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„Delay of gratification in a food exchange paradigm in kea (*Nestor notabilis*)“

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1. Abstract

The ability to forego an immediate reward in favour of a bigger or better one at a later point, showing advanced cognitive skills such as impulse control and forward-planning, can be assessed by the classic food exchange paradigm. While long regarded as an exclusive trait of humans or at least primates, in recent years the first bird species have been shown to be able to perform in such tasks and actually demonstrated results similar to primates. Here we test ten captive kea (*Nestor notabilis*), using the food exchange paradigm standardized in earlier experiments, but adding the use of a container to hold the initial item and a novel way to visually represent the passage of the waiting time. While the visual cue ended up having no significant influence on the bird's behaviour, the subjects nevertheless reached waiting times of up to 160 seconds, the longest to date for a bird species not using food caching to cope with the waiting time. They also showed significantly different results depending on the preference difference of the presented food items, as well as clearly non-random waiting times, displaying forward-planning and economic evaluation of the situation at hand. As in most other species, results were markedly better when exchanging for quality as opposed to quantity of the food reward. These results provide further evidence for temporal discounting in birds, and fit in with the data gained on corvids and Goffin's cockatoos in recent years.

2. Zusammenfassung

Die Fähigkeit, auf eine sofort verfügbare Ressource zu verzichten, und lieber auf eine größere Menge oder etwas Besseres zu warten, zeigt fortgeschrittene kognitive Fähigkeiten wie Impulskontrolle und Vorausplanung, und kann mit dem klassischen Food Exchange Experiment überprüft werden. Obwohl lange geglaubt wurde, es handle sich dabei um ein Talent, das auf Menschen oder zumindest auf Primaten beschränkt sei, wurde die Fähigkeit in einem Food Exchange Task zu warten in den letzten Jahren auch in den ersten Vogelspezies nachgewiesen, die außerdem den Ergebnissen von Primaten nicht weit nachstehen. Hier testen wir zehn in Gefangenschaft gehaltene Kea (*Nestor notabilis*) mit dem in früheren Experimenten standardisierten Food Exchange Paradigma, benutzen aber zusätzlich einen kleinen Behälter für das zu tauschende Futterobjekt und eine visuelle Repräsentation der ablaufenden Wartezeit. Obwohl der visuelle Hinweis auf die verstrichene Zeit keinen Einfluss auf das Verhalten der Vögel hatte, erzielten die Testsubjekte Wartezeiten von bis zu 160 Sekunden, die bis zu diesem Zeitpunkt längsten für Vögel die die Wartezeit nicht mittels Verstecken (caching) des Tauschobjekts überbrücken. Der Unterschied in der Präferenz des Tauschobjekts zeigte einen signifikanten Einfluss auf das Resultat, und die Länge der Wartezeiten in den Trials war eindeutig nicht-zufällig, was beides auf Vorausplanung und ökonomische Analyse der Situation hinweist. Wie in den meisten anderen Spezies war die Bereitwilligkeit zum Tausch für eine bessere Qualität des Futterobjekts höher als für eine größere Menge des gleichen Futters. Diese Resultate dienen als ein weiterer Nachweis für zeitliche Diskontierung bei Vögeln, und passen zu den bereits in Corviden und Goffin's Kakadus erzielten Ergebnissen der letzten Jahre.

3. Introduction

A bird in the hand might be worth two in the bush, but picking the easily available small reward over a more difficult to obtain long-term goal is not always the best choice, neither for humans nor for non-human animals (Frederick et al., 2002; Bramlett et al., 2012). Inhibiting consummation of a small food item to acquire more or better quality of food in the future requires impulse control and forward-planning (Kacelnik, 2003). Future rewards are valued based on the expected delay before acquiring them, a strategy called temporal discounting (Ainslie, 2001). Experimental paradigms to evaluate these abilities are offered by delay-of-gratification experiments, where subjects can pick an immediate small reward or decide to skip that and wait for a better one at a later point.

In the first delay of gratification study, done in the 1970s, human children aged three to four years old could earn an additional marshmallow if they could resist the temptation of eating a single one for 15 minutes (Mischel et al., 1972). One third of the children succeeded at the task, with age being the biggest determining factor for success. Follow-up studies in later years showed a high correlation between the subject's performance as children and their health and success in later life, as measured by such factors as higher SAT scores (Mischel et al, 1989), higher education (Ayduk et al., 2000) or a healthier BMI (Schlam et al., 2013). These results not only suggest that the impulse control and forward-planning needed to succeed at delay of gratification tasks are traits that can help people cope with various aspects of their lives, but also that they are stable over long periods of time in an individual life history.

While some authors have argued that the cognitive requirements for delay of gratification tasks are uniquely human features (Rachlin et al., 1991), later experiments in non-human animals showed that many species are in fact able to inhibit eating a small reward in favour of waiting for a larger or better one at a later point (Auersperg et al., 2013; Drapier et al., 2005; Dufour et al., 2007; Leonardi et al., 2011; Ramseyer et al., 2005; Wascher et al., 2012).

A variety of paradigms have been used to assess the ability to delay gratification in non-human animals. The most common ones are accumulation tasks and exchange tasks. In accumulation tasks, a food reward keeps accumulating at a given point until the subject decides to consume the accumulated quantity. African grey parrots *(Psittacus erithacus)* mostly did not wait at all in such a paradigm, and instead just consumed the first food item presented. Even when waiting, waiting times did not exceed a few seconds (Vick et al., 2010). In contrast, all five tested great apes (four chimpanzees *(Pan troglodytes)* and one Orang-Utan *(Pongo pygmaeus)* were able to wait for a delay of 180 s to receive the maximum quantity of food in the majority of trials in a similar study (Beran, 2002) in primates.

An experimental paradigm that comes closer to the initial experiments with human children are food exchange tasks, in which the subjects get a small food item from the experimenter that they have to hold on to, and which they can trade in for a better reward after a given time delay. Like in other tasks, ‘better reward’ can either mean a larger quantity of the same food (quantity exchange tasks), or a more preferred food item (quality exchange tasks). Some studies only test quantity exchange, some only quality exchange, and only a few exist that test both.

In a quantity exchange task, one out of four domestic dogs (*Canis familiaris*) was able to wait for up to 1090 seconds (18 min 10 s), but the other three subjects did not nearly come close to this delay time (Leonardi et al., 2012). In a quality exchange task, two out of six capuchins (*Cebus capucinus*) waited for more than ten minutes to trade for their most preferred food item, however they could not inhibit nibbling of the initial food item, and when this was not allowed their performance dropped significantly. Also, they performed much worse in quantity exchange, and their result in this respect could not be improved by largely enhancing the quantity of the reward (Ramseyer et al., 2006). On the contrary, other results from primates do indeed show an improvement when higher quantities are involved, up to endured delays of 8 minutes for 40 times the quantity of the initial item in chimps (*Pan troglodytes*) (Dufour et al., 2007), and even exceeding 20 minutes for a single individual, also getting 40 times the quantity, in long-tailed macaques (*Macaca fascicularis*) (Pelé et al., 2010).

The ability to perform in a food exchange task, or to reach waiting times beyond just a couple of seconds in any delay of gratification task, was long assumed to be limited to higher mammals and primates. Indeed, early experiments with delayed feeding tasks in White Carneaux pigeons (*Columbia livia*) had only three out of ten subjects waiting for a short interval of up to 15 seconds in order to obtain a prolonged feeding bout (Ainslie, 1974), domestic fowl were unable to wait for six seconds to get a seven second feeding access (Abeyesinghe et al., 2005), and African grey parrots mostly did not wait even for a few seconds in an accumulation task (Vick et al., 2010).

However, recently results similar to those achieved in higher mammals and primates were shown in a quality exchange task in corvids, where common ravens (*Corvus corax*) waited up to 160 seconds, and carrion crows (*Corvus corone*) even up to 320 seconds to exchange for a more preferred food item (Dufour et al., 2012). Interestingly, these delays could only be achieved in quality exchange task, while the birds barely exchanged at all when faced with a quantity exchange task (Wascher et al., 2012). As food hoarders, the corvids were allowed to cache the initial food item during waiting and retrieve it later to complete the exchange.

Goffin's cockatoos (*Cacatua goffini*), a non-food-hoarding psittacine, also showed little interest to wait for quantitative exchange, but individuals waited for up to 80 seconds for their most preferred food item in a quality exchange task (Auersperg et al., 2013). This result was especially impressive considering that the birds had to hold the initial food item in their beak, close to their taste organs, for the whole duration of the trial, and one could easily argue that this makes it even harder to resist the temptation of eating it, compared to primates, who can hold the food in their hand, or corvids, who were allowed to stash the item during the trial. The preference difference between the initial item and the reward was a big determining factor for the maximum length of the waiting time and the percentage of successful exchanges, showing economic evaluation and forward-planning.

In some of the studies mentioned above, the waiting times for all trials were analysed, to see whether the amount of time the animals waited before consuming the initial item in the failed trials (renouncement time) was random, or whether the subjects gave up earlier than expected by chance (Auersperg et al., 2013; Drapier et al., 2005; Dufour et al., 2007; Dufour et al., 2012; Leonardi et al., 2012). In all of these studies, the animals gave up significantly earlier than expected by chance, suggesting that they possess an internal representation of the remaining waiting time, and plan ahead whether to give up or wait for the whole duration.

While methodological differences between studies make it difficult to directly compare them, the general consensus of the results so far seems to be that cognitively advanced species tolerate higher waiting times, which could either be due to increased impulse control or different subjective measure of time in longer-living species. The maximum waiting times achieved in primates and dogs are longer than those in birds, yet in most cases, there seems to be a large variation between individual subjects, which could again represent differences in the individual ability to inhibit impulses, but which, in quality exchange tasks, could also be attributed to a variance in individual food preferences, since the individual's difference in food preference between the initial item and the reward seems to heavily influence the exchange rate and maximum endured waiting time (Auersperg et al., 2013).

Most species in general, but birds in particular, seem much less inclined to trade an initial food item for a higher quantity of the same item, as compared to trading for a more preferred food item. The low motivation to trade for higher quantities of a given food source could be explained by the lack of food deprivation, but it could also reflect a general foraging strategy of the studied animals.

To confirm the results obtained in corvids and Goffin's and put them into phylogenetic perspective, we tested another psittacine, the kea (*Nestor notabilis*), a New Zealand alpine parrot famous for its curiosity and intelligence (Huber & Gajdon, 2006). Unlike corvids, kea are not food hoarders, but allofeeding plays a big role in their social life, especially in the context of mating (Diamond and Bond, 1998), which might predispose them towards doing well in a food exchange experiment.

We used the same general food exchange paradigm as the earlier studies with corvids and cockatoos, with two modifications. To minimize the bird's disadvantage of having to hold the initial food item in the beak for the whole trial, compared to primates, who can use their hand, or corvids, who can stash it, we used a small container to hold the food. This was also supposed to eliminate the problem of the subjects nibbling on the initial food item and then trying to exchange an incomplete item.

Our experiment also included a visual representation of the waiting time (visual aid). In humans, information about the expected waiting time significantly reduces the overestimation of waiting time (Antonides et al., 2002), and the presence of feedback prolongs tolerable waiting time (Nah, 2004). To assess whether this also applies to kea, we added a visual cue to half of the trials, by putting a small computer screen next to the bird that would fill up with yellow on a black background within the given waiting time of a trial. We expected that this device would make it easier for the birds to wait in longer trials, thus increasing the maximum waiting time, and also that the waiting time for failed trials would drop, since the bird could decide earlier whether to wait or not.

In general, we predicted the maximum endured waiting times to be similar to those in the three other bird species tested so far. We also expected it to be dependant of the preference difference between the initial item and the reward, and that the kea would do better in a quality exchange compared to a quantity exchange task, as seen in most other species.

4. Material and Methods

4.1 Subjects and Housing

Overall, twelve captive kea – seven males, five females – participated in this study (Table 1). Two of them were juveniles, the rest adults. The individuals were marked with coloured leg bands and housed together. Two subjects (Frowin and John) dropped out after the first preference test, since it proved impossible to shape them for the food exchange task. The two that replaced them (Papu and Tammy) did not take part in the initial food preference test, but only in the second one after the food exchange task. Five of the subjects (Anu, Coco, Kermit, Sunny and Tammy) already had experience with the general testing paradigm from an earlier, unfinished and unpublished food exchange experiment (Amann 2009, University of Veterinary Medicine Vienna, unpublished).

Table 1: List of subjects

name	abbr.	sex	hatched	hand-raised	comment
Anu	An	male	2007 (adult)	yes	
Coco	Co	female	2007 (adult)	yes	
Frowin	Fr	male	2004 (adult)	no	dropped out
Kermit	Ke	male	2004 (adult)	yes	
John	Jo	male	1999 (adult)	no	dropped out
Lilly	Ly	female	2007 (adult)	yes	
Paul	Pa	male	2010 (juv.)	no	
Papu	Pu	female	2013 (juv.)	yes	not part of first preference test
Roku	Ro	male	2008 (adult)	no	
Sunny	Sy	female	2007 (adult)	yes	
Tammy	Ta	male	2007 (adult)	yes	not part of first preference test
Willy	Wy	female	2007 (adult)	yes	

Most of the subjects were hand-raised, and all were bred and raised in captivity. They are housed in a large outdoor aviary of 520 m², at the Haidlhof Research Station, Bad Vöslau (Austria), since August 2010. The aviary consists of nine connected compartments, two of which each are addressed to breeding pairs and experiments. With the exception of the breeding pairs, the birds are kept as one group in all remaining compartments, which can be flexibly separated by sliding gates made of wire mesh. Additionally, the experimental compartment used in the food exchange task (7 x 10 m) can be visually separated from the rest of the aviary by opaque sliding walls and subdivided in two compartments by sliding wire-mesh walls. Birds are fed three times a day with a mixture of fruits, vegetables, seeds and animal protein (eggs, minced meat), and receive water ad libitum.

4.2 Experimental overview and time schedule

The project was started in February 2014, all testing took place between March 2014 and June 2014. The first preference test was done in March 2014, the shaping phase for the food exchange task lasted from the end of March until the end of April 2014, followed by the food exchange experiment which was finished in mid-June. The second food preference test was then completed by the end of June 2014.

4.3 Food preference test

Like in earlier experiments, the preference for various food items was determined by a food preference experiment before the actual exchange task (Auersperg et al., 2013; Dufour et al., 2012, Wascher et al., 2012). For this, three different food items were tested in all possible combinations. Food pellets (NutriBird A19), small pieces of apple approximately the same size as the pellets, and pieces of peanuts (one quarter of a whole nut). Both the pellets and apple are part of the bird's regular diet, and peanuts are a common reward given to the birds in other experiments. To test for quantity distinction, one piece and three pieces of small food pellets (NutriBird G14) were used. All data was HD video recorded and coded in situ as well as from the videos.

For the first preference test, results from an uncompleted food preference test done in the winter of 2013/2014 (IMHAI student group, University of Veterinary Medicine Vienna, unpublished) were taken and completed by additional sessions for all preferences not yet determined. The items were presented on two wooden feeding boards, placed approximately one meter apart, the bird was put on a third wooden board two meters away from the others, and both food items were covered with cups. The experimenter then lifted both cups simultaneously and the subject was allowed to eat one of the food items. This was done for ten trials per session, balanced for side. The side of the food rewards was alternated based on a semi-random algorithm, which made sure that the same side did not come up more than three times in a row, in order not to establish a side preference. Even so, a training phase was required for most subjects, who showed strong side preference initially. Testing continued until the subject picked one item over the other in least eight out of ten trials in two consecutive sessions.

To test for a possible change in food preference during the course of the year, and to confirm the results of the first test, a second preference test was done after the food exchange task was completed. For this test, the two items were presented to the subjects in each hand of the experimenter, since the birds were already used to the paradigm of getting to pick one of two presented items from the experimenter's hands after completing the food exchange task.

4.4 Shaping for the food exchange task

To train the birds for the food exchange task, they were familiarized step by step with the procedure. Subjects received small food rewards as well as verbal praise during the shaping phase if they showed the desired behaviour at each step (explained below). Animals received trials according to their individual learning speed, to try and bring all of them to the same level before starting with the actual food exchange task.

The required steps were:

1. Subject takes the empty container from the experimenter's hand.
2. Subject drops the container back into the hand when the experimenter moves his hand under the container.
3. Subject actively places the container back into the experimenter's hand.
4. Subject holds on to the container for more than five seconds before giving it back.
5. The container is loaded with a small food item (apple). Subject gives back the loaded container without eating the initial item.

The reward was always immediately given to the bird by the experimenter, using the hand not presenting the initial item. The hand containing the reward was exchanged semi-randomly during the training.

4.5 Food exchange task

4.5.1 Basic setup

No verbal praise or any other reaction was given to the birds by the experimenter in the actual exchange task, no matter whether they chose to exchange or eat the initial item. The subjects were tested in a separate testing compartment, the experimenter wore sunglasses and avoided eye contact and any unnecessary movements during the trials. All data was HD video recorded and coded in situ, selected trials were later video-reviewed.

4.5.2 Food combinations

To cover many differences in food preference, as well as including quantity exchange, five different food combinations were tested in the food exchange task (Table 2).

For peanuts, one quarter of a whole peanut seed was used, sometimes slightly less in the case of exceptionally big seeds. Pellets were of similar size to the peanuts, and apple was cut in pieces approximately the same size as the peanut and apple rewards.

Table 2: Food combinations in the food exchange task. “Preference difference” applies to nine of the ten subjects, as it proved to be unstable in one subject during the course of the food exchange experiment.

initial item	reward	preference difference	code
apple	peanut	least preferred vs. most preferred	A-N
pellet	peanut	second preferred vs. most preferred	P-N
apple	pellet	least preferred vs. second preferred	A-P
pellet	apple	second preferred vs. least preferred (control condition)	P-A
1 small pellet	3 small pellets	quantity food exchange	1-3

4.5.3 Visual representation of waiting time (visual aid)

A small laptop was placed next to the feeding board where the bird sat during the trial, well within its visual field. It ran a program written in Visual Basic that randomized the trials, recorded the start and end time of each trial, and displayed a visual representation of the waiting time (visual aid) to the subject. The screen of the laptop (10.1”) filled up with bright yellow on a black background, starting on the bottom and reaching the top of the screen when the waiting duration for this trial was over. In trials without visual aid, the same program ran the same routine, but filled the screen with a colour identical to the background, thus giving no visual cue for the progress of the waiting time until the trial was over.

4.5.4 Trial procedure

The initial item was placed in a container made out of a plastic PET bottle cap, and held in place by three dulled pins covered with part of a second bottle cap (Figure 1). The loaded container and the reward were held in either hand by the experimenter, and both hands were opened and presented to the bird simultaneously. The subject was allowed to take the container out of one hand of the experimenter, who then activated the program recording the waiting time on the laptop next to the bird with this hand, and closed the hand until the waiting time was

Figure 1: The container used to hold the initial item

over (Figure 2). If the bird tried to take the reward instead of the container, the hand with the reward was moved out of reach, but the reward stayed visible to the bird for the whole duration of the trial. Once the waiting time was over, the experimenter opened his hand again and allowed the bird to place the container back into it. Upon completion, the subject was allowed to eat the reward from the other hand, and the experimenter registered the outcome of the trial on the laptop.

Subjects were allowed to drop the container for up to three seconds, but if a bird started eating the initial item, the reward was immediately removed and the trial counted as unsuccessful. If the bird tried to give back an empty container, the trial was also counted as unsuccessful, the subject was not allowed to eat the reward and instead was shown the empty container. If the initial item dropped out of the container, but the subject did not eat it, the trial was repeated. If only parts of the initial item fell out of the container but the bird did not eat any of it, the trial was counted as successful if more than half of the initial item was returned, and repeated if less than half was returned, in both instances, the subject was rewarded. If the trial had to be interrupted for any other reason, it was repeated.

4.5.5 Session design

Sessions were balanced for side of the hand giving the reward and the visual representation of waiting time, so four trials per food combination were run in each session. With five different food combinations, this added up to a maximum of twenty trials per session. Three sessions were run for each level of waiting time. The waiting time doubled at each delay stage, starting at five seconds.

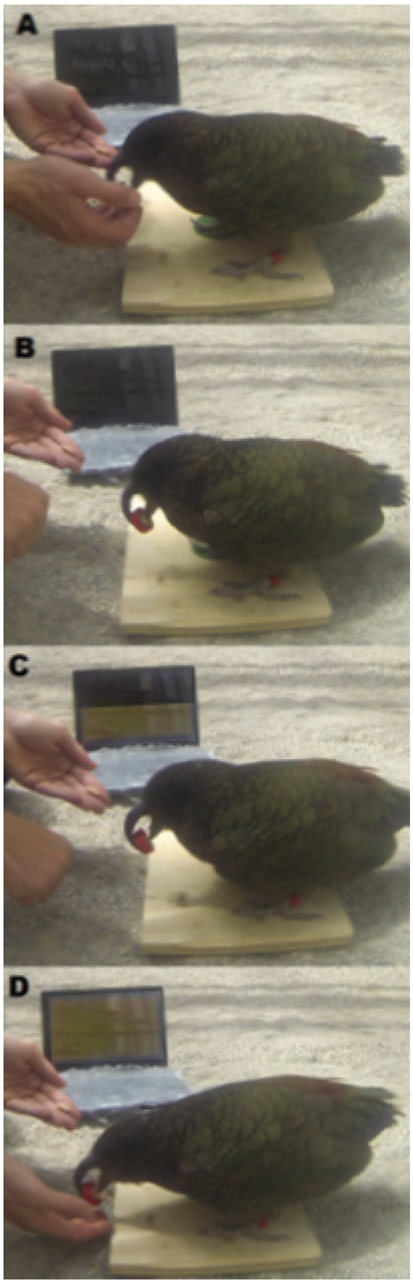

Figure 2: A) bird taking the container out of the experimenter's hand; B) bird starting to wait with the reward visible and the experimenter's other hand closed; C) screen showing the progress of the waiting time is already half filled-up; D) waiting time is over, the screen is filled with yellow, the bird is allowed to give back the loaded container and take the reward.

If a bird failed to exchange even a single time for all twelve trials at a given delay level, this food combination was not tested again for this subject in later levels. The control condition was exempt from this rule, but in order to not have too many control trials at later sessions, where the total number of trials was already low, the number of control trials was cut from four to two in sessions where only one other food combination á four trials remained to be tested.

4.5.6 Statistical methods

To evaluate the influence of different factors on the outcome of the exchange task, the exchange rates were compared using nonparametric statistics in IBM SPSS 21. The exchange rates for trials with and without visual aid and for both sides of reward presented were summed up for all individuals over all delay stages for each condition and compared using McNemar's test. The exchange rates for the different exchange conditions were also compared for each delay stage using McNemar's test.

The time at which subjects gave up waiting (renouncement time) was analysed, to see whether the birds decided early in a trial whether to wait or give up, which would result in shorter than expected waiting times in unsuccessful trials. The waiting time for each trial was automatically registered by the program used to randomize the trials and show the visual representation of waiting time. Two seconds were subtracted from the recorded waiting time to make up for the time it took the experimenter to activate and deactivate the timer. Trials with waiting times of over five seconds were video-reviewed for additional accuracy. Trials with unknown waiting time due to the bird non-visibly eating the initial item and then trying to exchange an empty container at the end of the trial were excluded from this analysis.

Like in earlier experiments (Dufour et al., 2007 and 2012; Pelé et al., 2010 and 2011; Auersperg et al., 2013), an adjusted Kolmogorov-Smirnov test was used to compare the observed survival function to the expected distribution of give-up times, assuming a constant give-up chance under null hypothesis (Haccou & Meelis, 1992). Significant differences between the observed and the expected distribution are specified by reaching a critical value (Siegel, 1956), and indicate that a subject renounced earlier or later than would be expected by chance.

5. Results

5.1 Food preference test

A preference between the tested items was shown in all subjects in the first food preference test. All ten individuals showed the same preference of picking pellet over apple, and peanut over anything else, as well as picking three small pellets over one in the quantity preference condition (Table 3). The results of the food exchange task later confirmed this data for all individuals taking part in the first food preference test.

Table 3: Results of food preference tests, shown as the ratio of one item picked over the other in ten trials per session. Frowin (Fr) and John (Jo) dropped out of the experiment and were replaced by Papu (Pu) and Tammy (Ta), who did not take part in the first preference test . *Data taken from recent IMHAI student project (IMHAI student group 2014, University of Veterinary Medicine Vienna, unpublished)

	first food preference test (winter 2013/2014)										second food preference test (summer 2014)									
	An	**Co**	**Fr**	**Jo**	**Ke**	**Ly**	**Pa**	**Ro**	**Sy**	**Wy**	**An**	**Co**	**Ke**	**Ly**	**Pa**	**Pu**	**Ro**	**Sy**	**Ta**	**Wy**
apple/pellet	0.5*	0.6*	0.0	0.3*	0.5*	0.1	0.5*	0.5*	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0
	0.1*	0.1*	0.0	0.2*	0.0*	0.0	0.1*	0.3*	0.0	1.0	0.0	0.0	0.3	0.0	0.1	0.7	0.0	0.0	0.3	0.2
	0.1*	0.2*		0.0*	0.1*		0.1*	0.1*					0.0			0.0			0.8	
								0.1*					0.0			0.3				
																0.3				
apple/peanut	0.2*	0.2*	0.7*	0.3*	0.4*	0.0	0.0	0.5*	0.2*	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
	0.1*	0.0*	0.2*	0.0*	0.0*	0.0	0.2	0.1*	0.0*	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
			0.0*	0.0*	0.1*			0.0*		0.0										
pellet/peanut	0.6*	0.2*	0.2	0.2	0.2	0.6*	0.6	0.4*	0.3	0.4*	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	0.4*	0.2*	0.1	0.0	0.0	0.4*	0.4	0.4*	0.2	0.3*	0.0	0.0	0.0	0.0	0.1	0.0	0.2	0.1	0.0	0.0
	0.2*					0.2*	0.1	0.2*	0.2	0.2*										
	0.1*					0.2*	0.0	0.1*		0.0*										
3/1 pellet	0.9	0.8	0.8	0.7	0.5	0.6	0.8	0.6	0.3	0.6										
	1.0	1.0	0.9	0.8	1.0	0.9	1.0	0.6	0.6	0.7										
				0.9	1.0	1.0		0.8	1.0	1.0										
								0.9	0.8	0.8										

In the second food preference test, done after the exchange task was completed, the same preference scale was confirmed in all but two subjects. These two individuals (Papu and Tammy, who replaced John and Frowin in the exchange task) did not show a clear preference between apple and pellet, which fits the behaviour they showed in the food exchange task.

The diet the kea at Haidlhof receive differs between summer and winter. This could influence their food preferences, however, no significant differences between the preferences for the three offered food items were found between winter (first food preference test) and summer (second food preference test). The two birds with the most unstable preference between apple and pellet seemed to change their preference on a daily or weekly basis instead. Overall, peanut was clearly preferred over the other two presented food items in all subjects at all times, and all preferences were again confirmed by the different exchange rates in the food exchange experiment.

5.2 Food exchange task

5.2.1 Effect of visual aid and side of the reward on overall exchange rate

No significant influence of the side of the hand presenting the reward on the exchange rate was found (McNemar's test, $p = 0.923$). Likewise, the presence of the visual representation of the waiting time had no significant influence on the exchange rate (McNemar's test, $p = 0.847$).

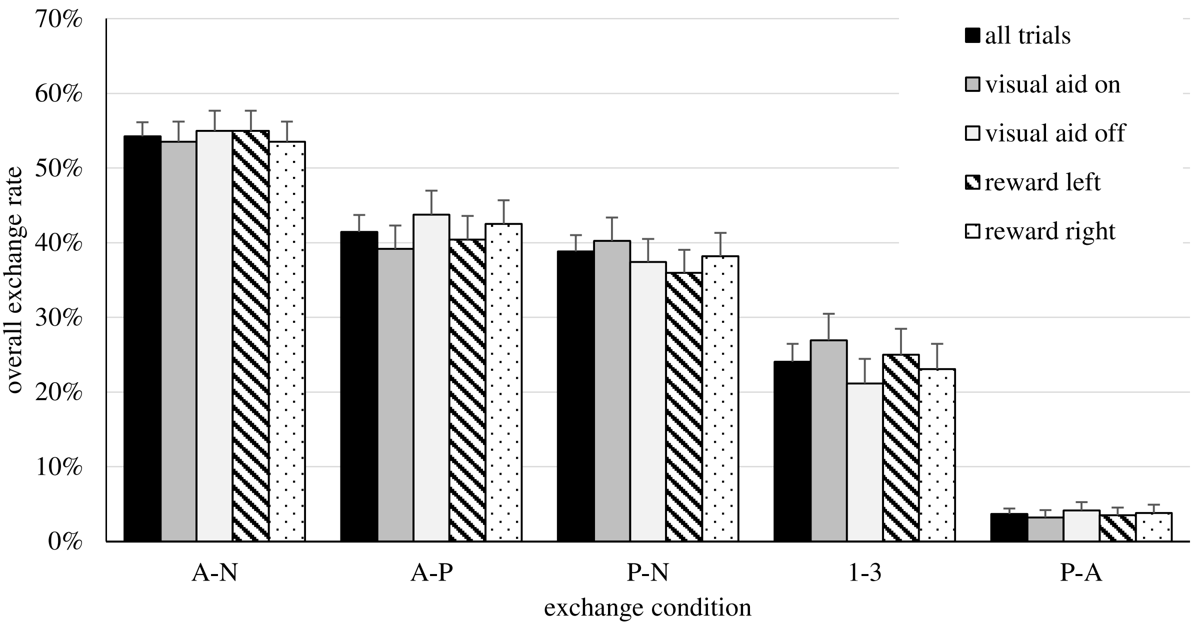

Figure 3: Overall exchange rates for all subjects in all sessions for the five exchange conditions, compared for visual aid and size of the reward. Error bars represent SE.

Even though the conditions with higher exchange rates include more sessions at higher delays, due to subjects dropping out in the other conditions, a difference of the overall exchange rate between the different conditions can already be seen in Figure 3. The birds rarely exchanged at all in the control condition.

5.2.2 Effect of preference difference on exchange rate

The condition with the highest difference in preference between initial item and reward (apple for peanut, "A-N") consistently had the highest exchange rate at all delay levels (Table 4, Figure 4). The differences to any other exchange condition were significant (McNemar's test $p = 0.000$) for all comparisons of "A-N" with any other exchange condition at any delay level up to 40 s, where comparisons become difficult due to very low sample sizes. The longest waiting times for each of the ten individuals were also achieved in this condition (Table 5).

Table 4: Development of average exchange rates for all subjects over different delay lengths. NT = not tested, since all individuals already dropped out of this condition.

delay	exchange rate					subjects left			
	A-N	A-P	P-N	1-3	P-A (control)	A-N	A-P	P-N	1-3
5 s	89.17%	61.67%	59.17%	33.33%	15.83%	10	10	10	10
10 s	91.67%	65.83%	69.44%	24.07%	2.50%	10	10	9	9
20 s	71.67%	35.19%	34.26%	15.00%	0.83%	10	9	9	5
40 s	43.33%	9.52%	5.56%	0.00%	0.00%	10	7	9	2
80 s	13.89%	0.00%	5.56%	NT	0.00%	9	4	4	0
160 s	1.19%	NT	0.00%	NT	0.00%	7	0	1	0
320 s	0.00%	NT	NT	NT	0.00%	1	0	0	0

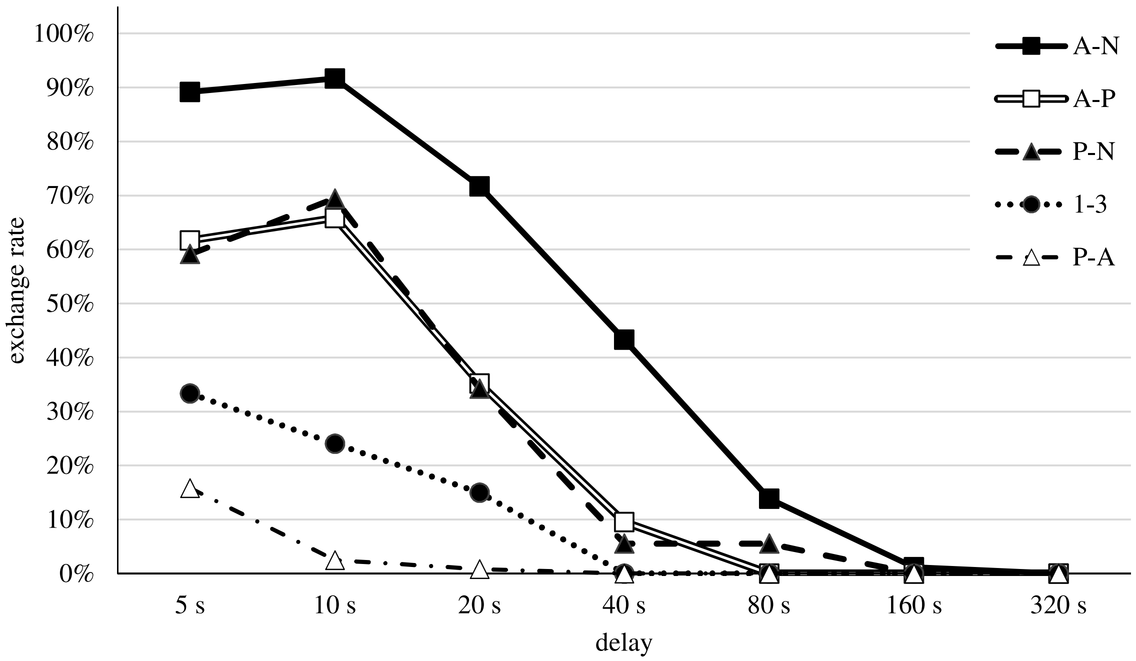

Figure 4: Development of average exchange rates for all subjects over different delay lengths.

While being significantly lower than the exchange rates for “A-N”, the overall exchange rates of the two conditions with a smaller preference difference (apple for pellet, “A-P”; pellet for peanut, “P-N”) were not significantly different between each other overall, even though some individuals preferred one condition over the other (see individual results in Appendix).

Quantity exchange (one pellet for three pellets, “1-3”) had lower exchange rates than the other non-control exchange conditions, and no individual tolerated delays longer than 20 s for this condition.

The control condition (pellet for apple, “P-A”) was not traded at all by five subjects and not more than a single time by another three subjects. Its exchange rate was significantly lower than that for any other condition (McNemar’s test $p < 0.005$ for all comparisons of “P-A” with any other exchange condition at any delay level, except those with an exchange rate of zero).

Furthermore, more than half of all exchanges in the control condition (12 of 23) came from a single individual (Tammy), and were in accord with a non-stable food preference in this individual in the second food preference test (Table 3).

Table 5: Maximum waiting time and delay at which the last successful exchange took place for all individuals

subject	maximum waiting time (sec)	last success at delay (sec)
Anu	80	80
Coco	80	80
Kermit	126	80
Lilly	80	80
Paul	59	40
Papu	80	80
Roku	160	160
Sunny	80	40
Tammy	155	80
Willy	40	20

The individual exchange rates for all subjects can be found in the Appendix.

5.2.3 Renouncement time analysis

In most cases where no exchange took place, the subjects ate the initial item right away, without waiting, resulting in a renouncement time of zero in 83.7 % of all trials at any delay stage above five seconds (Figure 5), and 78.3 % still when discounting the control trials. Some renouncement times were unknown due to the bird eating the initial item without the experimenter noticing, and trying to trade back an empty container after the waiting time elapsed. A complete table of the distribution of waiting times at all delay stages can be found in the Appendix.

The results of the Kolmogorov-Smirnov test (Table 6) also show that in most conditions, the birds had a renouncement time that was significantly different from the one expected assuming a constant giving-up chance. All significant results show that the birds waited shorter than expected by chance.

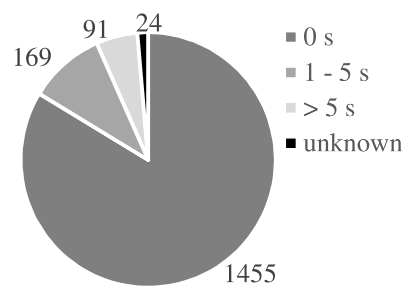

Figure 5: Distribution of renouncement times for all trials.

Table 6: Maximum values obtained from the Kolmogorov–Smirnov test comparing the observed renouncement times with those expected assuming a constant giving-up chance. NT = no trade at this condition/delay level, NF = no failed trial with known give-up time at this condition/delay level. *p < 0.05, **p < 0.01.

	delay	An	Co	Ke	Ly	Pa	Pu	Ro	Sy	Ta	Wy
A-N	**10 s**	NF	0.58	NF	0.20	NF	0.58	NF	0.29	0.29	NF
	20 s	0.27	NF	NF	1.73**	0.29	2.02**	NF	0.58	1.44*	1.73**
	40 s	0.84	0.23	0.47	2.31**	1.44*	1.15	1.73**	0.87	1.44*	NT
	80 s	3.18**	2.31**	2.31**	2.02**	NT	1.44*	1.76**	NT	2.35**	NT
	160 s	NT	NT	NT	NT	NT	NT	2.60**	NT	NT	NT
	delay	**An**	**Co**	**Ke**	**Ly**	**Pa**	**Pu**	**Ro**	**Sy**	**Ta**	**Wy**
A-P	**10 s**	0.29	NT	0.58	1.73**	NF	1.44*	0.26	NF	0.39	0.58
	20 s	0.87	NT	0.64	3.18**	0.83	NT	0.30	2.02**	NT	2.89**
	40 s	2.31**	NT	2.11**	3.18**	NT	NT	NT	2.11**	NT	NT
	delay	**An**	**Co**	**Ke**	**Ly**	**Pa**	**Pu**	**Ro**	**Sy**	**Ta**	**Wy**
P-N	**10 s**	1.21	0.53	0.29	0.58	1.44*	2.02**	NT	0.17	NF	1.15
	20 s	3.18**	1.81**	2.02**	0.87	2.89**	1.44*	NT	1.33*	2.60**	2.31**
	40 s	NT	2.02**	NT	NT	NT	2.31**	NT	NT	3.18**	NT
	80 s	NT	NT	NT	NT	NT	NT	NT	NT	2.89**	NT
	delay	**An**	**Co**	**Ke**	**Ly**	**Pa**	**Pu**	**Ro**	**Sy**	**Ta**	**Wy**
1-3	**10 s**	1.20	NT	NT	NT	1.73**	NT	NT	1.21	1.15	3.18**
	20 s	1.32*	NT	NT	NT	2.89**	NT	NT	NT	NT	NT

Another way to look at the renouncement time data is to calculate the percentage of failed trials after a given time has elapsed. For example, while the total percentage of failed trials at the 20 s delay level is 57.1%, this percentage shrinks to 5.6% if we only count trials where the subjects waited for more than five seconds, already discounting control trials (Table 8). This shows the reluctance of the birds to give up waiting once they started.

Table 7: Percentage of failed trials for all non-control trials at all delay stages after a given time elapsed.

					fail after waiting for > 5 s		**fail after waiting for > 10 s**		**fail after waiting for > 20 s**	
delay	**n total**	**n trade**	**n fail**	**total fail**	**n**	**%**	**n**	**%**	**n**	**%**
5 s	480	292	188	39.2%	-	-	-	-	-	-
10 s	456	290	166	36.4%	14	4.6%	-	-	-	-
20 s	396	170	226	57.1%	10	5.6%	6	3.4%	-	-
40 s	336	66	270	80.4%	31	32.0%	24	26.7%	16	19.5%
80 s	192	17	175	91.1%	20	54.1%	14	45.2%	10	37.0%
160 s	96	1	95	99.0%	12	92.3%	11	91.7%	7	87.5%
320 s	12	0	12	100.0%	2	100.0%	1	100.0%	1	100.0%

6. Discussion

The data gathered in this study demonstrates that kea not only possess the cognitive requirements to perform in a food exchange task, but also the impulse control needed to delay consummation of a food item for a prolonged duration of time. The renouncement time distribution shows that they make their decision to wait very early in a trial, and the significant differences in the exchange rates between test conditions with distinctive preference differences indicate that they base this decision on economic considerations including the immediate benefit, the future reward, and the expected waiting time. Taken together, these findings strongly suggest that kea are able to plan ahead, can control their impulses, and use temporal discounting in exchange tasks.

The exchange ratios in the quantity exchange condition were higher than in previous studies in birds, and the maximum endured delay times were the longest yet recorded in any bird species not using food caching to cope with the waiting time. The individual variation between subjects was smaller than in the previous experiments in Goffin's or corvids, where some subjects started to refuse any exchange already at very short delay times (Dufour et al.. 2007; Auersperg et al.. 2013).

All subjects scored their highest exchange rates and the longest waiting times trading apple for peanut, which was the exchange condition with the biggest preference difference between initial item and reward. The control condition was not traded more than a single time by eight of the ten individuals, for a total of 23 in 630 trials, and more than half of those came from a single individual (Tammy) who had changing food preferences in regard to apple and pellet. This reconfirms that the subjects made strategic decisions based upon their preference of the food items.

The renouncement time data from failed trials also supports this claim. In most cases, there was no renouncement time at all – the subjects ate the initial item right away, without waiting, in the overwhelming majority of failed trials. The Kolmogorov-Smirnov analysis of waiting times demonstrated that the birds waited significantly shorter than expected assuming a constant giving-up chance, confirming that they decided early in a trial whether to wait or not. After the first delay stage of five seconds, where the birds seemed to take some time getting used to the task, sometimes waiting for the whole duration and then deciding not to trade after all, results became markedly clear, with a renouncement time of zero in more than 87 % of all trials at any delay stage above five seconds, and more than 82 % still even discounting the control trials (see Appendix for exact data). If we look at the results in another way, the percentage of failed trials drops sharply once the waiting time exceeds five seconds, also confirming the bird's reluctance to give up waiting once they started.

The tendency of the birds to either instantly consume the initial item, or wait for the whole duration of the trial to exchange for the more preferred one, is also demonstrated by the waiting times for individual trials (Figure 6). Most birds show a clear pattern of "either-or", either waiting for the whole duration, or instantly consuming the initial item, and in most cases this pattern gets only broken when the waiting time is longer than the individual could expect, at the start of a new delay level. What happens then is that most of the birds attempt to wait one or at most two times at the new delay stage, sometimes even completing a successful trade, but then adjust their strategy to the new expected waiting time and stop waiting at all. Taken together, these patterns strongly suggests that the subjects possess an internal representation of the waiting time and use temporal discounting to make a decision whether the expected payoff will be worth the wait.

The visual representation of the waiting time failed to have any significant influence on the outcome of the trials. This could either be due to the bird's inability to make the connection between the visual cue and the waiting time, or because they paid little to no attention to it, instead mostly focussing on the experimenter and the expected reward. An auditory cue in addition to the visual one, for example a tone steadily rising in pitch, could have helped catching the subject's attention and should be incorporated in future experiments using this setup. Furthermore, the bird's tendency to make their decision to wait at the start of a trial, even before they could see whether there was a visual aid or not, and then to stick to that decision, would have diminished the effect of any help they got during the waiting time anyways. This, combined with the low number of successful trials at longer delay times, would have made it extraordinary difficult to statistically detect any impact of the visual aid, even if there was one.

Earlier studies often had issues with the subjects being unable to inhibit nibbling the initial item and then trying to return an incomplete food item (Auersperg et al, 2013; Ramseyer et al., 2006). Our solution, the addition of the container to hold the initial item, did ameliorate but not completely eliminate this problem. While most birds used the container in a way that made it impossible for them to manipulate the food item without putting it down (Figure 7A), some of the birds held the container in a fashion that enabled them to press their tongue on the food item during the waiting phase (Figure 7B), sometimes removing the initial item from the container (resulting in a repeat trial), or mashing the initial item. The latter was only a problem with pieces

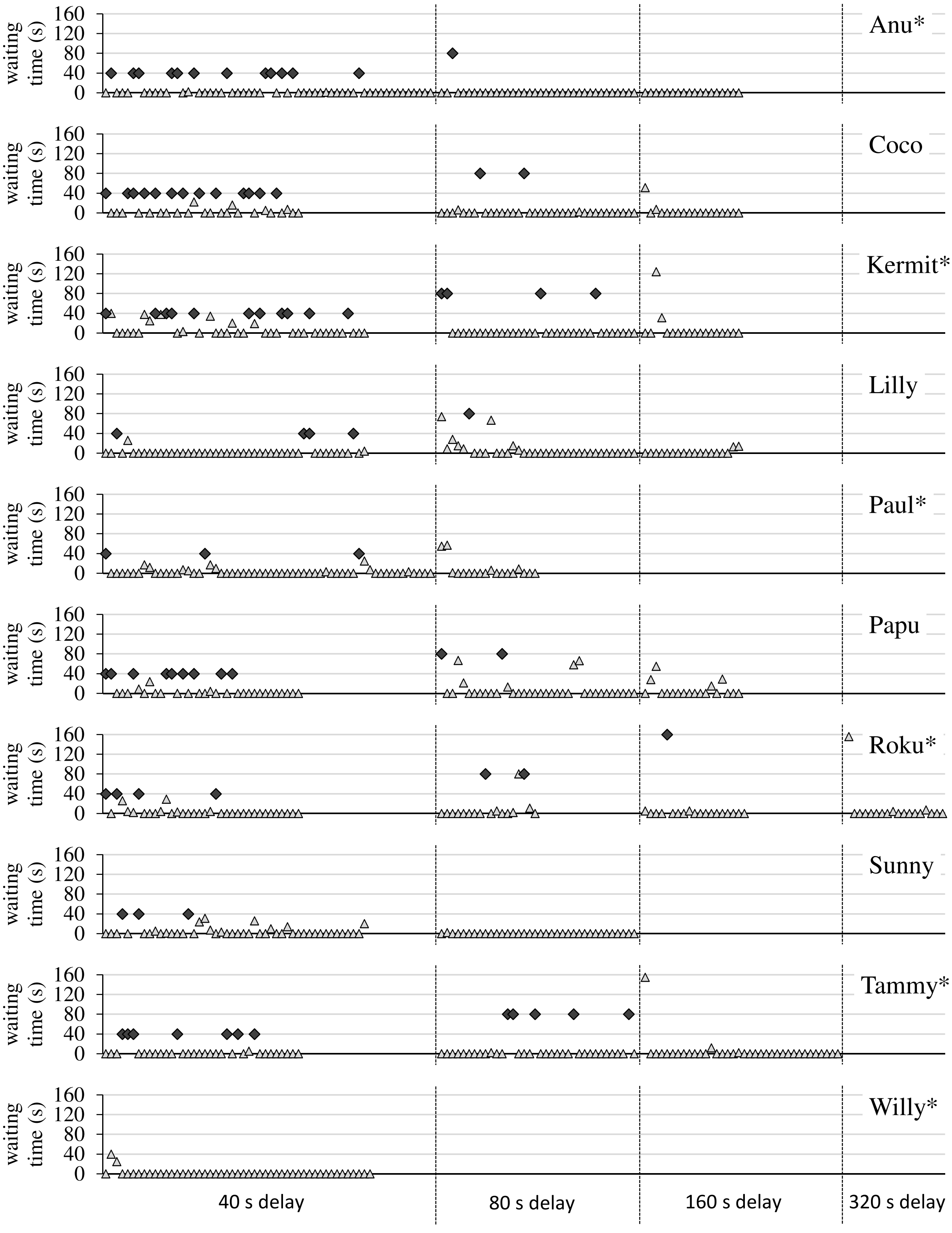

Figure 6: Waiting times for trials with a delay of 40 seconds and more. Light triangles show unsuccessful trials, dark rectangles represent successful exchanges. Not all individuals have the full number of trials at a given delay stage, since some of them were not tested for certain conditions, having already failed them in earlier delay stages. *Subjects displaying the pattern of waiting at most one or two times at a new delay stage, before giving up waiting altogether.

of apple, but sometimes it became very hard to judge whether the bird had actually eaten parts of the initial item or just mashed it.

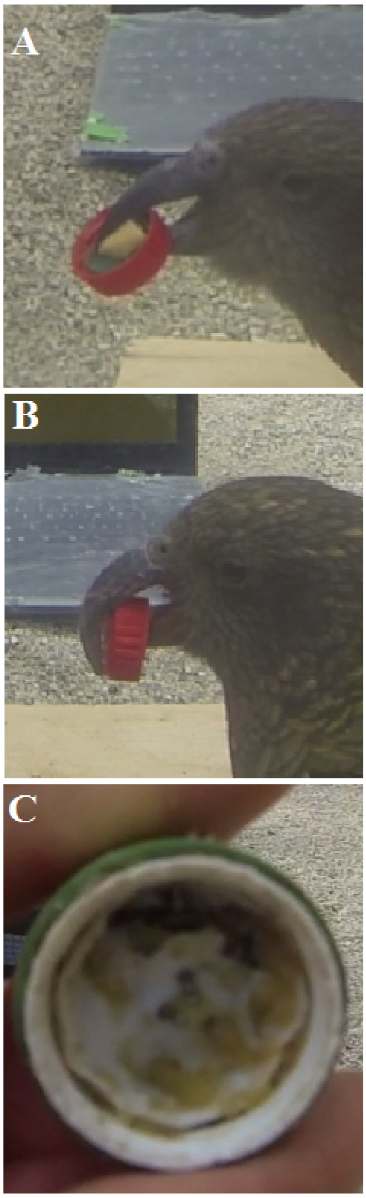

Figure 7: A and B: Different ways the subjects held the container in their beak. C: Container with remains of a piece of apple, returned by Roku in the only successful trial at the 160 s delay stage.

This issue was only present in two of the ten subjects, Coco and Roku, and especially pronounced in trials with a long waiting time, including the only successful trial at the 160 s delay stage, where Roku squished the piece of apple into a pulp (Figure 7C). While he did not visibly eat any pieces of apple during waiting, one could argue that the squished apple represents little gratification to delay. To counter that view, it is worth noting that in his failed trial at the 320 s delay stage, Roku mashed the piece of apple in a similar way, yet when he gave up to wait after 156 seconds he actually put down the container and consumed the tiny pieces of apple left. Either way, future studies could improve upon our experimental design by training the birds to hold the container in a way that makes it impossible for them to manipulate the food item without putting the container down, as shown in Figure 7A.

All bird species tested so far do not come close to the highest waiting times achieved in exchange tasks in primates, and the kea was no exception to this. One should keep in mind though, that a direct comparison of our results to those achieved in primates is complicated by the fact that most studies in primates only use quantity exchange paradigms or even accumulation tasks to test delay of gratification. Furthermore, the quantities used in primate studies, where the subjects got as much as 40 times the quantity of the initial food item as a reward (Dufour et al., 2007; Pelé et al., 2010), would have been impossible to do for us because of dietary restrictions. We only used three times the quantity of the initial item in our quantity exchange condition, in order not to overfeed the birds. Thus, the better performance of primates as far as quantity exchange is concerned, could be at least partly due to these methodological differences.

Comparing our findings to the previous studies in birds, our results fit in very well with the earlier experiments in corvids (Dufour et al.. 2012) and Goffin's cockatoos (Auersperg et al.. 2013). Birds generally seem to be less motivated to wait for a higher quantity of food compared to a more preferred reward, and the kea follow this pattern, even if both their exchange rate and tolerated waiting times exceeded those shown in other bird species. Maximum waiting times and exchange rates in kea are higher than in Goffin's cockatoos, and while at least one of the corvid subjects still traded at a delay of 320 seconds, all exchanges over 160 seconds of waiting time in corvids were achieved by caching the initial item, a coping strategy not allowed in this experiment. Thus, our study shows the longest waiting times in non-food-caching birds to date. However, considering the relatively small sample sizes and the slight methodological differences between the studies in birds, as well as the high inter-subject variation and the heavy impact of the preference difference of the presented food items on the maximum tolerated waiting time, one should rather look at the overall picture instead of particular data points, especially since it is impossible to exactly quantify the actual preference difference for a given individual.

Taken together, the food exchange studies done in birds so far show that at least some families of birds possess the ability to make economic decisions based on past experiences and future expectations, and the necessary impulse control to delay immediate gratification in favour of a long-term reward. Further studies in other bird species could enhance our understanding of the cognitive requirements for this kind of behaviour, and the possible impact of ecological factors such as foraging strategies on the result of food exchange experiments.

Acknowledgements

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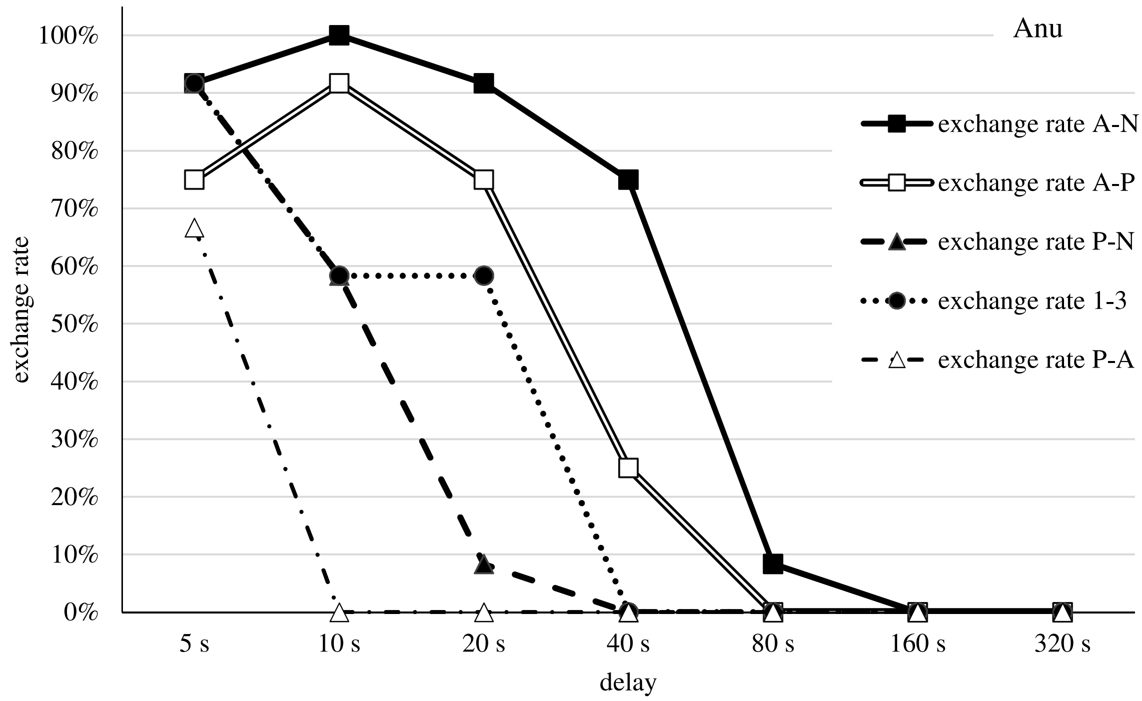
Appendix

Individual results



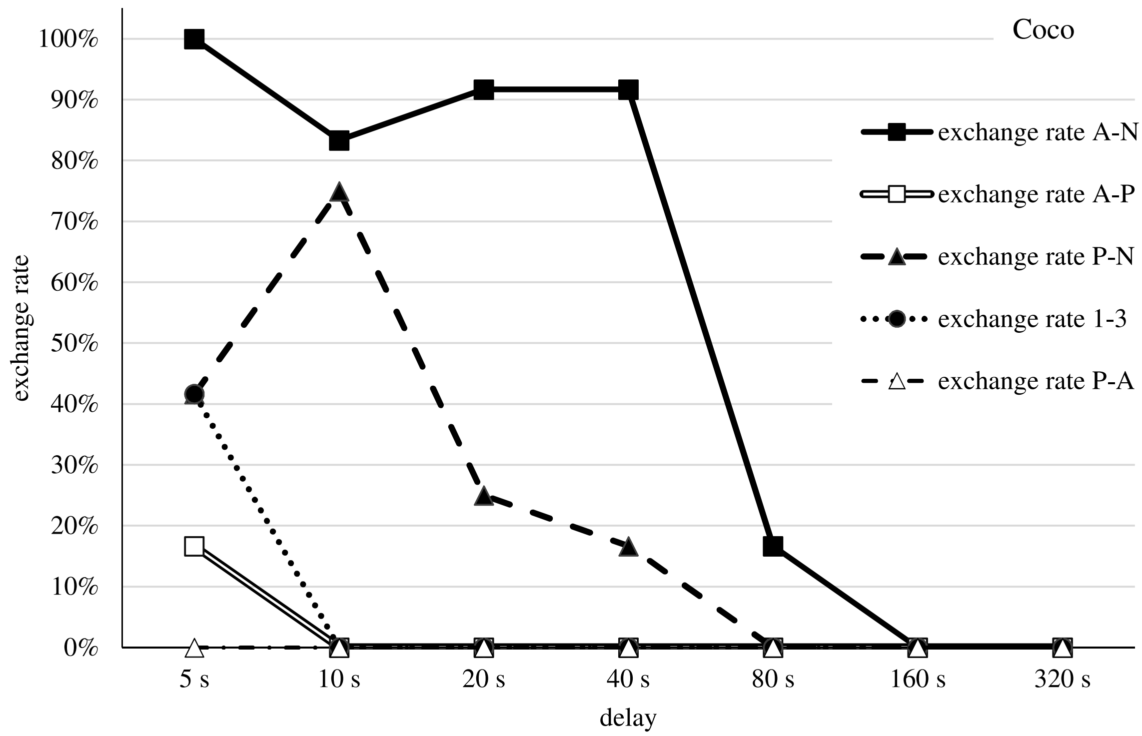


Figure 8: Exchange rates for all conditions over all sessions for Anu and Coco.

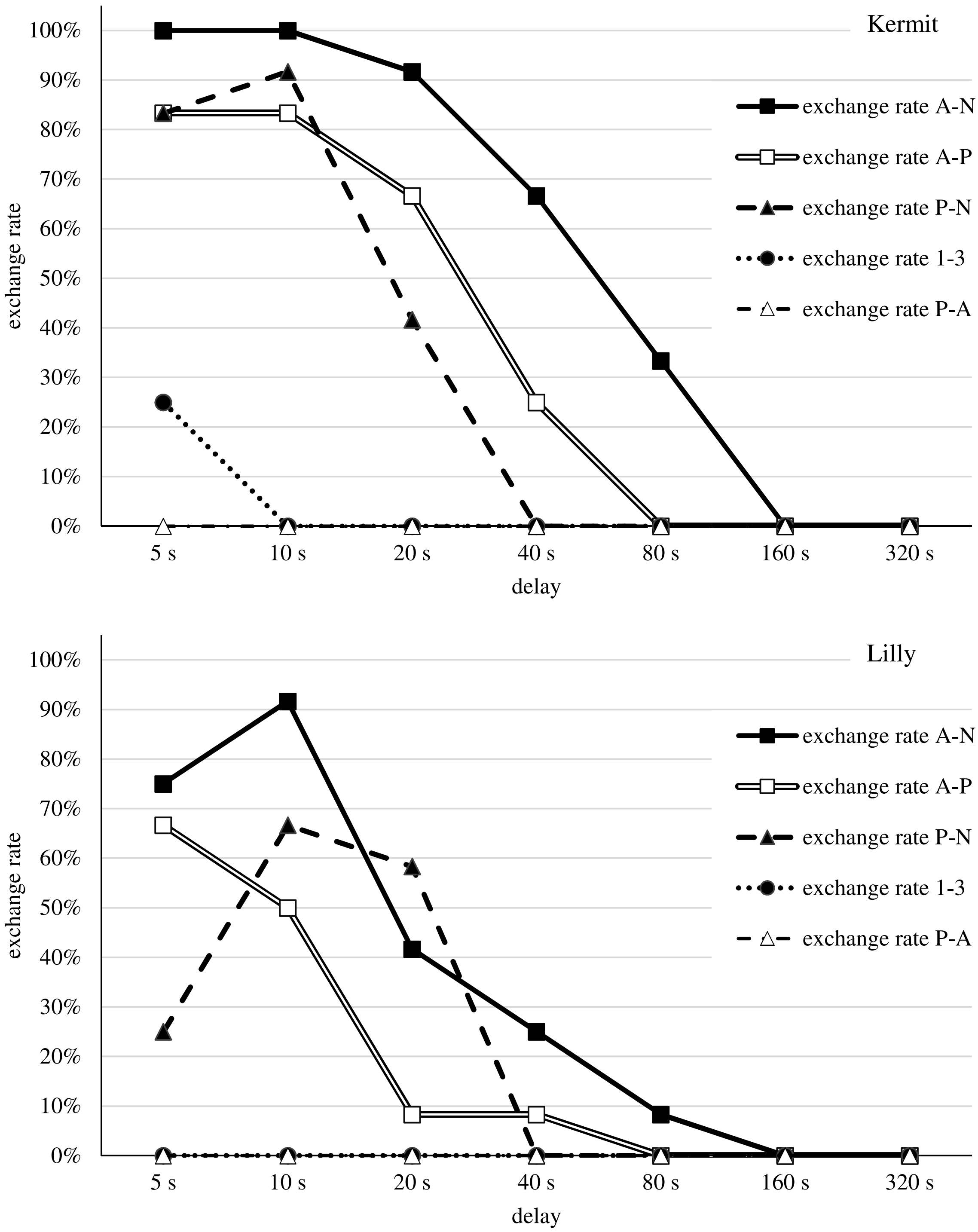


Figure 9: Exchange rates for all conditions over all sessions for Kermit and Lilly.

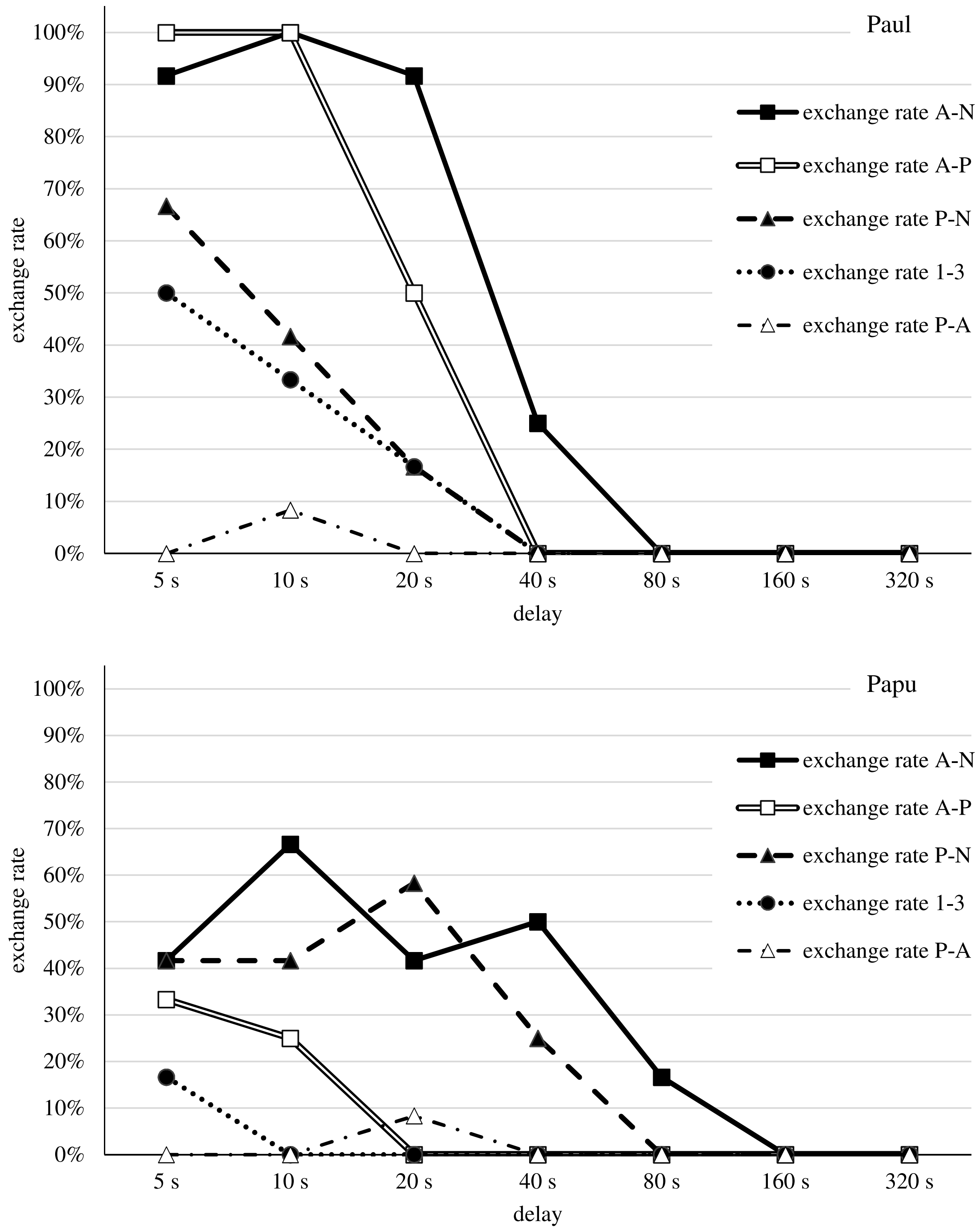


Figure 10: Exchange rates for all conditions over all sessions for Paul and Papu.

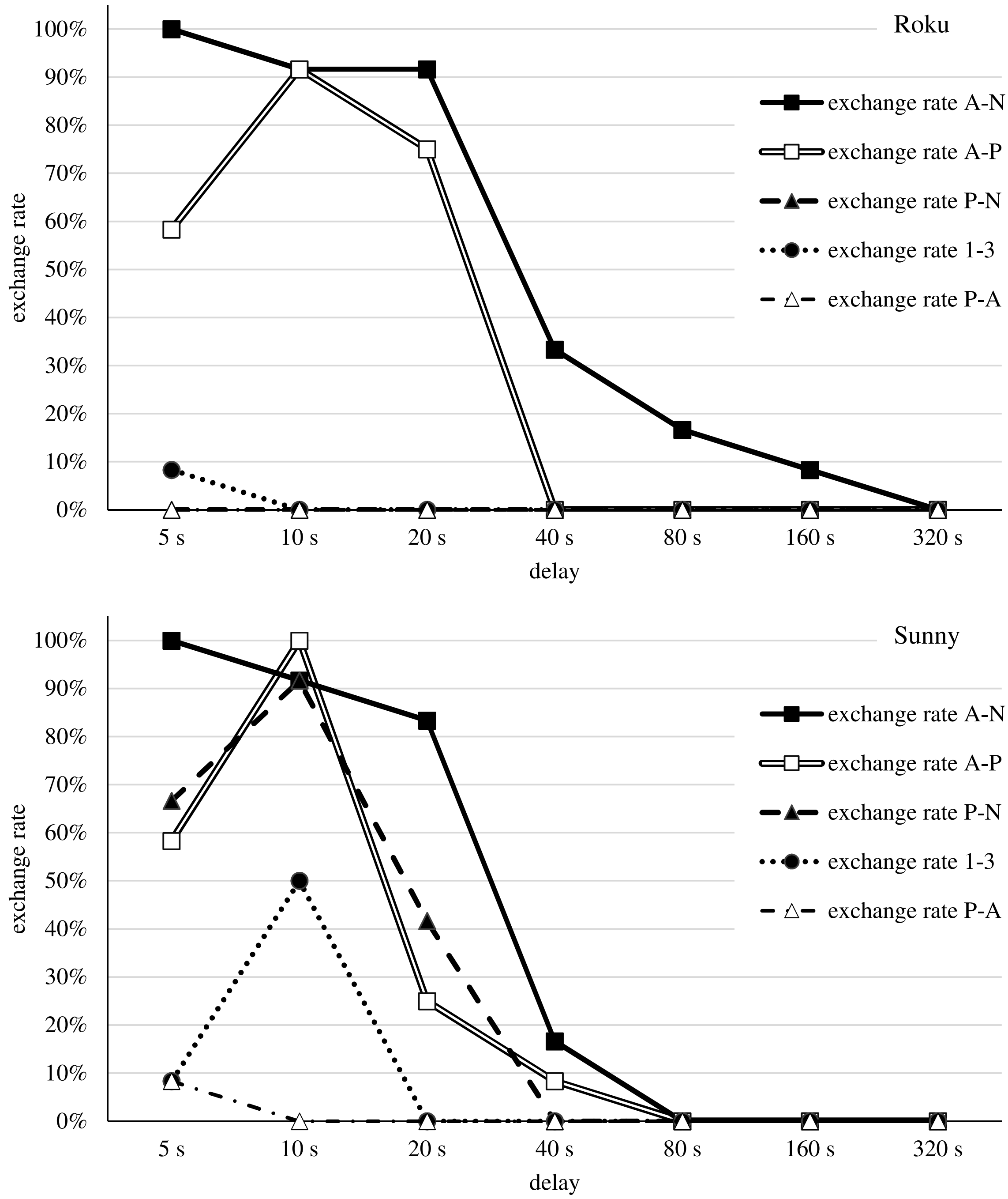


Figure 11: Exchange rates for all conditions over all sessions for Roku and Sunny.

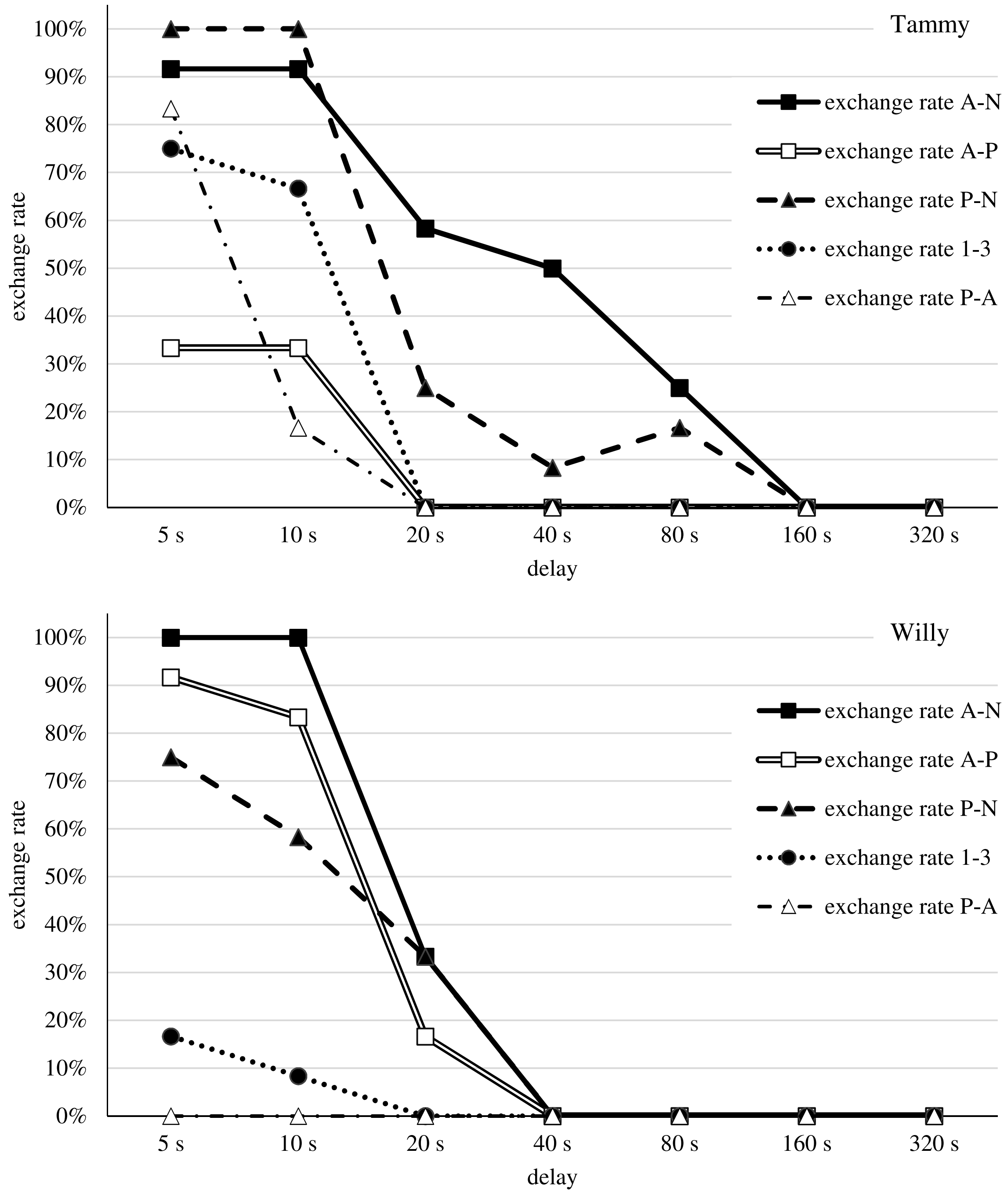


Figure 12: Exchange rates for all conditions over all sessions for Tammy and Willy.

Exact values for all trials

Table 8: Exchange rates and number of successful and failed trials for all conditions over all trials.

			A-N			A-P			P-N			1-3			P-A		
	subj	**ses**	**succ**	**fail**	**%**	**succ**	**fail**	**%**	**succ**	**fail**	**%**	**succ**	**fail**	**%**	**succ**	**fail**	**%**
all trials	**An**	18	44	28	61%	32	28	53%	19	29	40%	25	23	52%	8	58	12%
	Co	18	46	26	64%	2	22	8%	19	41	32%	5	19	21%	0	66	0%
	Ke	18	47	25	65%	31	29	52%	26	22	54%	3	21	13%	0	66	0%
	Ly	18	29	43	40%	16	44	27%	18	30	38%	0	12	0%	0	66	0%
	Pa	15	37	23	62%	30	18	63%	15	33	31%	12	36	25%	1	53	2%
	Pu	18	26	46	36%	7	29	19%	20	40	33%	2	22	8%	1	65	2%
	Ro	21	41	43	49%	27	21	56%	0	12	0%	1	23	4%	0	67	0%
	Sy	15	35	25	58%	23	37	38%	24	24	50%	7	29	19%	1	59	2%
	Ta	18	38	34	53%	8	28	22%	30	42	42%	17	19	47%	12	60	17%
	Wy	12	28	20	58%	23	25	48%	20	28	42%	3	33	8%	0	48	0%
	Total	**171**	**371**	**313**	**54%**	**199**	**281**	**41%**	**191**	**301**	**39%**	**75**	**237**	**24%**	**23**	**608**	**4%**

Table 9: Exchange rates and number of successful and failed trials for all conditions at the 5 s delay level.

			A-N			A-P			P-N			1-3			P-A		
	subj	**ses**	**succ**	**fail**	**%**	**succ**	**fail**	**%**	**succ**	**fail**	**%**	**succ**	**fail**	**%**	**succ**	**fail**	**%**
5 s lag	**An**	3	11	1	92%	9	3	75%	11	1	92%	11	1	92%	8	4	67%
	Co	3	12	0	100%	2	10	17%	5	7	42%	5	7	42%	0	12	0%
	Ke	3	12	0	100%	10	2	83%	10	2	83%	3	9	25%	0	12	0%
	Ly	3	9	3	75%	8	4	67%	3	9	25%	0	12	0%	0	12	0%
	Pa	3	11	1	92%	12	0	100%	8	4	67%	6	6	50%	0	12	0%
	Pu	3	5	7	42%	4	8	33%	5	7	42%	2	10	17%	0	12	0%
	Ro	3	12	0	100%	7	5	58%	0	12	0%	1	11	8%	0	12	0%
	Sy	3	12	0	100%	7	5	58%	8	4	67%	1	11	8%	1	11	8%
	Ta	3	11	1	92%	4	8	33%	12	0	100%	9	3	75%	10	2	83%
	Wy	3	12	0	100%	11	1	92%	9	3	75%	2	10	17%	0	12	0%
	Total	**30**	**107**	**13**	**89%**	**74**	**46**	**62%**	**71**	**49**	**59%**	**40**	**80**	**33%**	**19**	**101**	**16%**

Table 10: Exchange rates and number of successful and failed trials for all conditions at the 10 s delay level.

10 s lag			A-N			A-P			P-N			1-3			P-A		
	subj	**ses**	**succ**	**fail**	**%**	**succ**	**fail**	**%**	**succ**	**fail**	**%**	**succ**	**fail**	**%**	**succ**	**fail**	**%**
	An	3	12	0	100%	11	1	92%	7	5	58%	7	5	58%	0	12	0%
	Co	3	10	2	83%	0	12	0%	9	3	75%	0	12	0%	0	12	0%
	Ke	3	12	0	100%	10	2	83%	11	1	92%	0	12	0%	0	12	0%
	Ly	3	11	1	92%	6	6	50%	8	4	67%	0	0	N/A	0	12	0%
	Pa	3	12	0	100%	12	0	100%	5	7	42%	4	8	33%	1	11	8%
	Pu	3	8	4	67%	3	9	25%	5	7	42%	0	12	0%	0	12	0%
	Ro	3	11	1	92%	11	1	92%	0	0	N/A	0	12	0%	0	12	0%
	Sy	3	11	1	92%	12	0	100%	11	1	92%	6	6	50%	0	12	0%
	Ta	3	11	1	92%	4	8	33%	12	0	100%	8	4	67%	2	10	17%
	Wy	3	12	0	100%	10	2	83%	7	5	58%	1	11	8%	0	12	0%
	To-tal	**30**	**110**	**10**	**92%**	**79**	**41**	**66%**	**75**	**33**	**69%**	**26**	**82**	**24%**	**3**	**117**	**3%**

Table 11: Exchange rates and number of successful and failed trials for all conditions at the 20 s delay level.

20 s lag			A-N			A-P			P-N			1-3			P-A		
	subj	**ses**	**succ**	**fail**	**%**	**succ**	**fail**	**%**	**succ**	**fail**	**%**	**succ**	**fail**	**%**	**succ**	**fail**	**%**
	An	3	11	1	92%	9	3	75%	1	11	8%	7	5	58%	0	12	0%
	Co	3	11	1	92%	0	0	N/A	3	9	25%	0	0	N/A	0	12	0%
	Ke	3	11	1	92%	8	4	67%	5	7	42%	0	0	N/A	0	12	0%
	Ly	3	5	7	42%	1	11	8%	7	5	58%	0	0	N/A	0	12	0%
	Pa	3	11	1	92%	6	6	50%	2	10	17%	2	10	17%	0	12	0%
	Pu	3	5	7	42%	0	12	0%	7	5	58%	0	0	N/A	1	11	8%
	Ro	3	11	1	92%	9	3	75%	0	0	N/A	0	0	N/A	0	12	0%
	Sy	3	10	2	83%	3	9	25%	5	7	42%	0	12	0%	0	12	0%
	Ta	3	7	5	58%	0	12	0%	3	9	25%	0	12	0%	0	12	0%
	Wy	3	4	8	33%	2	10	17%	4	8	33%	0	12	0%	0	12	0%
	To-tal	**30**	**86**	**34**	**72%**	**38**	**70**	**35%**	**37**	**71**	**34%**	**9**	**51**	**15%**	**1**	**119**	**1%**

Table 12: Exchange rates and number of successful and failed trials for all conditions at the 40 s delay level.

40 s lag			A-N			A-P			P-N			1-3			P-A		
	subj	**ses**	**succ**	**fail**	**%**	**succ**	**fail**	**%**	**succ**	**fail**	**%**	**succ**	**fail**	**%**	**succ**	**fail**	**%**
	An	3	9	3	75%	3	9	25%	0	12	0%	0	12	0%	0	12	0%
	Co	3	11	1	92%	0	0	N/A	2	10	17%	0	0	N/A	0	12	0%
	Ke	3	8	4	67%	3	9	25%	0	12	0%	0	0	N/A	0	12	0%
	Ly	3	3	9	25%	1	11	8%	0	12	0%	0	0	N/A	0	12	0%
	Pa	3	3	9	25%	0	12	0%	0	12	0%	0	12	0%	0	12	0%
	Pu	3	6	6	50%	0	0	N/A	3	9	25%	0	0	N/A	0	12	0%
	Ro	3	4	8	33%	0	12	0%	0	0	N/A	0	0	N/A	0	12	0%
	Sy	3	2	10	17%	1	11	8%	0	12	0%	0	0	N/A	0	12	0%
	Ta	3	6	6	50%	0	0	N/A	1	11	8%	0	0	N/A	0	12	0%
	Wy	3	0	12	0%	0	12	0%	0	12	0%	0	0	N/A	0	12	0%
	Total	**30**	**52**	**68**	**43%**	**8**	**76**	**10%**	**6**	**102**	**6%**	**0**	**24**	**0%**	**0**	**120**	**0%**

Table 13: Exchange rates and number of successful and failed trials for all conditions at the 80 s delay level.

			A-N			A-P			P-N			1-3			P-A		
	subj	**ses**	**succ**	**fail**	**%**	**succ**	**fail**	**%**	**succ**	**fail**	**%**	**succ**	**fail**	**%**	**succ**	**fail**	**%**
80 s lag	**An**	3	1	11	8%	0	12	0%	0	0	N/A	0	0	N/A	0	12	0%
	Co	3	2	10	17%	0	0	N/A	0	12	0%	0	0	N/A	0	12	0%
	Ke	3	4	8	33%	0	12	0%	0	0	N/A	0	0	N/A	0	12	0%
	Ly	3	1	11	8%	0	12	0%	0	0	N/A	0	0	N/A	0	12	0%
	Pa	3	0	12	0%	0	0	N/A	0	0	N/A	0	0	N/A	0	6	0%
	Pu	3	2	10	17%	0	0	N/A	0	12	0%	0	0	N/A	0	12	0%
	Ro	3	2	10	17%	0	0	N/A	0	0	N/A	0	0	N/A	0	6	0%
	Sy	3	0	12	0%	0	12	0%	0	0	N/A	0	0	N/A	0	12	0%
	Ta	3	3	9	25%	0	0	N/A	2	10	17%	0	0	N/A	0	12	0%
	Total	**27**	**15**	**93**	**14%**	**0**	**48**	**0%**	**2**	**34**	**6%**	**0**	**0**	**0%**	**0**	**96**	**0%**

Table 14: Exchange rates and number of successful and failed trials for all conditions at the 160 s delay level.

			A-N			A-P			P-N			1-3			P-A		
	subj	**ses**	**succ**	**fail**	**%**	**succ**	**fail**	**%**	**succ**	**fail**	**%**	**succ**	**fail**	**%**	**succ**	**fail**	**%**
160 s lag	**An**	3	0	12	0%	0	0	N/A	0	0	N/A	0	0	N/A	0	6	0%
	Co	3	0	12	0%	0	0	N/A	0	0	N/A	0	0	N/A	0	6	0%
	Ke	3	0	12	0%	0	0	N/A	0	0	N/A	0	0	N/A	0	6	0%
	Ly	3	0	12	0%	0	0	N/A	0	0	N/A	0	0	N/A	0	6	0%
	Pu	3	0	12	0%	0	0	N/A	0	0	N/A	0	0	N/A	0	6	0%
	Ro	3	1	11	8%	0	0	N/A	0	0	N/A	0	0	N/A	0	6	0%
	Ta	3	0	12	0%	0	0	N/A	0	12	0%	0	0	N/A	0	12	0%
	Total	**21**	**1**	**83**	**1%**	**0**	**0**	**0%**	**0**	**12**	**0%**	**0**	**0**	**0%**	**0**	**49**	**0%**

Table 15: Exchange rates and number of successful and failed trials for all conditions at the 320 s delay level.

			A-N			A-P			P-N			1-3			P-A		
	subj	**ses**	**succ**	**fail**	**%**	**succ**	**fail**	**%**	**succ**	**fail**	**%**	**succ**	**fail**	**%**	**succ**	**fail**	**%**
320 s lag																	
	Ro	3	0	12	0%	0	0	N/A	0	0	N/A	0	0	N/A	0	6	0%
	Total	**3**	**0**	**12**	**0%**	**0**	**0**	**0%**	**0**	**0**	**0%**	**0**	**0**	**0%**	**0**	**6**	**0%**

Distribution of waiting times for all trials

Table 16: Distribution of renouncement times at all delay stages. Control trials are discounted at the bottom table. * Unknown renouncement time due to the bird eating the initial item without the experimenter noticing. and trying to trade back an empty container after the waiting time elapsed.

renouncement time distribution for all unsuccessful trials																			
				unk*		**0 s**		**1 - 5 s**		**6 - 10 s**		**11 - 20 s**		**21 - 40 s**		**41 - 80 s**		**81 - 160 s**	
delay	**n total**	**n trade**	**n fail**	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**
5 s	600	311	289	8	3%	182	63%	99	34%	-	-	-	-	-	-	-	-	-	-
10 s	576	293	283	5	2%	232	82%	29	10%	17	6%	-	-	-	-	-	-	-	-
20 s	516	171	345	8	2%	314	91%	13	4%	4	1%	6	2%	-	-	-	-	-	-
40 s	456	66	390	3	1%	338	87%	18	5%	7	2%	8	2%	16	4%	-	-	-	-
80 s	288	17	271	0	0%	245	90%	6	2%	6	2%	4	1%	2	1%	8	3%	-	-
160 s	145	1	144	0	0%	129	90%	3	2%	1	1%	4	3%	3	2%	2	1%	2	1%
320 s	18	0	18	0	0%	15	83%	1	6%	1	6%	0	0%	0	0%	0	0%	1	6%
renouncement time distribution for unsuccessful non-control trials																			
				unk*		**0 s**		**1 - 5 s**		**6 - 10 s**		**11 - 20 s**		**21 - 40 s**		**41 - 80 s**		**81 - 160 s**	
delay	**n total**	**n trade**	**n fail**	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**
5 s	480	292	188	8	4%	108	57%	72	38%	-	-	-	-	-	-	-	-	-	-
10 s	456	290	166	5	3%	126	76%	21	13%	14	8%	-	-	-	-	-	-	-	-
20 s	396	170	226	8	4%	196	87%	12	5%	4	2%	6	3%	-	-	-	-	-	-
40 s	336	66	270	3	1%	218	81%	18	7%	7	3%	8	3%	16	6%	-	-	-	-
80 s	192	17	175	0	0%	149	85%	6	3%	6	3%	4	2%	2	1%	8	5%	-	-
160 s	96	1	95	0	0%	80	84%	3	3%	1	1%	4	4%	3	3%	2	2%	2	2%
320 s	12	0	12	0	0%	9	75%	1	8%	1	8%	0	0%	0	0%	0	0%	1	8%

Curriculum Vitae

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Education

09/2012 - dato **University of Vienna,** Austria

- Master's degree "Behaviour, Neurobiology and Cognition", enrolled
- Master's degree "Anthropology", not completed

03/2008 – 03/2012 **Leopold-Franzens-University** Innsbruck, Austria

- Master's degree "Molecular cell- and developmental biology", not completed
- Bachelor's degree "Philosophy", not completed

09/2004 – 03/2008 **Leopold-Franzens-University** Innsbruck, Austria

- Bachelor's degree „Biology", completed

09/1995 – 07/2000 **Handelsakademie** Schwaz, Austria

- „Matura", completed („Guter Erfolg")

09/1991 – 07/1995 **Gymnasium Paulinum** Schwaz, Austria

- „Unterstufe", completed

Employment

09/2012 – dato **Fachhochschule Technikum Wien**, Austria

- IT-support and Moodle development

07/2000 – 10/2004 **Sandoz Kundl**, Austria

- IT-support and network administration

Practical experience

03/2014 – dato **University of Vienna,** Austria

- Master's degree project: "„Delay of gratification in a food exchange paradigm in Kea (*Nestor notabilis*)"

03/2013 – 07/2013 **University of Vienna,** Austria

- Project: „Social transmission of tool use in Goffin cockatoos (*Cacatua goffini*)."

01/2008 **Leopold-Franzens-University** Innsbruck, Austria

- Laboratory course in biochemistry

07/2007 **Leopold-Franzens-University** Innsbruck, Austria

- Two-week marine biology excursion to Madeira, Portugal

Publications

09/2014 Auersperg, A. M. I., von Bayern, A. M. I., Weber, S., Szabadvari, A., Bugnyar, T., & Kacelnik, A.

„Social transmission of tool use and tool manufacture in Goffin cockatoos (*Cacatua goffini*)."

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