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Paying attention pays off: Kea improve in loose-string cooperation by attending to partner

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Abstract

Previous studies showed that kea are able to cooperate in experiments based on the loose-string paradigm, but success rates were low, except when tested in stable dyads. We trained kea with low success rates to attend to the handling of the string by a human partner. This vastly improved subsequent coordination during cooperation with kea partners. Furthermore, we tested the kea dyads with a delayed entry set-up (delays of 2, 4 or 6 s) and with two different lengths of string. Increasing length of delay and reducing string length had negative effects on the success rate. This suggests that a complete understanding of the actions was not present as the kea were not able to fully overcome factors that inhibit coordination. Lastly, we tested the three subjects showing the greatest ability to wait for the partner in a partner-choice paradigm: one subject in the central position could pull a loose string with one partner after another in the order it preferred. As a result, the second subjects had much longer waiting times than previously experienced. We could show that the central kea learned to visit both set-ups and that the second partner was able to wait for the partner to arrive before attempting to pull on the string, averaging twice as long as in the standard delay. Taken together, the results from this study highlight that cooperation in the loose-string paradigm is largely dependent on coordination of the subjects. While attention to the partner's actions greatly improved performance, the greater waiting times achieved in the final set-up also suggest that utilizing more ecologically relevant (subject is busy VS subject is held back) delays could further improve the performance of non-human subjects in the delayed loose-string paradigm.

KEYWORDS

cooperation, coordination, kea, loose-string, parrot

1 | INTRODUCTION

Cooperative behaviours are widespread in social animals, for example cooperative hunting (e.g. in mammalian and avian carnivores;

Bednarz, 1988; Coulson & Coulson, 2013; Smith, Swanson, Reed, & Holekamp, 2012), cooperative predator defence (e.g. mobbing in birds; Wheatcroft & Price, 2018) or cooperative breeding (e.g. in birds and mammals; Clutton-Brock, 2002). Experimental studies testing intraspecific cooperation, defined as “two or more

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individuals act simultaneously in order to obtain a communal reward" (Noë, 2006), in captive animals have shown many different species capable of cooperative action, for example chimpanzees (*Pan troglodytes*; Hirata & Fuwa, 2007), Japanese macaques (*Macaca fuscata*; Kaigaishi, Nakamichi, & Yamada, 2019), elephants (*Elephas maximus*; Plotnik, Lair, Suphachoksakun, & De Waal, 2011), ravens (*Corvus corax*; Asakawa-Haas, Schiestl, Bugnyar, & Massen, 2016) and blue-throated macaws (*Ara glaucogularis*; Tassin de Montaigu, Durdevic, Brucks, Krashennikova, & Bayern, 2019). Despite the growing number of studies (for a recent review, see Massen, Behrens, Martin, Stocker, & Brosnan, 2019), the cognitive mechanisms leading to cooperation remain unclear (Albiach-Serrano, 2015; Covas & Doutrelant, 2019; Noë, 2006), as effects of and differences in methodology often do not allow for direct comparison of results.

Social factors describing the relationship between cooperating partners, for example tolerance, have often been found to predict how well cooperative behaviours occur in a test setting. Subjects that tolerate each other while feeding on shareable food sources have often been found to later cooperate successfully in a loose-string task (Massen, Ritter, & Bugnyar, 2015; Melis, Hare, & Tomasello, 2006b). In this task, first proposed by Satoshi Hirata (Hirata & Fuwa, 2007), an out-of-reach reward on a tray can only be obtained by cooperatively pulling on both ends of a string loosely attached to the tray; pulling only one end causes the string to slip out and cooperation is no longer possible. Chimpanzees that showed high levels of tolerance outside the test setting were those most likely capable of cooperating successfully to obtain a shared food reward in a loose-string pulling task (Melis et al., 2006b). A similar effect was found when testing rooks, where more tolerant individuals also cooperatively pulled the string more (Seed, Clayton, & Emery, 2008). Although these results suggest that tolerance is a predictive factor of cooperative success, studies on ravens showed that tolerance merely allowed for the close proximity required in the previous studies' set-up for cooperation to be attempted. In an initial study with ravens, tolerance, tested in a co-feeding context, was also found to strongly predict the success of individual dyads tested (Massen et al., 2015). However, in a follow-up study where the set-up was changed to no longer necessitate direct proximity, it was shown that cooperation itself was not affected by relationship measures that predict social tolerance, such as affiliation or kinship (Asakawa-Haas et al., 2016; Massen, Sterck, & De Vos, 2010). This contrast highlights the difficulty of comparing results from different studies that vary in their methodology, as even when working within the same group of subjects, small changes in experimental design can change the conclusions about the factors that are relevant to the outcome.

Kea have shown their ability to flexibly solve many different problems (Huber & Gajdon, 2006). Kea have also been tested in cooperative problem-solving tasks (Huber, Gajdon, Federspiel, & Werdenich, 2008) including cases of forced cooperation (coercion) when tested with the seesaw paradigm. In the first study with kea using the loose-string test, birds were trained on an apparatus where they were physically separated from the partner (Schwing, Jocteur, Wein, Massen, & Noë, 2016). They received string pulling training with an experimenter acting as the perfect partner, that is holding

the string throughout but only pulling when the kea subjects pulled too, in half of the trials (16 trials), and the opposite, that is not holding the string, in the others (16 trials). The success rate during subsequent testing in avian pairs was rather limited: every individual was successful in some trials and more than half of dyads were successful at some point, but only ~18% of all trials ended in successful cooperation (Schwing et al., 2016). Interestingly, Heaney, Gray, and Taylor (2017) also tested kea with a loose-string set-up and were able to achieve much higher rates of cooperation (avg. 82.5% in the first session). They too had separated the subjects from one another, but their methodology differed in other ways that might explain the much better performance of their subjects. First, the subjects were tested in stable dyads, that is each subject only cooperated with one other subject. And second, their subjects received more training (on average 125 trials) and were required to reach a success criterion before advancing to testing. These relatively small differences could have allowed their subjects to learn to coordinate better with their partners in the test setting, as they had more experience with the task itself while only having to learn to coordinate with one other individual. The current study was therefore designed to address the effect of experience of coordinating with a partner on dyadic success.

Mutual tolerance of being in each other's close proximity could have been another key difference between the two studies. In Schwing et al. (2016) where all possible dyads were tested, affiliation, calculated from the frequency of two birds sitting in close proximity during focal scans of the group and thus a measure of social tolerance, was found to be a predictive factor of success. Despite the subjects being physically separated by a window, they were nevertheless required to sit within one body length of each other. Heaney et al. (2017) chose dyads on the basis of tolerating each other in the close proximity of the test apparatus and were thus pre-selecting for proximity tolerance. Nonetheless, as the results from ravens suggest, proximity tolerance allows animals to cooperate in certain situations but is not essential for cooperation to occur (Asakawa-Haas et al., 2016; Massen et al., 2015) as physically separated subjects showed no effect of tolerance on cooperation. As the current study design physically separated the kea subjects, further investigation of effects of tolerance was not included.

Studies with chimpanzees suggest that the accuracy of coordination is another important factor for successful cooperation. When presented with a very short rope, these primates were initially unable to solve the task (Hirata & Fuwa, 2007), as even a small discrepancy in coordination led to one subject pulling the rope out of reach for the partner. Only after increasing the length of the rope, thus relaxing the coordination constraint, and then gradually decreasing it again were the subjects able to solve the short rope version as well. The authors themselves, Hirata and Fuwa, point at the coordination of behaviours as likely representing a greater hurdle in their study compared to other studies with chimpanzees where use of a longer rope, resulting in lesser coordination constraint, could explain higher success rates (Melis et al., 2006b).

Here we introduced a new training methodology designed to increase the attention paid to the partner's actions, thus possibly allowing the kea to coordinate more accurately. The human experimenter

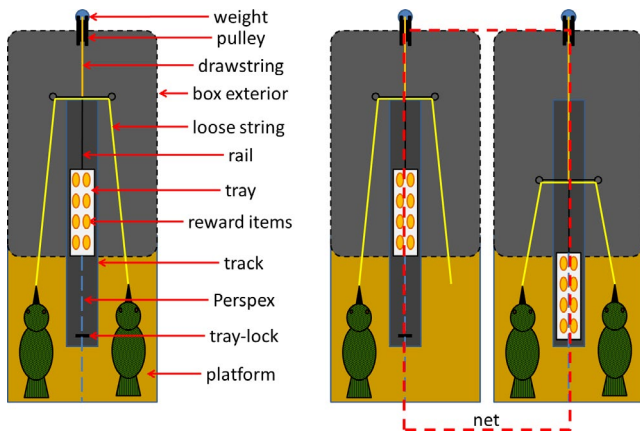


FIGURE 1 Diagram of apparatus set-up used for dyadic and standard delay (left) and triadic (right) testing (not to scale)

again acted as the partner, but cooperated in a way that would lead to success only if the kea subjects paid attention to the other string end. The effect of this was tested using all possible dyads from 6 subjects on the same apparatus as used in Schwing et al. (2016). To assess if this allowed the kea to understand a need for the partner, rather than just coordinating based on simultaneous access, we followed up with the standard delay paradigm, where one partner gains access to one end of the string before the other does. The delay paradigm, which can show a subject's ability to understand the need to wait for the partner, is dependent on the subject's ability to inhibit pulling the string prematurely. While the kea had not been tested using this paradigm before, they had shown their ability to inhibit immediate gratification in a delayed food-exchange paradigm (Schwing, Weber, & Bugnyar, 2017). Both the first round and the delay tests were done with both a long string, same as in the previous study, but also with a short string as in Hirata and Fuwa (2007) to look for effects of coordination on success. Lastly, we wanted to introduce a more natural delay for the partner by giving one bird positioned in the middle, the "initiator," the possibility to cooperate with two partners on separate apparatuses at either side. If the initiator chose to visit both apparatuses, the 2nd partner was faced with a delay based on the actions of the other birds rather than a pre-set waiting period. A very similar set-up (from a subject/partner perspective, yet different in other aspects of the methodology, e.g. the level of experience of the subjects or the number of partners) had already been utilized in a raven study (Asakawa-Haas et al., 2016) showing that all but one subject were capable of waiting as the 2nd partner, and more than half cooperated in that situation with the initiator.

We hypothesized that the new training would affect the kea's ability to coordinate their actions with a conspecific partner in solving a loose-string task. We predicted an improvement in the kea's performance in the standard loose-string tests compared to the first study (Schwing et al., 2016). We furthermore hypothesized that the kea would show signs of understanding the need for a partner to interact with their rope end in the delay set-up; notably, we predicted that they would be able to inhibit pulling while waiting for a delayed access of the partner to the rope. We further hypothesized that the length of the string would affect the

success rate and predicted that the short string length would have a negative effect on their success rate by placing a higher coordination constraint on the subjects. Finally, we hypothesized that changing the type of delay would have an effect on the subject's ability to wait for a partner and predicted that the animals would show a better performance in the tests in which their partner was delayed "naturally" by interacting with another group member than in the standard delay tests in which the partner was admitted to the test compartment after a fixed delay.

2 | MATERIALS AND METHODS

2.1 | Subjects and aviary

Six captive kea participated in this study: Kermit (Ke, adult male), Sunny (Sy, adult female), Willy (Wy, adult female), Roku (Ro, adult male), Paul (Pa, subadult male) and Pick (Pi, adult male). Subjects were members of a twenty-two kea group housed at the Haidlhof Research Station near Bad Vöslau in Austria, in a large outdoor aviary (52 × 10 × 4 m). All of the subjects were familiar with cooperation experiments having participated in an earlier study using the loose-string apparatus (Schwing et al., 2016). The number of subjects was chosen on the basis of being able to test all subjects in a single day. Previous experience has suggested that too long a delay between testing days can have a negative effect on learning a complex task in kea. As other studies have used similar number of subjects (e.g. Heaney et al., 2017), we chose the number of subjects to allow for increased testing frequency.

The experiments were conducted in a testing compartment (6 × 10 × 4 m), which was visually isolated from the rest of the aviary by sliding opaque walls. Outside of testing, all birds had access to this compartment and were thus 100% habituated to the environment. The kea were fed three times a day with seeds, fruits, vegetables, eggs, meat or cream cheese depending on the season and the specific individual diets. Water was provided ad libitum, also during the test.

2.2 | Apparatus

The two identical apparatuses used were the same as in Schwing et al., (2016). Both apparatuses consisted of a wooden box (80 × 150 × 100 cm), containing a metal plate with a sliding tray on which the rewards were placed (Figure 1), one pellet for the individual training and eight pellets attached with cream cheese for the dyadic, delay and triadic tasks. A transparent Plexiglas® window between the birds allowed them to see each other but limited physical contact between them. The ends of the string were placed on the platforms. If a bird pulled alone, the string would slip out without moving the tray. If the birds pulled together, the tray would slide out and lock at the end point, so the partners could release the string and retrieve the reward. A weight (200 g) attached to the tray via a separate string within the box made it slide back if was not locked

in position. This weighted tray represents a difference between this apparatus and other, more standard, loose-string set-ups, including Heaney et al., 2017. The main effect of the weight is that if the subjects have pulled the tray part-way, and then only one lets go, the tray sliding back causes the string end no longer held to slide out of reach more quickly than by the pulling of the other subject alone. This does not represent a categorical difference in the nature of the task, as only in situations where one subject lets go of the string/rope and the other immediately stops pulling, allowing the first subject to pick up their end before it is pulled out of reach, would it result in a different outcome than with our apparatus. Nonetheless, it likely did, in some cases at least, increase the difficulty of succeeding in the task for the kea in Schwing et al., 2016 compared to other subjects tested. However, as the study was mainly concerned with the effect of the training to increase the attention towards the partner's actions, it was decided to keep the same apparatus, for the sake of a more direct comparison.

Transparent Plexiglas plates covered the string ends at the beginning of each trial, preventing immediate access to the string. Two different lengths of string were used in the dyadic and delay tasks: a long string (19.5 cm of the rope accessible on the platform) and a short string (5 cm of the rope accessible on the platform). For the triadic task, we created a new compartment between the two apparatus (distance between apparatuses ~2 m) using a net (Figure 1), so that all three subjects were still physically separated. The bird in the middle could choose freely whether or not to interact with either apparatus/partner and in which order.

2.3 | Procedure

2.3.1 | Individual training

Habituation to the boxes and the loose-string system was not necessary as all birds had experience with it from the previous study (Schwing et al., 2016). All subjects ($N = 6$) did participate in a novel individual training with a human partner designed to increase their attention to the partner's actions with the string. The general procedure was as follows:

- a trial started as soon as the transparent Plexiglas plate was raised by the experimenter in front of the subject, giving access to the string end
- the experimenter waited for a set amount of time (0, 2, 4 or 6 s) before picking up the string
- the experimenter held the string for 2 s before putting down the string down, or, if the bird pulled the string within these 2 s, held the string until the tray locked and the trial was successful.

While the 0-s delay acted as a motivational trial, as it most closely resembled the original training the birds had received in the previous study, the other times were chosen to draw the kea's attention to the human partner's interaction with the string. Note that, as the times

differed by 2 s, while the string was then only held for 2 s, this prevented any alternative strategy (e.g. waiting for any particular amount of time) for the subject other than to wait until the human partner was holding the string and then to pull their own end quickly; without an overlap for the different waiting times, the kea could only succeed if they watched the actions of the human partner and only pulled when the partner interacted with the string. Each situation was done thrice in one session, and the order of the twelve trials was randomized within a session.

A trial ended in one of three ways: (a) the subject started pulling their string end within the 2 s the human partner was holding the string, locking the tray and reaching the reward (all situations); (b) the subject did not pull the string within the 2 s (all situations); and (c) the subject pulled the string before the human partner picked up the string (not possible at 0-s delay). All birds received 10 training sessions with 12 trials each. Criteria to advance to testing were set at retrieving the reward in 10 out of 12 trials within a session, which was achieved in 3 (Ke), 4 (Sy), 8 (Wy) and 10 sessions (Pa, Ro, Pi).

2.3.2 | Dyadic tests

All six subjects reached the advancement criterion and took part in the dyadic test sessions. Unfortunately, it was not possible to test one dyad as territorial behaviour in the breeding season meant that two subjects (Sy and Pa) were incompatible in close proximity even when physically separated. The remaining 14 dyads were tested in 4 session each, using a 2×2 design to balance position of each bird on the apparatus (left/right) with the two string lengths (short/long), resulting in 56 sessions, each consisting of ten trials; within a session position and string length were consistent. A trial was ended (a) after 5 min of neither bird interacting with their string, or (b) after 30 s if a subject pulled out the string or both subjects pulled and the tray locked in place; the theoretical situation where one or both birds interacted with the string but did not pull was not observed. The experimenter was present during trials but stood at approximately 2 m distance behind the apparatus.

2.3.3 | Delay tests

The same six birds took part in the delay test sessions. The procedure was the same as the dyadic tests except the opening of one Plexiglas[®] plate was delayed for one of the subjects.

Each test session for each dyad consisted of eight trials with four different time delays:

- Time delay 0 (motivation trial): the two birds were on the apparatus and the experimenter opened the two Plexiglas[®] plates simultaneously.
- Time delay 2 s: the two birds were on the apparatus and the experimenter opened the Plexiglas[®] plate on the side of the bird A

(subject), then waited 2 s before opening the Plexiglas[®] plate on the side of bird B (partner).

- Time delays 4 and 6 s: the same situations as situation 2 but the experimenter opened the second Plexiglas[®] plate 4 and 6 s after the first Plexiglas[®] plate.

Each situation was done twice in one session to counterbalance the role of the birds (partner and subject), while each dyad was again tested in the same 2×2 design as before to counterbalance relative position and string length, resulting in 56 sessions at 8 trials each.

2.3.4 | Triadic tests

Four individuals took part in the triadic test. We chose the four best performing birds of the delay task, Ke, Wy, Sy and Ro. During this task, three birds could work together in two dyads: one initiator (the bird inside the net who can cooperate with the two other birds) and two remaining birds (partner 1 [P1] and partner 2 [P2]) were situated on the left side and on the right side of the initiator.

At the beginning, we worked with four trios: Sy, Wy & Ke; Wy, Ke & Ro; Sy, Ke & Ro; and Sy, Wy & Ro. However, although all four subjects had passed the habituation criteria, when tested as initiator, in the first session one subject (Ro) already showed signs of being too distracted by the set-up to cooperate with the partners. Therefore, we excluded him from further testing and the analysis.

In total, we carried out 66 sessions with the three remaining subjects, switching the role of each bird (22 as initiator and 44 as partner) and to counterbalance the position (right/left) of the two partners (11 sessions each).

2.3.5 | Behavioural and background data

For the individual training, we coded whether the birds successfully cooperated with the human partner (tray locked). For the dyadic and the delay tests, we recorded the number of successful cooperations (tray locked) and cooperation attempts (both birds held the string at the same time but did not lock the tray properly).

For the triadic test, we recorded the number of successful cooperations (tray locked) with P1 and P2. We also recorded the behaviour of the initiator (middle subject) with regard to P2 (went to P2 after P1 or did not go) as well as when possible (the video was frequently obscured by the position of the subject) the behaviour of P2 with regard to the partner (no behaviour towards partner, pulled early but stopped, pulled early but stopped and looked to partner's side, first looked to partner's side) and with regard to the timing of the pulling (before partner arrived, when Plexiglas cover was released, when partner also pulled).

In addition to these experiments, we gathered observational data using continuous focal animal sampling (Altmann, 1974) to assess affiliative and dominance relationship, as these parameters may predict cooperative success (Massen et al., 2015; Schwing et al., 2016). Focal

protocols were performed on a weekly basis by all kea researchers and students. We followed each bird for 2-min continuous sampling including three instantaneous scans at 1-min intervals. The data used for this study covered the time from April 2015 to April 2016. From these protocols, we used two parameters: the nearest neighbour value to calculate an affiliative score and the number and direction of displacements in order to calculate the rank of the birds.

Each displacement of one bird by another provided two data points, one for each bird. We calculated the Clutton-Brock Index (CBI; Clutton-Brock, Albon, Gibson, & Guinness, 1979) from these, since this has previously been used in the determination of the hierarchy in wild kea (Gajdon, Fijn, & Huber, 2006). For an individual i , we used this formula:

$$CBI_i = (B + b + 1) / (A + a + 1)$$

where B is the number of individuals dominated by i ; b is the number of individuals dominated by the ones subordinate to i ; A is the number of individuals dominating i ; and a is the number of individuals displacing birds dominant to i .

The identities of nearest neighbours, defined as any individuals within one metre of the focal bird during protocol scans, were extracted from the focal samples for all subjects. The absolute number of protocols during which two individuals were recorded as nearest neighbours was used as the affiliative score in the analysis.

The original study used a divisible reward, which was used here as well to focus on the effect of the training, despite no significant effects of reward division on success having been observed in the first study (Schwing et al., 2016); a trend for an effect of reward division on next trial attempt at cooperation was found; however, it was not significant and there was no effect for next trial success. The number of reward pieces taken by each bird was coded for each trial (where visible from the camera's perspective).

2.4 | Data collection and analysis

We ran GLMMs for the dyadic and delay tests to determine factors influencing overall success (binary target). Social measures of the dyad (gender combination, rank distance, affiliation, kinship) and the string length were entered as fixed factors in both dyadic and delay test modelling; in addition to these, in the delay models, the delay in s was added as a fixed factor, both stand-alone and as an interaction effect with string length, as well as the identity of the partner that had delayed access. Session number within each dyad and dyad ID was entered as random factors to account for repeated measures. Post hoc pairwise comparisons of categorical factors were also performed with sequential Bonferroni corrections. Final selection of fixed factor inclusion was based on best model fit rather than factor significance; we used accuracy score for binomial and corrected Akaike information criteria for linear model factor selection. Using the same social fixed factors, random factors and method of model selection, we also ran a GLMM to look for possible effects of reward

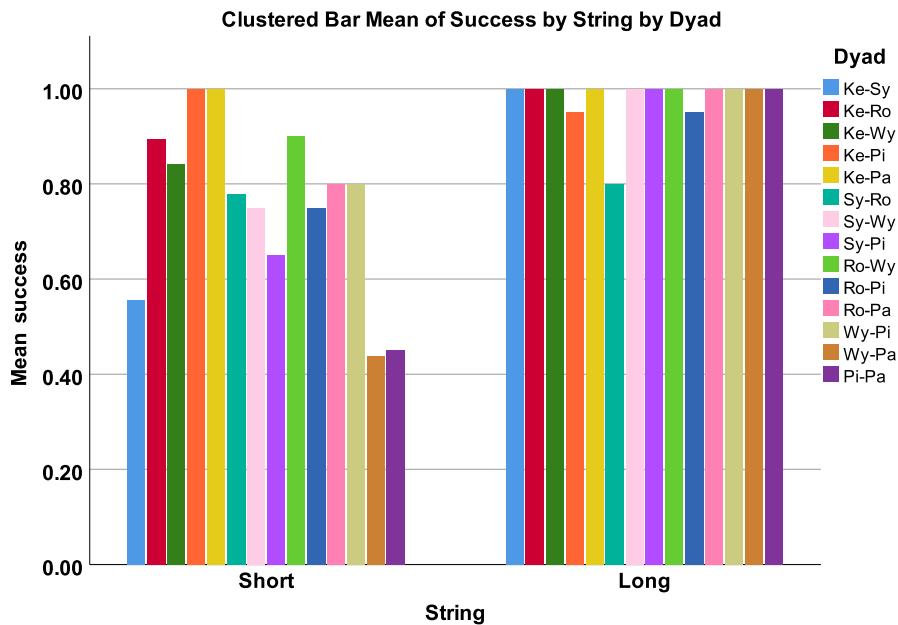


FIGURE 2 Mean success of dyads with the short (left) and long (right) string. In a previous study (Schwing et al., 2016), only ~18% of trials were successful with a long string

division (fixed factor) on the success of the following trial (target variable) in the dyadic set-up (similar to Schwing et al., 2016).

Analysis of the behaviours shown during the triadic test to look at the actions of the initiator and the second partner over time was done using chi-square test overall and Dunn's test. All reported p -values are two-tailed, and the significance threshold was fixed to $\alpha \leq .05$.

2.5 | Ethical statement

The experiment was approved by the University of Veterinary Medicine Vienna's institutional ethics committee in accordance with Good Scientific Practice guidelines and national legislations. All subjects that participated in our experiments were housed in accordance with the Austrian Federal Act on the Protection of Animals (Animal Protection Act-TSchG, BGBl. Nr.118/2004). Furthermore, as the present study was strictly non-invasive and based on behavioural observations, none of the experiments were classified as animal experiments under the Austrian Animal Experiments Act (92, Federal Law Gazette No. 501/1989) and consequently did not require further permission.

3 | RESULTS

3.1 | Training

3.1.1 | Dyadic test

Overall model fit with success as the target variable was best (88.2% accuracy, $F_{1-106} = 32.491$, $p < .001$) with a single fixed factor: string length had a significant effect on the overall success ($\beta = 3.938$, $F_{1-106} = 32.491$, $p < .001$). Pairwise comparison showed that the subjects had significantly more success ($F_{1-17} = 21.386$, $p < .001$) with the long string ($\bar{x} = 98.1\%$, $SE = 0.9\%$) than the short ($\bar{x} = 77.7\%$, $SE = 4.6\%$). The

GLMM with the best fit for success in the following trial as the target variable was the intercept only model.

3.1.2 | Delay test

Overall model fit with success as the target variable was best (86.3% accuracy, $F_{12-875} = 18.583$, $p < .001$) with five fixed factors. String length had a significant effect on the overall success ($F_{1-875} = 164.299$, $p < .001$). Pairwise comparison showed that the dyads had significantly more success ($F_{1-875} = 420.772$, $p < .001$) with the long string ($\bar{x} = 87.1\%$, $SE = 4.2\%$) than the short ($\bar{x} = 15.3\%$, $SE = 5.0\%$) (Figure 2). Partner ID had a significant effect on the overall success ($F_{5-875} = 5.087$, $p < .001$). Pairwise comparison showed that subjects waiting to cooperate with Ke ($\bar{x} = 75.4\%$, $SE = 10.0\%$) had significantly more success ($F_{5-875} = 6.236$, Ke-Pa: $p = .001$, Ke-Pi: $p < .001$) than when waiting for Paul ($\bar{x} = 40.6\%$, $SE = 13.3\%$) or Pi ($\bar{x} = 37.6\%$, $SE = 12.5\%$). Delay had a significant effect on the overall success ($F_{3-870} = 41.074$, $p < .001$; Table 1). Pairwise comparison of success across delay times (Figure 3) showed that compared to no delay ($\bar{x} = 97.9\%$, $SE = 1.0\%$), 2-s ($\bar{x} = 41.3\%$, $SE = 9.3\%$), 4-s ($\bar{x} = 24.4\%$, $SE = 7.2\%$) and 6-s ($\bar{x} = 12.6\%$, $SE = 4.4\%$) delays were all significantly less successful ($F_{3-875} = 195.126$, 0-2: $p < .001$, 0-4: $p < .001$, 0-6: $p < .001$). Furthermore, compared to 2-s delay, both 4-s and 6-s delays were significantly less successful (2-4: $p = .011$, 2-6: $p < .001$), and 6-s delay was also significantly less successful than 4-s delay (4-6: $p = .013$). While adding to the model fit sex combination and the interaction of affiliation, rank difference and age difference were not significant overall.

3.1.3 | Triadic test

In the triadic set-up, all three subjects showed a development over time as the initiator and/or when acting as the second partner. Ke

TABLE 1 Success/fail of subjects waiting in the delay task with different string lengths

Delay	Kermit			Sunny			Roku			Willy			Pick			Paul							
	0	2	4	6	8	10	12	14	16	18	20	2	4	6	0	2	4	6					
Short	2	18	18	18	0	14	16	16	2	18	19	20	4	18	20	19	3	20	20	20	5	14	15
Success	17	2	2	2	15	2	0	0	18	2	1	0	16	2	0	1	16	0	0	0	10	2	1
Long	0	4	4	7	0	3	5	8	0	5	6	14	1	4	8	10	1	5	12	14	0	5	7
Success	20	15	16	13	16	13	11	8	20	14	13	6	19	16	12	10	19	15	8	6	16	11	8

showed little change as the initiator, visiting both partners in most trials from the first session onwards, while both Sy and Wy initially did not visit the second partner, but did so significantly more from the second session onwards and did so in all trials in the 8th (Sy) and 11th (Wy) sessions (Figure 4, Table 2). All three subjects learned to wait to cooperate, in the role of the second partner, already waiting in every trial in the 4th (Wy), 5th (Ke) and 9th (Sy) sessions (Figure 5, Table 3). Waiting times for the second partner were on average 12.1 s ($SD = 6.7$ s, Min = 4.0 s, Max = 67.0 s) in trials with a successful second cooperation, and on average 13.0 s ($SD = 4.9$ s, Min = 5.0 s, Max = 32 s) in trials without a successful second cooperation. As the second partner in successful trials, Ke waited on average 16.7 s ($SD = 12.4$ s, Min = 7.0 s, Max = 67.0 s), Sy waited on average 10.9 s ($SD = 3.9$ s, Min = 6.0 s, Max = 25.0 s) and Wy waited on average 11.3 s ($SD = 3.4$ s, Min = 4.0 s, Max = 24.0 s).

4 | DISCUSSION

In general, the kea were able to greatly improve their success rate after introducing the new training methodology featuring delayed responses by the experimenter acting as a partner, when compared to the first study by Schwing et al. (2016). When using the long rope, as was used in this previous study, all birds and all dyads were shown to be successful, and the overall success rate over all trials was close to 100%. The kea waited consistently for their partner in the standard delay trials with a long string. However, when using the short string, no kea succeeded more than twice in any delay, and only three subjects succeeded at the 6-s delay with the short string at all (Table 2). In the triadic set-up, the kea showed their ability not only to learn to visit both apparatuses, but also to wait on average twice as long as in the standard delay paradigm.

The effect of the training on the kea's performance highlights the difference with spontaneous success in a cooperative task and also the potential effect when the subjects' attention was guided through training to be attentive to the actions of the partner. This increased attention may hint towards a possible understanding of, at least to some degree, the need to wait for the partner to interact with their string end; to what degree the kea understood how the actions of the partner affected the outcome cannot be concluded here. Other studies have also utilized training methodologies, which likely resulted in a similar learning effect with regard to coordinating with the actions of the partner. In many primate studies (e.g. Hare, Melis, Woods, Hastings, & Wrangham, 2007; Melis, Hare, & Tomasello, 2006a; Melis et al., 2006b), but also the Heaney et al. (2017) study with kea, the subjects were likely able to learn about the need for a partner in training by first being presented with a set-up where they could solve the task on their own by pulling the two ends of the rope simultaneously. Success in the subsequent test situation, where the subjects only had access to one end of the rope each, was probably facilitated by some basic understanding of the effect of pulling both ends of the rope simultaneously. In contrast, the first kea study (Schwing et al., 2016) involved training trials where the experimenter

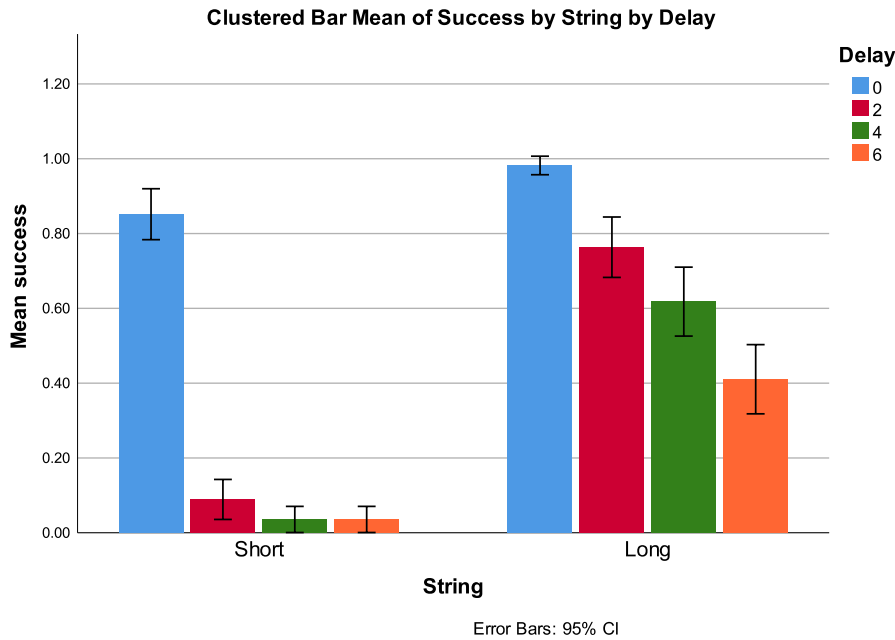


FIGURE 3 Mean success rate in the delay tasks (0, 2, 4 and 6 s) with the short (left) and the long (right) string

did not hold the other end of the rope, thus making success impossible. The lack of inhibition of pulling the rope in these trials indicates that the kea had not learned the decisive difference between the contrasting actions of the human partner (holding or not holding the other rope end) during training before being tested with other kea as partners. Other cooperation studies in which animal subjects had no such learning opportunities often showed low success rates. In the Hirata and Fuwa study (Hirata & Fuwa, 2007), the chimps were not able to succeed with a short rope until they had had numerous successes with long ropes, that were then gradually shortened.

The result of the delay paradigm further suggests that the kea had learned to attend to the partner's actions and thus the need for the partner to pull the other end of the rope. An alternative explanation, a greater experience with waiting compared to the previous study, is less likely because, while the delay set-up does require the subjects to wait, the crucial aspect is to coordinate with the partner. As long as the kea still needed to react to the partner pulling, they still needed to attend to the partner's actions. The training the kea had received, while utilizing waiting times, could not be solved by any specific amount of waiting but only if the waiting was until the human partner held the string. Thus, the waiting is incidental while the attention to the partner's actions is crucial (see ESM for more details on differences in training here vs. other delay studies). While one bird, Kermit, showed close to perfect inhibition with the long string, the other subjects showed a decline in inhibition with increasing delay length. As we were interested in seeing how well the kea would transfer their understanding for a need for a partner from a pure coordination to a situation where they needed to inhibit the previously learned behaviour, we did not give them shaping training to specifically teach them this aspect of the task with a conspecific partner. In other studies, with shaping training, the subjects had to reach a criterion before moving to the next longer waiting time (e.g. Heaney et al., 2017; Plotnik et al., 2011). As neither study reports

detailed training results, it is not possible here to compare our kea's success directly. However, Kermit having had success in most delay trials was likely comparable to Plotnik et al.'s (2011) elephants (low number of trials needed to reach criterion) and the Heaney et al. (2017) kea (low error rate in training). Both elephants and kea, having been trained to wait for up to 25 s, showed higher success rates when presented with either random delay times they had previously experienced sequentially, and novel delay times up to 45 and 65 s, respectively. While the delay time in the triadic set-up was variable, as it completely depended on the activity of the initiator in the

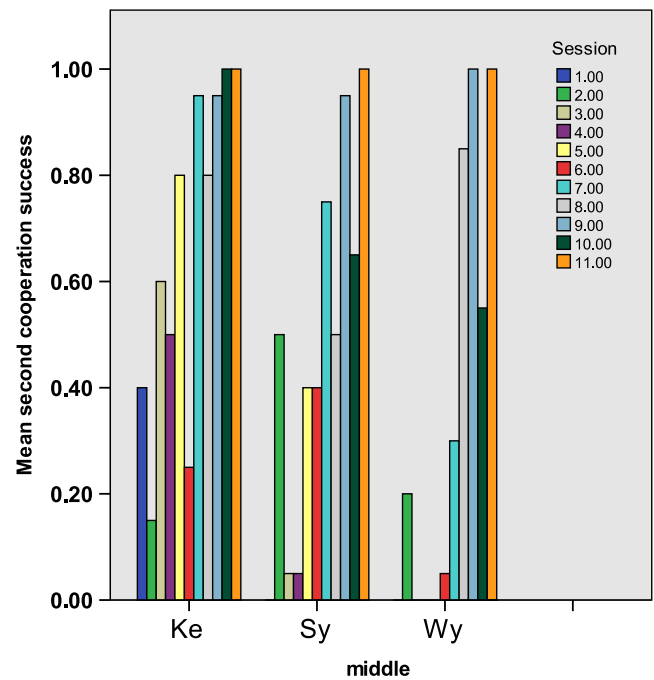
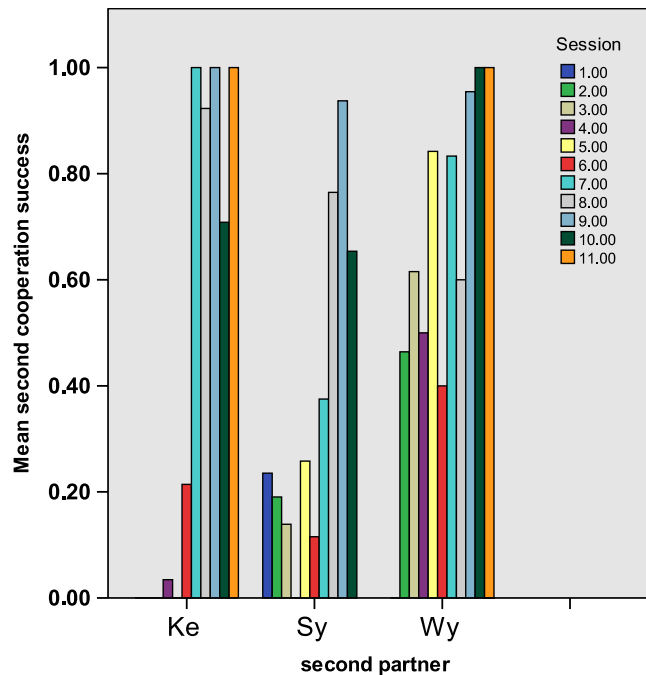


FIGURE 4 Mean success in the second cooperation by initiator subject (middle bird)

TABLE 2 Behaviour of the initiator across sessions with regard to the 2nd cooperation

Initiator	Behaviour (count)	Session											Total	
		1,00	2,00	3,00	4,00	5,00	6,00	7,00	8,00	9,00	10,00	11,00		
Ke	Goes	20 _a	13 _{a,b}	20 _a	11 _b	20 _a	20 _a	20 _a	20 _a	20 _a	20 _a	20 _a	20 _a	204
	Does not go	0 _a	7 _{a,b}	0 _a	9 _b	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	16
	Total	20	20	20	20	20	20	20	20	20	20	20	20	220
Sy	Goes	1 _a	11 _{b,c}	10 _{a,b,c}	4 _{a,c}	10 _{a,b,c}	18 _{b,d}	20 _d	20 _d	19 _{b,d}	13 _{b,c,d}	20 _d	146	
	Does not go	19 _a	9 _{b,c}	10 _{a,b,c}	16 _{a,c}	10 _{a,b,c}	2 _{b,d}	0 _d	0 _d	1 _{b,d}	7 _{b,c,d}	0 _d	74	
	Total	20	20	20	20	20	20	20	20	20	20	20	220	
Wy	Goes	0 _a	10 _{b,c,d}	0 _a	0 _a	0 _a	3 _{a,d}	6 _{a,c,d}	18 _{b,e}	18 _{b,e}	14 _{b,c,e}	20 _e	89	
	Does not go	20 _a	10 _{b,c,d}	20 _a	20 _a	20 _a	17 _{a,d}	14 _{a,c,d}	2 _{b,e}	2 _{b,e}	6 _{b,c,e}	0 _e	131	
	Total	20	20	20	20	20	20	20	20	20	20	20	220	
Total	Goes	21 _{a,b}	34 _{b,c}	30 _{a,b,c}	15 _a	30 _{a,b,c}	41 _c	46 _{c,d}	58 _{d,e}	57 _{d,e}	47 _{c,d}	60 _e	439	
	Does not go	39 _{a,b}	26 _{b,c}	30 _{a,b,c}	45 _a	30 _{a,b,c}	19 _c	14 _{c,d}	2 _{d,e}	3 _{d,e}	13 _{c,d}	0 _e	221	
	Total	60	60	60	60	60	60	60	60	60	60	60	660	

Note: Each subscript letter denotes a subset (within each individual's or the total performance) of session categories whose column proportions do not differ significantly from each other at the 0.05 level.

**FIGURE 5** Mean success in the second cooperation by the 2nd cooperation partner

middle and the first partner chosen, waiting times experienced were on average 2 times longer than those in the standard delay set-up, and at times exceeded 60 s, matching the longest waiting times for Heaney et al.'s (2017) kea and Plotnik et al.'s (2011) elephants.

The kea showed stark individual differences in their ability to coordinate with their partner. When taking the effects of the string length and the delays together, four birds showed greater success than the other two. This indication of individual ability was further shown in the triadic set-up, as one subject (Kermit) was the first to visit both partners, while another (Willy) was the first to wait for

the second partner (see ESM for more details). The results from the triadic set-up also suggest that the partner being delayed by being occupied rather than having restricted access to the string could be easier to adjust to for the subjects, as the waiting times were much greater for the 2nd partner in the triadic set-up than in the standard delay set-up. The low number of subjects does not allow for far reaching conclusions on this point, but it would be interesting for future research to look more closely at the different strategies required to solve a task on the basis of ecological relevance of the delay. Our results possibly suggest that for cooperation, different personalities could benefit from one another in reaching the common goal. This would likely, however, depend to a large degree on the constraints and presentation of the task. Two studies on ravens (Asakawa-Haas et al., 2016; Massen et al., 2015) show a similar effect based on differences in set-up presentation when compared with one another. In the first study (Massen et al., 2015), utilizing a dyadic set-up, the subject waited for a delayed partner in less than 2% of trials. The second study (Asakawa-Haas et al., 2016), utilizing a triadic set-up, showed an increased ability to wait, with the second partner doing so in almost 10% of trials. Although the ravens were not shown to wait as consistently as the kea, the ravens' ability to wait increased within the study (~4% in exp. 1 and ~14% in exp. 2) and was shown to be significantly affected by experience. This suggests that the higher number of trials combined with the lower number of possible partners could explain the kea's higher waiting ability. A more comparable methodology in terms of experience of the subjects, both with the set-up and the individual partners, would be needed to uncover any true species-level differences in this ability.

A striking result is the lack of significant interactions of any of the social measures (i.e. rank distance, affiliation, kinship). The small number of subjects might have not been enough to produce effects strong enough to affect the outcome when the effects of non-social factors were so strong. Nonetheless, compared to Schwing et al. (2016),

TABLE 3 Behaviour of the 2nd partner across sessions before arrival of initiator

2nd partner	Behaviour (count)	Session											Total
		1,00	2,00	3,00	4,00	5,00	6,00	7,00	8,00	9,00	10,00	11,00	
Ke	Waits	6 _{a,b}	0 _b	0 _b	1 _b	10 _{c,d}	6 _{a,b,d}	6 _{a,c,d}	13 _{c,d}	22 _c	24 _c	30 _c	118
	Pulls early	14 _{a,b}	11 _b	11 _b	26 _b	0 _{c,d}	8 _{a,b,d}	0 _{a,c,d}	0 _{c,d}	0 _c	0 _c	0 _c	70
	Leaves	2 _a	0 _a	0 _a	2 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	4
	Total	22	11	11	29	10	14	6	13	22	24	30	192
Sy	Waits	10 _{a,b}	4 _{a,b}	6 _b	1 _{a,b}	18 _{a,c,d}	11 _{a,b,d}	14 _{a,c,d}	14 _{c,d}	16 _c	22 _{c,d}		116
	Waits > leaves	1 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	1
	Pulls early	19 _{a-c}	12 _{a-c}	30 _c	10 _{b,c}	13 _{a,b,d}	15 _{a-c}	10 _{a,b,d}	3 _{a,d}	0 _d	4 _{a,d}		116
	Leaves	4 _a	5 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	9
	Total	34	21	36	11	31	26	24	17	16	26		242
Wy	Waits	1 _a	17 _{a-c}	8 _{a-e}	20 _{c,e,f}	17 _{a-f}	10 _a	28 _{b-f}	27 _{a-f}	22 _{d,e,f}	10 _{a-f}	30 _f	190
	Waits > leaves	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	1 _a	0 _a	0 _a	0 _a	0 _a	1
	Leaves	3 _a	11 _{a,b}	5 _{a-d}	0 _{b,d,e}	2 _{a-e}	10 _a	1 _{c-e}	3 _{a-e}	0 _{c-e}	0 _{a-e}	0 _e	35
	Total	4	28	13	20	19	20	30	30	22	10	30	226
Total	Waits	17 _a	21 _a	14 _a	22 _a	45 _b	27 _a	48 _b	54 _{b,c}	60 _c	56 _{b,c}	60 _c	424
	Waits > leaves	1 _a	0 _a	0 _a	0 _a	0 _a	0 _a	1 _a	0 _a	0 _a	0 _a	0 _a	2
	Pulls early	36 _a	34 _a	46 _a	36 _a	15 _b	33 _a	11 _b	6 _{b,c}	0 _c	4 _{b,c}	0 _c	221
	Leaves	6 _a	5 _a	0 _a	2 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	0 _a	13
	total	60	60	60	60	60	60	60	60	60	60	60	660

Note: Each subscript letter denotes a subset (within each individual's or the total performance) of session categories whose column proportions do not differ significantly from each other at the 0.05 level.

where affiliation had been found to be correlated with success, after learning to attend to the partner in this study, the kea would have not required a social facilitation of proximity to coordinate anymore. This is similar in effect to the ravens, where in the initial study, strong effects of social factors on successful cooperation were found (Massen et al., 2015). However, when the constraints of proximity were removed, such social factors were also no longer found to play a role (Asakawa-Haas et al., 2016). In a chimpanzee study, spontaneous cooperation was found to rely on tolerance (Melis et al., 2006b). However, in a follow-up study where the same subjects were used (Melis et al., 2006a), all subjects received several rounds of additional training, including a shaping training using a standard delay paradigm. When subsequently tested on their ability to actively recruit a partner, by releasing them from an adjacent room, they chose to do so based on their previous success in cooperating with a specific individual. As this included many instances of changing their choice of partner, the acutely stable social factors could not have played a role.

In contrast, the lack of an effect of reward division on next trial success was largely expected. The original study had found no effect of reward division on success (and only a trend regarding an effect on cooperation attempts), and a recent study on inequity aversion in kea (Heaney, Gray, & Taylor, 2019) did not find evidence of such. As the authors of that study point out the sample size tested so far might obscure an underlying sensitivity to inequity. However, they also point out that given the lack of known cases of cooperation in wild kea, that not finding such an effect would follow the theory

that inequity aversion evolved together with cooperation (Brosnan, 2011), and a species lacking cooperation in the wild would also likely not be sensitive to unequal reward division.

In conclusion, the kea have shown that they have the ability to attend to, and at least to some degree understand, the need for the partner to interact with the other end of string and thus wait for them. The effect of the string length highlights that coordination is likely the main limitation even after the importance of attending to the partner's actions has been learned. However, the more ecologically relevant delay implemented in the triadic set-up also suggests that adjusting the constraints of a set-up to better reflect a natural setting might allow animals to show even greater cooperative abilities than have already been shown.

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CONFLICT OF INTEREST

There is no conflict of interest to declare with regard to the authors and this publication.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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