 (3)
Nino <sup>§</sup>	Female	2011 (1)
Peter <sup>*,†,‡</sup>	Female	2007 (5)
Resa <sup>†</sup>	Female	2009 (3)
<b>Ravens</b>		
Cassandros <sup>§</sup>	Male	2004 (8)
Columbo <sup>§</sup>	Female	2004 (8)
Dora <sup>*,†</sup>	Female	2004 (8)
Hugin <sup>*,†</sup>	Male	1995 (17)
Rumo <sup>*,†</sup>	Male	2008 (4)

\* Individual participated in the qualitative exchange task (Dufour et al., 2012).

† Individual participated in the quantitative exchange task (Wascher et al., 2012).

‡ Individual participated in the inequity condition of a qualitative exchange task (Wascher & Bugnyar, 2013).

§ Individual never participated in any study involving exchange tasks.

We introduced the accumulation paradigm to all subjects during a training phase. To demonstrate the procedure, the experimenter placed both plastic lids out of the bird's reach while transferring the items from the storing into the serving lid without delay, that is, the reward grew at a rate of one item every second. When all four pieces had been transferred, the experimenter moved the serving lid within reach of the bird, so it could take the food. In contrast to demonstrations, in training trials the experimenter placed the serving lid in reach of the subject, so it was able to take the food at any time during a trial. As in the demonstrations, the experimenter delivered food items without delay. As soon as the subject touched an item, the accumulation ended by the experimenter removing the storing lid. During the intertrial interval (a few seconds), the bird was able to eat or take the food. If the subject waited until the accumulation ended, this meant that all four pieces of food were in place and able to be reached by the subject; the reward then remained there for 5 s to give the bird the chance to take it. We noted the items that the subject did not take as being refused.

The training phase consisted of 8–12 sessions with approximately 5–10 trials, demonstrating and training the method. The type of the demonstrations and training trials varied randomly, incorporating trials in which food of the same sort accumulated, food of ascending quality accumulated, and trials in which we added increasingly larger food pieces throughout the trial. As assumed by Anderson et al. (2010), and Evans and Beran (2007), the gradually increasing attractiveness of ascending sizes helps individuals to understand the task intuitively. Initial sessions basically consisted of demonstration trials, whereas in later training sessions we increased the number of training trials while we reduced the number of demonstrations to three per session: a single opening, a mid-session and a final demonstration trial. At the end of the training phase, we considered all subjects to have understood the idea of the task, since all subjects succeeded in gaining more than one food item in at least three training trials.

In the actual test, the procedure was similar to the training phase, although we presented no further demonstrations. In the first condition, the food accumulated with a delay of 2 s between each piece. The succession scheme was analogous to the exchange task, with delays increasing as follows: 2 s, then 5, 10, 20, 40, 60, 80, 160, 320, 640, 1280 s. If the subject succeeded in waiting at least once at a given stage, and did not refuse the reward, it proceeded to the subsequent stage; with the exception that we tested all subjects in the first two delay conditions, regardless of their performance in

the 2 s condition. Each delay condition contained four sessions of 10 trials; two quality (task 2A) and eight quantity trials (task 2B). In the latter, we tested each food quality (low, mid1, mid2, high) twice in randomized order in each session.

### Statistical Analysis

We calculated a series of eight generalized linear mixed models (GLMMs) to assess the effects of fixed factors on the subjects' behavioural responses, namely waiting (y/n), and the maximum delay condition reached. Data distributions and link functions are presented in Table 2. In the exchange task 'waiting' meant a successful exchange, whereas in the accumulation task we considered waiting as successful if the subject waited for at least the second of the four possible food items and accepted at least one piece of the reward. The GLMM factors we took into account are presented in Table 2. In addition, we included interactions between the fixed factors that were present in the final model (Table 2). In Appendix Table A1, we report parameter coefficients, standard errors and confidence intervals for all fixed GLMM factors. We considered subjects' identity as a random factor (for covariance, standard errors and confidence intervals see Appendix Table A2), to account for individual differences in overall performance. As the number of individuals waiting in at least one trial of a delay condition decreased dramatically from the 10 s delay condition onwards (Table 3), we ran three separate GLMMs for the first three delay conditions (2 s, 5 s and 10 s). Here, almost all subjects were included, allowing for analysis of the factors age, sex and species on the subjects' performance.

To investigate the influence of the declared value of the potential reward on subjects' waiting performance, we incorporated the treatment option of the respective tasks as a fixed factor. Namely, this included any of the seven possible combinations in the qualitative exchange task, any of the 12 combinations of the reward's quantity and given food type in the quantitative exchange task, and the quality of items that were accumulated (four variants). We determined the final model by applying the backward stepwise selection procedure to eliminate the least significant terms. The best model was assessed by comparing second-order Akaike's information criteria (AICc; Burnham & Anderson, 2004); this identifies the model that best explains the variance of the dependent variable as that with the lowest AICc value. To investigate the correlation between age and experience, we used a Pearson correlation. We conducted statistical analysis using SPSS 21.0; the significance level for all tests was set at 0.05.

**Table 2**  
GLMM settings and factors taken into account

GLMM	Data used	Fixed factors and interactions	Response variable	Data distribution and link function
1	Entire data set	Delay condition, experience, sex, species, test paradigm (accumulation/exchange), reward type (quantity/quality)	Waiting (y/n)	Binomial response distribution with probit link
2	Entire data set	Experience, sex, species, test paradigm, reward type	Delay condition reached	Multinomial response categories with probit link function
3	2 s delay condition	Age, experience, sex, species, test paradigm, reward type, age*paradigm, age*reward type, experience*reward type, paradigm*reward type	Waiting (y/n)	Binomial response distribution with probit link
4	5 s delay condition	Age, experience, sex, species, test paradigm, reward type	Waiting (y/n)	Binomial response distribution with probit link
5	10 s delay condition	Age, experience, sex, species, test paradigm, reward type, paradigm*reward type	Waiting (y/n)	Binomial response distribution with probit link
6	Qualitative exchange	Delay, species, sex, age, trial number, combination	Waiting (y/n)	Binomial response distribution with probit link
7	Quantitative exchange	Delay, species, trial number, combination	Waiting (y/n)	Binomial response distribution with probit link
8	Quantity accumulation	Delay, species, trial number, food quality	Waiting (y/n)	Binomial response distribution with probit link

**Table 3**  
Number of successful subjects and percentages of trials in which subjects succeeded in waiting, given per delay condition

Task	Delay condition										Overall performance
	2 s	5 s	10 s	20 s	40 s	60 s	80 s	160 s	320 s	640 s	
<b>1 exchange</b>	10	9	8	7	2	nt	1	1	1	1	Successful subjects
1A quality (%)	57.62	29.63	16.67	18.10	23.81	nt	28.57	14.29	9.52	4.76	40.07
1B quantity (%)	18.74	8.61	1.37	1.11	0.00	nt	0.00	0.00	0.00	0.00	8.49
<b>2 accumulation</b>	12	10	6	3	3	2	2	1	1		Successful subjects
2A quality (%)	57.29	39.77	65.00	50.00	25.00	37.50	50.00	37.50	50.00		48.44
2B quantity (%)	9.11	3.68	1.25	4.69	5.21	1.56	0.00	0.00	3.13		4.91

nt = not tested; the 60 s delay condition was tested only in the accumulation task. The conditions reported are those where one subject waited at least once.

**RESULTS**

*Effects of Reward Type on Waiting Performance*

Percentages of trials with successful waiting, as well as the number of subjects tested in each task and delay condition are summarized in Table 3. Generally, subjects waited more often in trials that offered a reward of higher quality than in those with a reward of higher quantity (GLMM1:  $F_{1,4341} = 657.666$ ,  $P < 0.001$ ; Fig. 1). For both reward types, the decision to wait was affected by the duration of the delay (GLMM1:  $F_{9,4341} = 35.057$ ,  $P < 0.001$ ; Fig. 2); the waiting performance decreased with advancing delay condition.

*Maximum Delay Condition Reached*

The maximum delay condition reached was 640 s, achieved in the qualitative exchange task, and 320 s in the accumulation task. Considering the entire data set, individuals waited longer when it led to a reward of higher quality compared with a higher quantity (GLMM2:  $F_{1,35} = 10.031$ ,  $P = 0.003$ ). We also found an effect of sex (GLMM2:  $F_{1,35} = 4.338$ ,  $P = 0.045$ ); the two individuals maintaining the longest delays in each task were both female.

*Effects of Individual Characteristics on Test Performance*

We examined the delay conditions in which all or most of the subjects were tested (2 s, 5 s, 10 s; GLMM 3, 4 and 5), to investigate effects of species, age, experience and sex on performance.

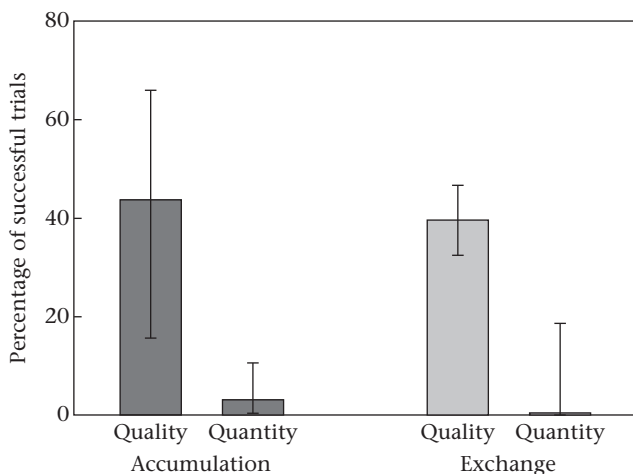
Comparable with the overall results, individuals waited significantly longer in each of the first three delay conditions when they thereby optimized the quality over the quantity of the reward (2 s delay, GLMM3:  $F_{1,1607} = 241.46$ ,  $P < 0.001$ ; 5 s delay, GLMM4:  $F_{1,1022} = 107.74$ ,  $P < 0.001$ ; 10 s delay, GLMM5:  $F_{1,657} = 89.517$ ,  $P < 0.001$ ). In the 2 s delay condition, we found a nonlinear effect of age (GLMM3:  $F_{5,1607} = 2.584$ ,  $P = 0.025$ ). Although age did not correlate with experience, that is, participation in previous exchange experiments (Pearson correlation:  $r_{10} = 0.184$ ,  $P = 0.568$ ), we found experienced subjects did wait more often in the 2 s delay condition (GLMM3:  $F_{1,1607} = 17.538$ ,  $P < 0.001$ ). In addition to this finding, subjects performed better in the exchange than the accumulation task (GLMM3:  $F_{1,1607} = 14.106$ ,  $P < 0.001$ ). None of these effects was found in the 5 s delay condition.

We found an interaction between the type of the reward and the paradigm in the 2 s delay condition (GLMM3:  $F_{1,1697} = 6.051$ ,  $P = 0.014$ ), and in the 10 s delay condition (GLMM5:  $F_{1,657} = 12.331$ ,  $P < 0.001$ ). In both delay conditions, the subjects consistently performed better in the qualitative context, although in the 10 s condition this was less pronounced in the exchange task, owing to the sharp decrease in performance in qualitative exchanges. Also, in the 10 s delay condition, the test paradigm affected performance (GLMM5:  $F_{1,657} = 7.679$ ,  $P = 0.006$ ), but here, conversely to the 2 s delay condition, individuals waited more in the accumulation task.

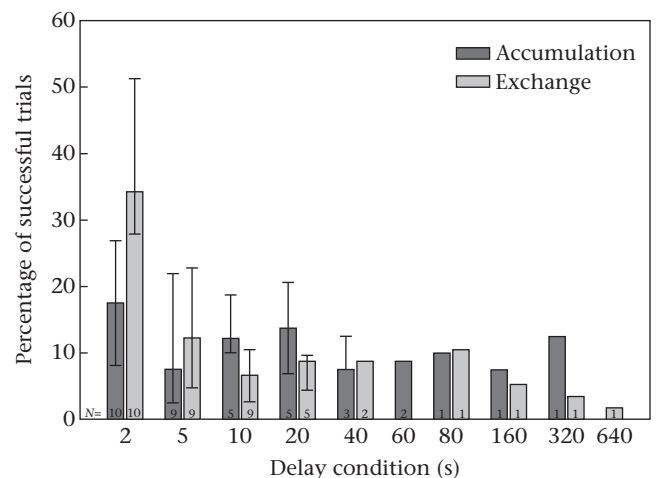
*Task 1: Exchange Task*

*Task 1A: qualitative exchange task*

In the qualitative exchange task, waiting performance was determined by delay condition (GLMM6:  $F_{8,1203} = 29.171$ ,



**Figure 1.** Percentage of successful trials in each task depending on reward type. Bars represent medians; error bars are based on interquartile ranges (25th and 75th percentiles) and indicate individual variation.



**Figure 2.** Number of subjects tested (inside bars) and median percentage of successful trials per delay condition. Interindividual variation is presented as interquartile ranges (25th and 75th percentiles).

$P < 0.001$ ) and by the specific quality combination of the exchangeable food (GLMM6:  $F_{6,1203} = 30.688$ ,  $P < 0.001$ ). In accordance with our prediction regarding relative gain, the subjects performed best when the reward was highly preferred, and the lowest percentage of successful exchanges occurred in the preference-reversed condition, 'mid2–mid1' (Fig. 3).

#### Task 1B: quantitative exchange task

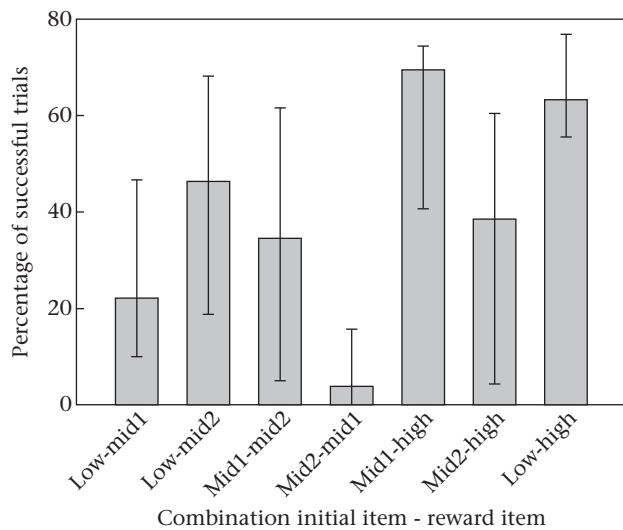
In the quantitative exchange task, in which one piece of food could be exchanged for a larger quantity of the same food, the type of food had no effect on waiting performance. Besides delay condition (GLMM7:  $F_{8,1516} = 11.444$ ,  $P < 0.001$ ), we found significant effects of species (GLMM7:  $F_{1,1516} = 40.743$ ,  $P < 0.001$ ), sex (GLMM7:  $F_{1,1516} = 12.741$ ,  $P < 0.001$ ) and age (GLMM7:  $F_{5,1516} = 14.331$ ,  $P < 0.001$ ). Performance was better in ravens, females exchanged more than males, and the average age of subjects that ever succeeded in this task (mean age: 4.1 years,  $N = 6$ ) was slightly lower than the average age of subjects that never succeeded in this task (mean age: 6.5 years,  $N = 4$ ). The subject succeeding most (40.4% of all successful trials) was one of the oldest subjects (8 years), a female raven.

#### Task 2: Accumulation Task

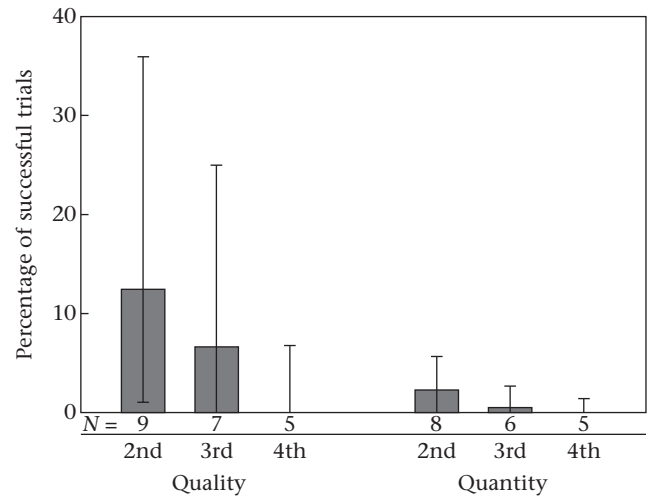
In the accumulation task, in the majority of the successful trials, the delay was tolerated up to the second piece of food, whereas subjects rarely waited until all four items had been accumulated (Fig. 4). Although the proportion of successful waiting in order to optimize reward quantity was as poor as in the exchange task, we found a clear pattern with regard to the food quality: corvids did wait in more than half of the cases when accumulating items were of low quality (GLMM8: delay condition:  $F_{9,1556} = 4.048$ ,  $P < 0.001$ ; food quality:  $F_{4,1556} = 10.419$ ,  $P < 0.001$ ; Fig. 5).

## DISCUSSION

The present study demonstrates corvids' ability to control impulsive behaviour, even over prolonged periods of up to 10 min. Both tasks suggest that carrion crows and common ravens are generally willing and able to delay gratification when it leads to a



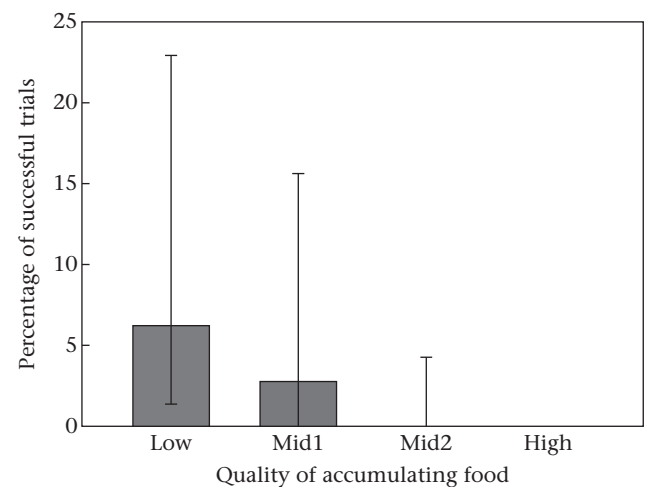
**Figure 3.** Subjects' performance given as the percentage of successful trials in each combination treatment of the qualitative exchange task. Results are plotted over all delay conditions. Bars show medians; error bars indicate individual variance, calculated as 25th and 75th percentiles.



**Figure 4.** Median percentage of successful trials in the accumulation task, split up according to the number of food items obtained in each task. Error bars show inter-individual variation (interquartile ranges; 25th and 75th percentiles).

higher quality, but not higher quantity of food. In line with previous studies on impulsivity in mammals and birds, we found that waiting appears to be more difficult with increasing delay times, and subjects tend to take the less preferred but immediate reward. In our study, the crucial parameters determining the birds' decisions were the reward's value and the duration of the delay.

Importantly, the present study is the first to simultaneously compare avian performance in the main experimental delay maintenance paradigms: the exchange and accumulation task. In accordance with our predictions, we found that crows and ravens generally behaved similarly in both experimental paradigms. However, in the rather short delay of 2 s, the subjects performed better in the exchange task, whereas in the 10 s delay condition, performance was better in the accumulation task. It remains unclear which of the tasks' specific features may account for this, but it has to be taken into account that individuals that did not wait in the early delay conditions were not tested in the 10 s delay. However, as the type of paradigm affected neither the overall exchange



**Figure 5.** Subject's performance in the accumulation task regarding optimization of reward quantity, depending on the food quality. Bars show the median percentage of successful trials, interindividual variation calculated as interquartile range (25th and 75th percentiles) is indicated in error bars.

performance, nor the delay condition reached by an individual, our results show that, in corvids, the ability to cope with a delay in gratification is unaffected by the experimental paradigm.

In our experiment, the three subjects that failed first were birds that already had experience in delay maintenance tasks. Overall, our results do not support the assumption that age or experience influenced the performance in the two delay maintenance tasks, although our sample size is not large enough to discard the possibility of a learned component. The same issue applies with the species and sex effects. Although females seemed to perform better in coping with a delay of gratification, this should be treated with caution. The effect of sex with regard to longest waiting period sustained may result from the fact that the two individuals reaching the longest delay conditions were female (one female raven: accumulation task, 320 s; one female crow: exchange task, 640 s). Similarly, effects of species, sex and age in the quantitative exchange should not be overinterpreted as they arise from one female raven performing substantially better than most of the tested subjects. Finally, we did not find any effect of trial number, suggesting that the subjects' performance was not affected by satiation.

In our study, we made one methodological adjustment compared with the previous accumulation studies (e.g. Vick et al., 2010). Here, we increased the delay duration between the different reward items being accumulated, instead of simulating the delay by increasing the number of items that the subject could gain. This adjustment aimed at keeping the birds motivated and to avoid satiation, making the accumulation task more comparable to the exchange task. In the accumulation task, birds most frequently waited only for the second of the four items, which is hardly surprising, considering that the delay was already twice as long for the third item, and three times longer for the fourth than for the second item. Dufour et al. (2012) previously showed that corvids anticipate the delay and 'decide' accordingly whether to wait or not, as has been found in primates (chimpanzees: Dufour et al., 2007; long-tailed macaques: Pelé et al., 2010; Tonkean macaques and capuchins: Pelé et al., 2011), and, just recently, in another bird species, the Goffin cockatoo (Auersperg et al., 2013).

We found that the reward type (quality/quantity) substantially influenced the subjects' performance, indicating that corvids attribute food quality differently from quantity, with optimization of reward quality being more important than quantity. This is consistent with the results of previous studies with corvids (Dufour et al., 2012; Wascher et al., 2012), cockatoos (Auersperg et al., 2013) and capuchins (Drapier et al., 2005). In the quantitative exchange task, the frequency of successful exchanges was relatively low, and we did not find an effect of the number of potential reward items (two, four or eight) on the subjects' performance. In the accumulation task, the waiting performance was also markedly lower in a quantitative context. In contrast to the exchange task, we did find that the quality of accumulating food items affected waiting performance. In this case, although subjects did occasionally sustain delays in trials in which pieces of a less preferred food were provided, they almost always acted impulsively when they had access to a highly preferred food. This again suggests that crows and ravens prefer one immediate piece of highly preferred food over waiting for more pieces.

For qualitative exchanges, we tested different combinations of the initial item and reward, and found corvids behaved according to their food preferences and the relative gain. Independent of the delay condition, the birds exchanged more often when the potential reward was highly preferred, the initial item was of low quality and when the relative value of the reward was clearly distinct from the initial item. This suggests that corvids take the loss of (the initial) food into consideration when deciding whether to wait for a

more valuable reward. They may therefore base their decision to wait or not on a comparison of the available options, as also described in grey jays, *Perisoreus canadensis* (Shafir, Waite, & Smith, 2002) and capuchins (Drapier et al., 2005). Successful exchanges in later delay conditions (longer than 40 s) were limited to combinations in which the initial item was the least preferred food. Likewise, subjects did not exchange in the reversed preference combination (mid2–mid1) when the delay was longer than 10 s. This may account for the unusually small percentage of successful trials in later delay conditions in the qualitative exchange. However, we expected a drop in success rates, since in an earlier study applying the qualitative exchange task to crows and ravens, subjects succeeded in fewer than 50% of the trials with a delay of more than 40 s (Dufour et al., 2012).

To conclude, we found that carrion crows and common ravens were able to control impulses and wait up to 10 min for a reward of higher quality, which is comparable with previous findings in primates. However, it is noteworthy that only a few subjects waited in the longer delay conditions and these individuals did so in only a very limited number of trials. In a quantitative context, corvids' waiting performance was as poor as that of all previously tested avian species. The present study contributes towards a better understanding and interpretation of this pattern, since our findings suggest that it may not be attributed to the experimental paradigm. Similarly, the difference found between parrots (Goffin cockatoos and grey parrots, Auersperg et al., 2013; Vick et al., 2010) may also be caused by reward type, rather than the experimental paradigm or cognitive limitations. Supposedly, requirements enabling inter-temporal perspectives have evolved independently among birds (Auersperg et al., 2013), as well as between birds and primates (Dufour et al., 2012). Apart from ecological aspects related to foraging and storing of food, these capabilities are required in social contexts, for instance reciprocal altruism (Stevens & Hauser, 2004), competition for resources (Mischel, 1974) and inhibitory control in subordinates in the presence of dominants (Amici, Aureli, & Call, 2008).

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## APPENDIX

**Table A1**

Parameter coefficient, standard error (SE) and lower and upper 95% confidence interval (CI) for all factors in each generalized linear mixed model (GLMM)

GLMM	Factor	Coefficient	SE	Lower CI	Upper CI
GLMM1	Test paradigm	−0.224	0.072	−0.365	−0.083
	Reward type	−1.42	0.057	−1.532	−1.307
	Delay 2	−2.228	0.35	−2.913	−1.542
	Delay 5	−1.525	0.352	−2.215	−0.835
	Delay 10	−0.942	0.355	−1.638	−0.246
	Delay 20	−1.175	0.358	−1.876	−0.474
	Delay 40	−1.021	0.369	−1.743	−0.298
	Delay 60	−0.71	0.411	−1.516	0.095
	Delay 80	−0.708	0.391	−1.474	0.058
	Delay 160	−0.588	0.415	−1.401	0.224
	Delay 320	−0.71	0.407	−1.507	0.087
	Species	0.709	0.418	−0.112	1.529
	Sex	−0.738	0.421	−1.564	0.088
	Experience	0.634	0.15	0.341	0.927
	GLMM 2	Test paradigm	−5.298	1.61	−8.453
Reward type		0.574	0.249	0.086	1.062
Species		6.69	3.794	−0.749	14.129
Sex		−21.952	1142.822	−2262.425	−2218.52
Experience		6.052	1.629	2.859	9.245
GLMM 3	Test paradigm	−9.066	41.929	−91.308	73.177
	Reward type	−10.516	31.621	−72.54	51.507
	Species	1.663	2.228	−2.707	6.032



Table A1 (continued)

GLMM	Factor	Coefficient	SE	Lower CI	Upper CI
	Sex	-2.934	1.758	-6.383	0.514
	Age 1	-14.543	52.704	-117.919	88.833
	Age 3	-16.909	52.613	-120.107	86.289
	Age 5	-17.754	52.629	-117.984	88.475
	Age 8	-16.449	52.591	-119.603	86.705
	Experience*Age 3	4.577	2.802	-0.919	10.073
	Test paradigm*Age 1	10.023	41.934	-72.228	92.274
	Test paradigm*Age 3	5.748	41.953	-76.541	88.038
	Test paradigm*Age 4	7.451	41.931	-74.794	89.696
	Test paradigm*Age 5	9.824	41.933	-72.426	92.073
	Test paradigm*Age 8	7.682	41.932	-74.565	89.928
	Reward type*Age 1	4.745	31.636	-57.307	66.797
	Reward type*Age 3	7.778	31.624	-54.252	69.808
	Reward type*Age 4	9.424	31.622	-52.602	71.45
	Reward type*Age 5	6.062	31.628	-55.976	68.099
	Reward type*Age 8	8.544	31.624	-53.485	70.574
GLMM 4	Test paradigm	-0.408	0.258	-0.913	0.098
	Reward type	-2.195	0.227	-2.639	-1.75
	Species	-0.827	1.431	-3.635	1.981
	Sex	-1.667	0.96	-3.551	0.218
	Experience	0.423	0.513	-0.584	1.431
	Age 1	0.719	2.224	-3.645	5.083
	Age 3	-0.367	2.004	-4.3	3.565
	Age 4	-0.602	1.509	-3.562	2.359
	Age 5	1.09	2.184	-3.195	5.375
	Age 8	-1.788	1.48	-4.692	1.115
GLMM 5	Test paradigm	-1.19	0.947	-3.049	0.669
	Reward type	-4.868	0.79	-6.418	-3.318
	Species	-1.667	3.972	-9.463	6.13
	Sex	0.379	2.599	-4.722	5.481
	Experience	2.037	1.109	-0.14	4.213
	Age 1	1.711	4.825	-7.76	11.182
	Age 3	3.051	4.772	-6.317	12.418
	Age 4	3.406	3.8	-4.054	10.866
	Age 5	4.075	4.916	-5.574	13.725
GLMM 6	Test paradigm*Reward type	2.047	0.964	0.155	3.938
	Species	0.044	2.262	-4.394	4.481
	Sex	-2.372	2.268	-6.821	2.077
	Experience	2.858	3.2	-3.421	9.136
	Age 1	-1.629	3.75	-8.987	5.729
	Age 3	-1.385	3.2	-7.664	4.893
	Age 4	-1.341	2.265	-5.786	3.104
	Age 5	1.959	2.996	-3.919	7.836
	Delay 2	-4.766	1.077	-6.879	-2.653
	Delay 5	-2.985	1.082	-5.107	-0.862
	Delay 10	-1.915	1.088	-4.05	0.221
	Delay 20	-2.186	1.097	-4.338	-0.035
	Delay 40	-2.498	1.127	-4.709	-0.286
	Delay 80	-2.358	1.175	-4.662	-0.054
	Delay 160	-1.335	1.237	-3.763	1.092
	Delay 320	-0.038	1.492	-2.964	2.889
	Trial 1	9.478	43.968	-76.785	95.742
	Trial 2	9.596	43.968	-76.668	95.859
	Trial 3	9.544	43.968	-76.720	95.807
	Trial 4	9.397	43.968	-76.866	95.661
	Trial 5	9.624	43.968	-76.639	95.888
	Trial 6	9.228	43.968	-77.036	95.491
	Trial 7	9.513	43.968	-76.75	95.777
	Trial 8	9.122	43.968	-77.141	95.385
	Trial 9	9.185	43.968	-77.079	95.448
	Trial 10	9.852	43.969	-76.415	96.118
	Trial 11	8.893	43.969	-77.372	95.158
	Combination 1	2.202	0.286	1.641	2.764
	Combination 2	0.922	0.275	0.384	1.461
	Combination 3	1.63	0.28	1.081	2.179
	Combination 4	4.036	0.37	3.311	4.761
	Combination 5	0.703	0.276	0.162	1.244
	Combination 6	1.99	0.281	1.439	2.541
GLMM 7	Species	3.394	1.938	-0.407	7.195
	Delay 2	-10.545	237.339	-476.097	455.007
	Delay 5	-8.696	237.34	-474.248	456.857
	Delay 10	-6.257	237.34	-471.811	459.296
	Delay 20	-8.06	237.341	-473.615	457.494
	Delay 40	2.698	282.94	-552.303	557.699
	Delay 80	-0.036	336.117	-659.346	659.273
	Delay 160	-0.001	335.645	-658.384	658.383

**Table A1** (continued)

GLMM	Factor	Coefficient	SE	Lower CI	Upper CI
GLMM 8	Delay 320	0.004	335.591	-658.274	658.282
	Trial 1	0.458	0.693	-0.902	1.819
	Trial 2	1.267	0.717	-0.14	2.674
	Trial 3	0.369	0.657	-0.92	1.658
	Trial 4	0.888	0.704	-0.494	2.269
	Trial 5	0.496	0.678	-0.835	1.826
	Trial 6	0.831	0.7	-0.542	2.205
	Trial 7	0.149	0.663	-1.151	1.45
	Trial 8	0.603	0.703	-0.776	1.982
	Trial 9	0.891	0.702	-0.486	2.269
	Trial 10	0.225	0.662	-1.074	1.523
	Trial 11	1.319	0.734	-0.121	2.76
	Combination 1	0.696	0.732	-0.741	2.132
	Combination 2	-0.684	0.684	-2.026	0.658
	Combination 3	0.145	0.72	-1.268	1.558
	Combination 4	0.861	0.762	-0.634	2.357
	Combination 5	-0.558	0.708	-1.948	0.832
	Combination 6	-0.115	0.718	-0.161	1.292
	Combination 7	-0.095	0.741	-1.548	1.359
	Combination 8	0.369	0.702	-1.009	1.747
	Combination 9	-0.47	0.712	-1.867	0.928
	Combination 10	-0.622	0.677	-1.95	0.706
	Combination 11	0.211	0.7	-1.162	1.583
	Species	0.07	0.862	-1.761	1.621
	Delay 2	-9.682	88.149	-182.587	163.224
	Delay 5	-8.357	88.15	-181.262	164.549
	Delay 10	-6.26	88.153	-179.172	166.653
	Delay 20	-8.112	88.15	-181.019	164.794
	Delay 40	-8.244	88.15	-181.151	164.663
	Delay 60	-6.455	88.155	-179.371	166.461
	Delay 80	1.532	106.161	-206.702	209.767
	Delay 160	0.071	124.614	-244.359	244.502
	Delay 320	-8.944	88.154	-181.858	163.97
	Trial 1	3.281	1.619	0.104	6.457
	Trial 2	2.689	1.545	-0.34	5.719
	Trial 3	3.051	1.556	-0.001	6.103
	Trial 4	3.825	1.81	0.275	7.376
	Trial 5	3.425	1.576	0.333	6.517
	Trial 6	3.126	1.588	0.012	6.24
	Trial 7	3.384	1.594	0.257	6.511
	Trial 8	2.681	1.545	-0.35	5.712
	Trial 9	3.397	1.693	0.075	6.719
Trial 10	2.322	1.556	-0.731	5.374	
Combination 1	14.948	535.412	-1035.263	1065.158	
Combination 2	15.776	535.412	-1034.434	1065.986	
Combination 3	17.152	535.412	-1033.059	1067.362	
Combination 4	18.618	535.413	-1031.594	1068.831	

**Table A2**

Covariance, standard error (SE) and the lower and higher 95% confidence interval (CI) for the random factor subject in each generalized linear mixed model (GLMM)

GLMM	Covariance	SE	Lower CI	Upper CI
GLMM 1	0.446	0.229	0.163	1.222
GLMM 2	27.08	0.379	26.348	27.832
GLMM 3	2.442	2.415	0.351	16.967
GLMM 4	0.848	0.766	0.144	4.983
GLMM 5	7.477	6.331	1.422	39.303
GLMM 6	2.498	2.586	0.329	18.997
GLMM 7	6.886	4.147	2.116	22.415
GLMM 8	1.708	1.037	0.52	5.612