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Blue-throated macaws (*Ara glaucogularis*) succeed in a cooperative task without coordinating their actions

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Abstract

Social complexity may select for socio-cognitive abilities. The “loose string” task has become a comparative benchmark paradigm for investigating cooperative problem-solving abilities in many species, thus enhancing our understanding of their evolution. It requires two individuals working together to solve a problem, specifically by pulling the two ends of a string simultaneously to move a reward towards them. A dyad's performance therefore depends on the individuals' ability to coordinate their pulling action. Many species, including corvids and parrots, have been tested in this paradigm, but most appear insensitive to the exact cooperative nature of the task. We tested another parrot species, blue-throated macaws, to further our understanding of social cognition in psittacids. Five birds were tested with different partners in a dyadic setting. The study included two control conditions examining the cognitive mechanism underlying their seemingly cooperative behaviour. All birds were able to simultaneously pull the strings, but their performance did not drop when they were denied mutual visual access, and they failed to obtain food when they needed to wait for their partner. Moreover, the parrots decreased their latency to pull with increasing experience. These findings suggest that the birds may have applied an associatively learnt rule, or relied on acoustic cues, rather than coordinating their actions with the partner. This may not necessarily prove a lack of understanding the partner's role, given that their failure to wait in the delay control test might be explained by their poor inhibitory control abilities. Relationship quality (i.e. affiliation and food tolerance) did not influence dyadic success. Future studies are needed in order to disentangle macaws' potentially limited cooperative abilities from their lack of inhibitory control.

KEYWORDS

affiliation, avian cognition, blue-throated macaws, cooperative problem-solving, parrots, psittacids

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1 | INTRODUCTION

Cooperative behaviour is defined as an “act performed by one individual that increases the fitness of another” (Bergmüller, Johnstone, Russell, & Bshary, 2007). Cooperation often presumes joint actions of two or more individuals that lead to a net gain for all participants. Because of this joint nature, coordination can also be beneficial to allow cooperation to occur. For example, during cooperative hunting individuals take complementary roles and adjust to the others’ behaviour when hunting for the same prey. If two or more predators target the same prey and coordinate their actions (instead of acting simultaneously but independent), they may increase the chances of succeeding (e.g., cooperative hunting for lizards in brown-necked ravens (Yosef & Yosef, 2009)). But for them to benefit on average across such instances, an adaptive mechanism that facilitates coordination needs to exist.

Researchers have focused on identifying the underlying mechanisms or proximate causes of cooperation using artificial experimental settings. In such controlled experimental settings, cooperative behaviour is often examined with apparatuses that afford food rewards when engaged jointly but not when engaged solitarily. In the benchmark test of cooperative behaviour, the loose-string paradigm (Hirata & Fuwa, 2007), an out-of-reach platform that holds food items is connected to the animals’ area with two ends of a string. The string is looped around the platform so that each animal has access to one end of the string, which, when pulled jointly brings it within reach; however, if one end of the string is pulled solitarily, it makes the other end inaccessible. While success in this basic task alone can be achieved by unintentional coordination, further control conditions can disambiguate between intentional or uncoordinated engagement. For instance, *delay or solitary controls* can reveal if the animals are sensitive to the presence of a cooperative partner. In those tasks, a focal animal is released before and/or without the partner and should inhibit engagement with the apparatus (Plotnik, Lair, Suphachoksakun, & de Waal, 2011). If the animals are intentionally coordinating their engagement with the apparatus, they should wait until their partner is present before jointly manipulating the apparatus. So far, chimpanzees, *Pan troglodytes* (e.g., Melis, Hare, & Tomasello, 2006a; Melis, Hare, & Tomasello, 2006b), bonobos, *Pan paniscus* (Hare, Melis, Woods, Hastings, & Wrangham, 2007), orangutans, *Pongo pygmeus* (ChalmeauLardeux, Brandibas, & Gallo, 1997), capuchin monkeys, *Cebus apella* (Mendres & de Waal, 2000), cotton-top tamarins, *Sanguines oedipus* (Cronin, Kurian, & Snowdon, 2005), Asian elephants, *Elephas maximus* (Plotnik et al., 2011), domestic dogs, *Canis familiaris* (Ostojčić & Clayton, 2014), wolves, *Canis lupus*, (Marshall-Pescini, Schwarz, Kostelnik, Virányi, & Range, 2017), spotted hyenas, *Crocuta crocuta* (Drea & Carter, 2009), coral trout, *Plectropous leopardus* (Vail, Manica, & Bshary, 2014) and keas, *Nestor notabilis*, (Heaney, Gray, & Taylor, 2017) were able to wait for a cooperative partner in loose-string paradigms. Consequently, it can be assumed that such underlying mechanisms for cooperation are common across species (Noë, 2006). For gaining a further understanding about the coordination of action required for succeeding in the task,

an *opaque barrier control* can be implemented. In this control, the animals’ visual coordination is disrupted, which can reveal whether the cooperative behaviour is dependent on visual coordination when the partner is available and if auditory communication is used between partners. Cooperative success broke down in capuchin monkeys when an opaque barrier was inserted between partners; thus, suggesting that they were coordinating their actions based on visual signals (Mendres & de Waal, 2000).

Inter-individual relationships have shown to be relevant for cooperative behaviour across species and designs. Relationship quality is evaluated by observing animals’ tendency to come into proximity of one another, display prosocial behaviour or willingness to share food. More affiliative dyads of kea (Schwing, Jocteur, Wein, Noë, & Massen, 2016) and wolves (Marshall-Pescini et al., 2017) were more successful in cooperating with each other than less affiliative dyads. Furthermore, inter-individual tolerance (i.e., in food context) seems to be important for dyadic success (Melis et al., 2006b). Certain features of the experimental design (i.e., distribution of rewards and option for partner choice), however, seem to affect the importance of relationship quality for predicting cooperative success. Bonobos outperformed a less tolerant chimpanzee group when food rewards were clumped together and easier to monopolize, while performing similarly when divided and shareable (Hare et al., 2007). Also, rooks, *Corvus frugilegus* (Seed, Clayton, & Emery, 2008) and ravens (Massen, Ritter, & Bugnyar, 2015) were more successful in cooperative tasks when paired with more tolerant individuals. In particular, ravens tended to cooperate only when in physical proximity of a tolerant friend and not necessarily when the friend was also the partner (Asakawa-Haas, Schiestl, Bugnyar, & Massen, 2016). Consequently, tolerance for proximity rather than relationship quality might be the driving force behind variation in cooperative success.

In order to gain an understanding of the evolutionary origin of cooperative abilities and the potential for convergent evolution between primate and birds, we need to gain more information about cooperation across different corvid and parrot species. Several studies have shown that corvids (e.g., ravens, Massen et al., 2015; rooks, Seed et al., 2008) and some parrot species (i.e., kea and African grey parrots) are able to solve the loose-string paradigm. Schwing et al., (2016) found that kea could successfully solve the loose-string paradigm and preferentially did so with affiliative partner; however, the birds were not sensitive to the presence of a partner and attempted to solve the task if no partner was present or the partner arrived only after a delay. Likewise, Péron, Rat-Fischer, Lalot, Nagle, and Bovet (2011) found that while African grey parrots succeed in the cooperative test condition, they could not inhibit engagement with the apparatus when the partner was absent or act according to the availability of the partner (solve the problem solitarily when alone and cooperatively when in dyads). These results suggest that parrots are able to cooperate even though they seem to have problems with the task’s contingencies, although they seem to be able to improve with training (Heaney et al., 2017; Schwing et al., this issue).

With the current study, we sought to add to the yet limited knowledge about cooperative abilities of parrots by testing a

previously untested species from a different cladistic branch within the psittaciformes superfamily, the blue-throated macaw, *Ara glaucogularis*, using the loose-string paradigm. Blue-throated macaws are gregarious birds that form monogamous pair-bonds and have been observed in pairs but also family flocks (Yamashita & Machado de Barros, 1997). Little is known about the social organization of blue-throated macaws, potentially due to the low population numbers and remote habitat in Bolivia. Nonetheless, considering that they live in groups, thus having various social relationships (i.e., mate, family group members), and the proposed need for enhanced social cognition (incl. cooperative abilities) in groups with constant group members (e.g., Emery, Seed, Bayern, & Clayton, 2007), we hypothesize that blue-throated macaws exhibit cooperative behaviours.

The blue-throated macaws were tested in three conditions. In the *cooperative test*, the birds were given the opportunity to jointly pull on the strings of the apparatus in order to obtain food rewards. Furthermore, two control conditions were deployed for disentangling unintentional coordinated behaviours from intentional cooperation (i.e., *delayed control*—need for a partner; *opaque barrier*—cooperation based on visual coordination). We also included social variables into the analyses, namely food tolerance (i.e., co-feeding) and affiliation scores (i.e., positive social interaction in a group setting). We predict that dyads that share resources (=high food tolerance) and exchange more affiliative interactions (=high sociality index) are better in solving the cooperative test than less tolerant/less affiliated ones.

2 | METHODS

2.1 | Subjects

Six subadult blue-throated macaws (*Ara glaucogularis*) were tested between October 2018 and February 2019. While the group consisted of five males and one female bird with an average age of 4.67 ± 0.82 years; only five birds could be tested in the current study (one male was afraid of the apparatus despite extensive training). Consequently, only the five remaining birds (4M/1F) were tested in all possible dyads within the group ($N = 10$ dyads; see Table 1). All birds were hand-raised and subsequently socialized in groups in the Loro Parque Fundación, Tenerife, Spain.

2.2 | Housing conditions

All birds were housed in one social group within two interconnected aviaries at the Max Planck Comparative Cognition Research Station in the Loro Parque in Puerto de la Cruz, Tenerife. The two aviaries ($1.8 \times 3.4 \times 3$ m each) were interconnected by 1×1 m windows, which could be closed for separating individuals for testing. Both aviaries had access to the outside, hence allowed the birds to adapt to the natural light cycle and outside weather conditions. In addition, each aviary was lit with UV-light lamps (Arcadia 54W Freshwater Pro and Arcadia 54W D3 Reptile).

The birds had access to water ad libitum and were fed twice a day with a mix of fruits, vegetables and seeds in the evening. All

TABLE 1 Composite sociality index (CSI) and food tolerance scores (=mean duration of co-feeding) of the dyads participating in the study

Dyad	Bird 1	Bird 2	CSI	Food tolerance
1	Charlie	Lady	3.82	0.00
2	Long John	Charlie	2.69	0.05
3	Mowgli	Charlie	26.80	0.01
4	Mr. Huang	Charlie	8.92	0.07
5	Lady	Long John	4.86	0.14
6	Mowgli	Lady	5.96	0.01
7	Mr. Huang	Lady	24.08	0.01
8	Long John	Mowgli	6.05	0.02
9	Mr. Huang	Long John	11.73	0.14
10	Mowgli	Mr. Huang	5.04	0.04

birds were familiar with handling procedures necessary for transporting the birds from their aviary to the test rooms. The birds were tested once or twice per day, depending on availability, either in the morning (10:30–12:30) or in the afternoon (14:30–16:30). The last feeding was at least 1 hr before starting a training or test session. All applicable international, national and/or institutional guidelines for the care and use of animals were followed. In accordance with the German Animal Welfare Act 32/2007 of the 7th November 2007, Preliminary Title, Article 3, the study was classified as non-animal experiment and did not require any approval from a relevant body.

2.3 | Behavioural observations

In order to gain insights into the social dynamics within the group, we conducted 21.33 hr of observations during different times of the day (i.e., morning, midday, afternoon and evening). One observation session lasted for 16 min., in which affiliative behaviours (i.e., sitting in body contact, allopreening, feeding each other, play) between birds were continuously recorded. The observations were separated into two parts; the first 10.67 hr of observations (=40 observations) were conducted before starting the experiment, while the second part of the observations (10.67 hr; 40 observations) was conducted at the end of the experiment. For each dyad, we calculated the composite sociality index (CSI; Silk, Cheney, & Seyfarth, 2013) as a measure for affiliation (see Table 1 for CSI scores across dyads).

2.4 | Experimental setup

Testing and training took place in an indoor test room ($2.5 \times 1.5 \times 1.5$ m) equipped with lamps covering the birds' full range of visible light (Arcadia 54W Freshwater Pro and Arcadia 54W D3 Reptile). The test rooms were sound-buffered and contained a one-way glass system on one side to allow zoo visitors to observe ongoing experiments without visually distracting the birds. Inside of the test room, a table ($87 \times 49 \times 150$ cm) was placed in front of a window facing into the adjacent test room in which the experimenter was sitting. The table had two perches attached to the backside of

it, equidistant to the middle barrier. During tests, a transparent (or opaque for the opaque barrier test) barrier was inserted at the middle of the table and held in position by a metal sliding construction. The Plexiglass barrier contained two holes in it (7 cm diameter, at 7 cm height with 21 cm in between holes), thus, allowing the birds limited tactile contact. A curtain separated the rest of the room. The experimenter was sitting in the adjacent test room behind a small table with the apparatus on it. The transparent glass window separating the test rooms contained a cut-out of 50 cm with a thickness of 1 cm which was covered with mesh (86 × 20 cm), thus allowing the birds to manipulate the strings through the mesh without grabbing the whole apparatus. The apparatus could be slid into the test room through a gap of 5 cm below the mesh partition, thus allowing the birds to grab the reward on top of the apparatus.

We used two different apparatuses for this study, at first, a vertical apparatus was used (see Figure S1), but due to technical problems, we had to switch to a horizontal setup (see Figure 1). The horizontal apparatus consisted of a wooden board (40 × 40 cm) mounted on two metal ball-bearing slides, thus allowing a smooth sliding motion in the direction of the puller. A hemp string (3 mm diameter) was fed through two metal loops attached to the ends of the wooden platform (see Figure 1a). The ends of the string were pushed through the mesh at fixed positions and protruded 4 cm into the test room (see Figure 1b). The platform moved towards the birds only if both ends of the string were pulled at the same time. If only one end was pulled, the other end of the string was pulled out of reach and the platform did not move. The apparatus was mounted on top of a small table (85 cm) in order to line up precisely with the table in the test room (see Figure 1b). Two pieces of walnut (1/8 of a walnut), a highly preferred reward, were placed at the left and right end of the board. A transparent divider was inserted in the middle of the table, thus allowing visual, olfactory and auditory contact between the birds, but preventing birds from monopolizing the apparatus. The bird's testing position (left/right) was randomized and counterbalanced across test sessions. All training and test sessions were videotaped by a camera mounted to the wall behind the experimenter.

2.5 | General procedure

At the beginning of every trial, the experimenter removed an opaque panel, which prevented the birds from seeing the apparatus and called the birds' name to get their attention (always calling bird on the left side first). Once the birds were standing in front of the mesh, she showed two pieces of walnut to the bird(s) before placing them on the platform. If the birds did not approach the mesh after their name was called three times in a row, the experimenter retracted her hands with the reward and waited for 30s before showing the rewards again in front of the mesh and calling the birds' names one more time.

Each session (training and test sessions) started with two *motivational trials*, in which the experimenter moved the platform within reach of the birds and they were allowed to consume the rewards. The *test trials* started immediately after the motivational trials and the birds now needed to pull both ends of the string in order to gain access to the rewards on the platform. After showing the rewards to the birds, the experimenter simultaneously fed both ends of the string through the mesh and removed her hands, placed them in her lap and remained passive until the trial ended (=either possible outcome occurring). The birds could access the string ends as soon as it was fed through the mesh. If the birds pulled the string ends simultaneously, the platform moved within reach and the birds could eat the pieces of walnut (=successful trial). If a bird did not pull within 1 min (=not touching string) or pulled solitarily (=string out of reach for partner), the trial ended and was noted as a failure. In case, the birds were inattentive and not coming forward while calling their names, one motivational trial was conducted to increase the birds' motivation to engage with the apparatus again, before proceeding with the next trial. Between trials, the experimenter prepared the apparatus (i.e., straightening the string and making sure that both ends were equally long) and removed the panel before the next trial began.

2.6 | Training

Prior to starting the training, we tested the birds' ability to spontaneously solve the task arranged in a vertical setup (see Figure S1). In

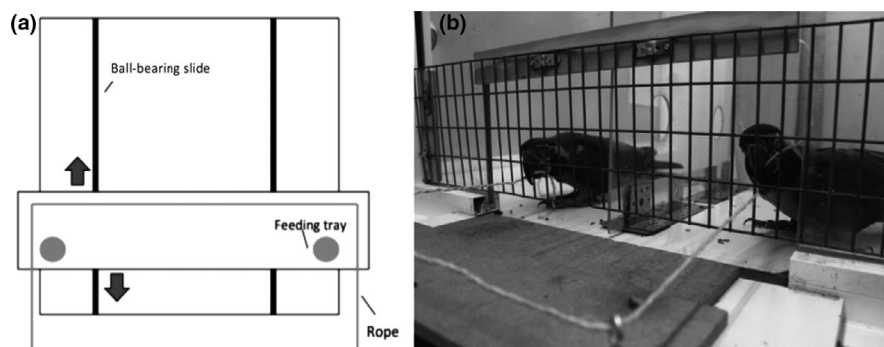


FIGURE 1 (a) Schematic drawing of the string-pulling apparatus. A string is fed through two metal loops, which are attached to a mobile platform. Accordingly, if only one end of the string is pulled, the other end weaves out of the loop and the platform does not move. The food rewards are placed on two small wooden trays on each side of the mobile platform and are only reachable to the birds once they have pulled the platform towards them. (b) Setup during the cooperative test condition. A transparent divider with two holes separates the birds while the strings are fed through the mesh in predefined places. The experimenter is sitting behind the apparatus facing the birds

TABLE 2 Overview of training steps and test conditions

	Order	Description	Number of trials	Criterion
Training (individually)				
Step 1	1	String ends intertwined	5 trials per session	3 successful trials in 2 consecutive sessions
Step 2	2	String ends 2 cm apart		2 successful trials in 2 consecutive sessions; if not back to step 1
Test conditions (in dyads)				
Cooperative test	1	Partner visible	10 trials per session; 4 sessions	
Delayed control	2/3 ^a	Partner access after 5s	10 trials per session; 2 sessions	Only if successful in test
Opaque barrier control	2/3 ^a	Partner invisible		

^aThe order of delayed and opaque barrier test was randomized across dyads (i.e., some dyads experienced the delayed test following the cooperative test, while other dyads were tested in the opaque barrier test first).

this setup, the birds needed to pull the platform up until it reached the bottom of their cage for accessing the rewards (see Appendix S1 for details). The birds were tested in three dyads (with the highest social score) and exposed to the apparatus for five trials during two sessions. Following this spontaneous vertical test, we decided to switch to the horizontal setup due to technical problems with the vertical apparatus. Nonetheless, the parrots gained experience in interacting with the string-pulling apparatus, although arranged in a different setup. Consequently, we decided to skip an additional spontaneous test with the horizontal setup and instead began training the parrots directly.

Training was conducted in the test rooms before starting with the test conditions with each bird individually. Before starting the training, the birds were habituated to the apparatus using positive reinforcement. The birds were fed in the test room while the apparatus first remained motionless on the other side, then the apparatus was moved in a second step and finally the birds were fed from the apparatus. Only if a bird showed no signs of fear when interacting with the apparatus (i.e., feeding from and not reacting to movements of the apparatus), the first training step started. One bird did not proceed to the first training step as he was uncomfortable in the test room and showed signs of fear when interacting with the apparatus (despite two months of extensive habituation).

In the *first training step* (see Table 2.), the birds were trained to pull the platform in order to receive the rewards placed on top of it. The middle barrier was not inserted during training, and the bird was allowed to move across the whole table. The two ends of the string were intertwined with each other, so that only one end protruded through the mesh. Birds could consume both pieces of walnut if they pulled successfully during training. Each training session consisted of 5 trials, and in order to proceed to the next training step, birds had to succeed in pulling the platform in three out of five trials in two consecutive sessions.

In the *second training step*, the ends of the string were separated and placed through the mesh at a distance of 2 cm from each other. Since the string was naturally curled, the ends protruding into the test room were further apart than 2 cm. Accordingly, the birds

needed to grab both ends with their beak and pull, in order to succeed. As with the first step, five trials were conducted per session, and birds needed to succeed in two out of five trials in two consecutive sessions to reach criterion and proceed to testing. If a bird failed to reach this criterion in two sessions, he/she fell back to the first training step, and after successful completion of the first training step proceeded again to the second training step.

2.7 | Testing

Each dyad was tested in four test sessions, and depending on their success, additionally in the two control conditions. The order of control conditions was assigned pseudo-randomly and counterbalanced across dyads. In order to assess whether blue-throated macaws are able to cooperate with each other, we selected dyads with the highest CSI first (as cooperation should be most likely between affiliative partners). Subsequently, we tested the birds with other partners in order to investigate whether relationship quality has an effect on cooperation success.

In the *cooperative test condition*, the experimenter fed the string through the mesh with a distance of 45 cm end to end; thus, the birds could not reach both ends of the string (in addition to being separated by the Plexiglas panel) and needed to pull simultaneously with the partner in order to succeed (see Video S1).

In the *delayed control*, the second bird's access to the string was blocked for 5 s before allowing him/her access to the string. Consequently, the subject had to refrain from pulling the string until the partner could reach the apparatus. A transparent barrier was inserted perpendicular to the middle barrier (31 cm distance or halfway from mesh), which could be removed from outside of the test room following the delay duration (see Video S1). Birds were randomly allocated to the role of either subject or delayed partner in each session.

In the *opaque barrier control*, the transparent barrier in between birds was exchanged for an opaque wooden barrier (see Video S1). Accordingly, the birds had to coordinate their actions without relying on visual feedback.

2.8 | Food tolerance tests

Food tolerance tests were conducted in order to assess tolerance levels for each dyad. These tests were repeated twice for each dyad during the period they were tested with the cooperative string-pulling task. For the tolerance test, a second table was added onto the back of the birds' table so that they could walk around the transparent barrier in the middle. A metal bowl of 12 cm diameter filled with 10 g of seeds (Loro Parque Ara Mix) was shown to the birds in front of the transparent barrier. If both birds were attentive (i.e., in front of the barrier looking towards the bowl), the bowl was placed 10 cm behind the curtain and the curtain was opened, thus allowing simultaneous access the bowl. We recorded the duration of co-feeding (=both heads lowered into the bowl) and used this measurement as the food tolerance score (correcting for variable test durations by calculating the rate of co-feeding). The tolerance test ended after 5 min or when both birds left a 30 cm radius of the bowl.

2.9 | Analyses

The videos were coded using Solomon Coder (2015 by András Péter). For the test and control conditions, we coded the number of successful pulls (i.e., both birds pulling until the platform was within reach) and failures. The failures were further divided into two different categories: (a) one individual pulls alone or (b) no pulling within 1 min. In addition, we coded the latency to approach (=time from calling each bird by name up to their arrival in front of the mesh) and latency to pull (=time from inserting strings to first pulling behaviour). Furthermore, we coded frustration-related behaviours (i.e., biting) and attention-getting signals (i.e., vocalisations and begging). A second coder coded 20% of the videos for reliability (all Cohen's kappa for frequencies >0.8; all ICC (consistency) for durations >0.6).

All analyses were performed using R (R Core Team, 2014) and the packages "lme4" (Bates, Maechler, Bolker, & Walker, 2014) and "ggplot2" (Wickham, 2009). In the first step, we wanted to find out whether any variables predicted the birds' success in the task. We ran a generalized linear mixed model (GLMM) with a binomial error distribution with the combined frequency of successes and failures as the response variable and the following variables as predictors: condition (factor: cooperative, delayed, opaque), number of session for each bird (counting consecutively across partners), CSI and food tolerance score. Individuals nested within dyads were included as a random effect. In the second step, we looked at the different types of failures in two separate GLMMs. Here, we used the same model structure as before but with the number of failures (pull alone and not pulling) set as response variables respectively and condition and number of sessions per bird as predictors.

Finally, we ran linear mixed models (LMM) for analysing the behaviours observed during the test. Separate LMM were run for the latency to approach (mean per session; log-transformed), the latency to pull the strings (mean per session; reciprocal-square root transformed) and frustration-related behaviours (rate per test duration; cube root transformed). For the attention-getting signals

(rate per test duration), we had to use a generalized least square model (GLS) as the residuals could not be normalized. These models included condition and number of sessions as predictors and individuals nested with dyads as random effects. We used the Akaike information criterion (AIC) to reduce the full models in order to find the best fit. Furthermore, aggressive behaviours were coded but happened too rarely (0.74 occurrences per session) in order to be able to analyse.

3 | RESULTS

3.1 | Training

All parrots solved the first training step (intertwined strings) within the first two sessions. The second training step (strings 2 cm apart) was harder to solve for the birds, and an average of 9.0 (range: 5–12) sessions was needed until the criterion was reached. In total, on average 18 sessions (range: 9–20) were conducted before the parrots reached criterion due to birds falling back to the first training step if they failed to reach criterion within two sessions (see Methods).

3.2 | Test

The parrots solved the task in the cooperative test condition in 73.75% of all trials. All, but one dyad (Charlie–Mowgli), were successful in the cooperative test condition, within the first session (see Appendix S1 for data).

While the birds were successful in the cooperative test, they were less successful in the delayed control, with only 0.93% success rate (Figure 2; GLMM: $\beta = -5.67$, $SE = 0.67$, $z = -8.41$, $p < .001$). Interestingly, the birds were even more successful in the opaque barrier control (87.22%) compared with the cooperative test (73.75%; GLMM: $\beta = 1.52$, $SE = 0.35$, $z = 4.30$, $p < .001$), also when excluding the dyad, which failed the test and hence was not tested in the control conditions. In addition, birds were more successful with increasing session number (GLMM: $\beta = 0.22$, $SE = 0.05$, $z = 4.34$, $p < .001$); thus, indicating that experience facilitated string-pulling success.

In addition, we found that dyads with a higher CSI (=more affiliative relationship) showed a lower success rate than dyads with a lower CSI (Figure 3; GLMM: $\beta = -0.10$, $SE = 0.03$, $z = -3.08$, $p = .002$). However, this effect was caused by the only dyad that failed in the test condition (Mowgli–Charlie), as the effect of the CSI diminished when this dyad was excluded from the analysis (Wald χ^2 Test: $\chi^2 = 0.02$, $df = 2$, $p = .894$). Food tolerance (=food sharing behaviours) did not affect cooperative success (Wald χ^2 test: $\chi^2 = 2.76$, $df = 1$, $p = .097$).

3.3 | Types of Failures

When birds failed to solve a trial, this was most often due to one bird pulling alone (67.89%) instead of both birds failing to pull within the time limit (32.11%). We detected a condition x session

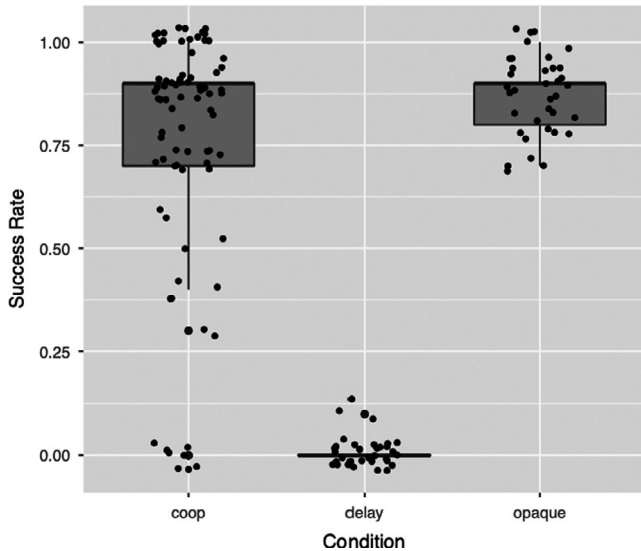


FIGURE 2 Success rate of all dyads across the three test conditions (coop = cooperative test; delay = delayed test; opaque = opaque barrier test). Black dots represent individual data points; black bars indicate median values, whiskers display upper and lower hinge and boxes show the interquartile range

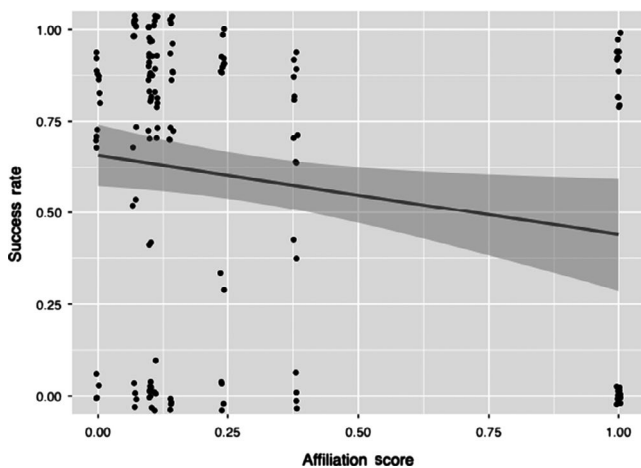


FIGURE 3 Correlation between success in test (all conditions combined) and the affiliation score. The higher a social score is, the more affiliative is the relationship between two birds. Black points represent the data points, the blue line indicates the regression line (smoothing loess function) with the grey shade marking the 95% confidence intervals

interaction (Wald χ^2 test: $\chi^2 = 9.58$, $df = 2$, $p = .008$) for the failures to pull. With increasing session number for each bird, more failures to pull occurred in the delayed control compared with the cooperative test (GLMM: $\beta = 0.233$, $SE = 0.08$, $z = 3.02$, $p = .003$) but not in the opaque barrier control (GLMM: $\beta = 0.131$, $SE = 0.10$, $z = 1.31$, $p = .191$).

Failures due to one bird pulling alone occurred more often in the delayed control compared with the cooperative test (GLMM: $\beta = 1.67$, $SE = 0.35$, $z = 4.84$, $p < .001$), while no difference was found between opaque and cooperative condition ($\beta = -0.73$, $SE = 0.57$, $z = -1.29$, $p = .200$).

3.4 | Motivation

We found that the variable latency to approach (=time from removing the opaque panel until they are in front of the mesh) was compromised by the birds' responsiveness to the experimenter's calls; consequently, this variable showed big individual differences (range: 2–192 s). Despite this potential confounding effect of responsiveness, the latency to approach differed across test conditions (Wald χ^2 Test: $\chi^2 = 12.04$, $df = 2$, $p < .001$) but not across sessions ($\chi^2 = 0.97$, $df = 1$, $p = .324$). In particular during the delayed control, it took longer for the birds to approach (mean \pm SD: 48.55 ± 38.78 s total per test session) compared with the cooperative condition (21.78 ± 28.07 s; LMM: $\beta = 1.08$, $SE = 0.21$, $df = 136.10$, $t = 5.17$, $p < .001$), but also in the opaque control, the latency to approach was longer than in the cooperative condition (40.69 ± 48.84 s; LMM: $\beta = 0.59$, $SE = 0.21$, $df = 132.01$, $t = 2.88$, $p = .005$).

3.5 | Behaviours during the test

In order to gain further insights into how the birds coordinated their pulling actions, we analysed their behaviours during the tests. In particular, we looked at attention-getting signals and frustration-related behaviours. We found neither an effect of condition (ANOVA: $F_{(2,148)}$: 0.497 , $p = .610$) nor session ($F_{(1,148)}$: 1.559 , $p = .214$) on attention-getting behaviours. For the frustration-related behaviours, we found that the birds displayed more frustration during the delayed control than in the cooperative test (LMM: $\beta = 0.25$, $SE = 0.05$, $df = 122.54$, $t = 5.12$, $p < .001$), while no differences emerged between the opaque control and cooperative test ($\beta = -0.04$, $SE = 0.05$, $df = 125.80$, $t = -0.91$, $p = .366$). In later sessions, the birds exhibited fewer frustration behaviours than in earlier sessions ($\beta = -0.02$, $SE = 0.01$, $df = 58.64$, $t = -2.12$, $p = .039$).

Furthermore, we analysed the time until the birds started to pull the strings, which was of particular relevance in the delayed control compared with the cooperative test. We found a main effect of condition (Wald χ^2 test: $\chi^2 = 106.28$, $df = 2$, $p < .001$) and session number of the bird ($\chi^2 = 5.60$, $df = 1$, $p = .018$) on the speed of pulling. The birds started to pull the strings after a longer time in the delayed control (mean \pm SD: 6.06 ± 7.71 s; LMM: $\beta = -0.40$, $SE = 0.07$, $df = 134.88$, $t = -5.95$, $p < .001$), while they started to pull sooner in the opaque barrier control (0.76 ± 0.54 s) compared with the cooperative test (2.28 ± 5.71 s; LMM: $\beta = 0.17$, $SE = 0.07$, $df = 136.60$, $t = 2.64$, $p = .009$). In addition, the birds started to pull faster with increasing session number (LMM: $\beta = 0.02$, $SE = 0.01$, $df = 89.38$, $t = 2.43$, $p = .017$).

4 | DISCUSSION

Blue-throated macaws, like other birds and mammals, were able to solve a loose-string problem repeatedly with different partners. They continued to solve the task when the visual access between partners was blocked, while they collectively failed to wait for a

partner in the delayed control. Thus, the parrots did not demonstrate sensitivity to the task's contingencies (i.e., the need for coordinating their actions with their partner) but may have learned to solve the task by applying a simpler rule, namely to pull as soon as strings are made available.

The blue-throated macaws' success rate was relatively high with 73.6% compared with other bird species tested in the same paradigm (e.g., kea: 18.9% with little training (Schwing et al., 2016; rooks: 41.0% Seed et al., 2008), but similar to ravens (74.6% Asakawa-Haas et al., 2016) and extensively trained kea (87.5% Heaney et al., 2017). Unfortunately, we could not test for the parrots' ability to spontaneously solve the paradigm, as they had some previous experience using a vertical setup. Nonetheless, two dyads were able to pull the platform up in the spontaneous cooperation test using the vertical setup, indicating that the macaws are potentially able to solve the problem without prior training (see Appendix S1). Interestingly, and contrary to the predictions, the parrots' success even increased in the opaque control up to 87.2% success. If success in the cooperation task depends on visual coordination between the partners, one would expect it to break down if visual access is blocked. Furthermore, we did not observe more attention-getting behaviours in this condition, which would be one way to ensure coordination between partners. Of course, it is possible that the birds coordinated their actions by relying on tactile feedback (instead of visual or vocal coordination) when pulling the string; however, the short latency to pull rather indicates that they pulled as soon as they grabbed the string and did not wait for tactile feedback (i.e., pressure on string). It is not out of range to assume that the birds could have noticed the presence of the partner by hearing them walking on the table or because both partners were coming in the test room together. Consequently, they may have relied on acoustic rather than visual cues for coordinating engagement with the apparatus. Furthermore, birds became more successful in later sessions, thus with increasing experience. Taken together, these results show that the birds solved the task without actively coordinating their actions based on visual or vocal feedback and learned to solve the problem efficiently with increasing exposure. A confounding factor in this regard is that in order to get the birds' attention, they were called by name at the beginning of each trial. Only if both birds were standing in front of the mesh, the trial was initiated. It could be argued that, this calling might have facilitated the birds' coordination, as they were both in the same position and attentive at the same time. This factor has not received much attention so far, as the task requires the animals to be in a specific spot (equidistant from the apparatus), in order to give both individuals the same chance for success (e.g. releasing the animals at the same time (e.g., Heaney et al., 2017; Marshall-Pescini et al., 2017). Future studies need to assess whether this "assisted" coordination affects the performance in cooperative problem-solving tasks. Another relevant finding in this context is that the parrots pulled the string very quickly after it was made available (2.3 s in cooperative and 0.8 s in opaque control), supposedly leaving very little time for coordination with a partner. Unfortunately, little information about the latency to pull in studies using the loose-string

paradigm is available, and while potentially species-specific ecological adaptation affects reaction times (as well as experimental setups), coordination times would still be an interesting aspect to consider particularly to provide an assessment of whether animals would potentially be able to coordinate in such a short time. In any case, pulling fast is a good strategy if the birds were indeed pulling blindly concerning their cooperation partner, as a consequence of simple reinforcement learning. This was particularly true for our setup, in which strings were short so that a single pull moved the other end out of reach. It has been shown that string length affected cooperation success in kea tested with a similar setup (Schwing et al., this issue). Shorter strings impaired cooperative string-pulling success in kea. The sooner the birds pull after a string end becomes available, the lower is the chance that one of them has already pulled the other end out of reach, and the higher is their chance of being rewarded. Consequently, they are reinforced to pull as fast as possible. This is in accordance with the finding that the birds pulled the strings faster in the opaque barrier control compared with the cooperative test, which was carried out before. Interestingly, capuchin monkeys' success rate decreased in the opaque barrier test compared with when the partner was visible (Mendres & de Waal, 2000); thus, suggesting that the birds, contrary to capuchin monkeys, did not rely on visual cues for solving the task.

The loose-string paradigm certainly poses an interesting milestone in testing for cooperative abilities in comparative cognition research. Nonetheless, it is important to note that all studies carry procedural differences inherent to species-specific constraints, and often even the task and success criteria themselves differ; thus, rendering interpretations pertaining to proximate causes of cooperative behaviour across species difficult. Furthermore, its pervading dilemma is that it can be solved by chance occurrence of simultaneously pulling rather than requiring coordinated cooperation (e.g., Chalmeau, Visalberghi, & Gallo, 1997; Noë, 2006; Visalberghi, Quarantotti, & Tranchida, 2000). Indeed, most species did not seem to show sensitivity to the need or had to learn first about the partner's role (e.g., Hirata & Fuwa, 2007; Massen et al., 2015; Seed et al., 2008), which precludes ruling out associative accounts. In order to tease apart the animals' sensitivity to the need of a partner, we tested the birds in a delay control, in which the partner gained access to the string only after 5 s. Consequently, the subject had to wait until the partner had access to the string for successfully pulling the platform within reach. We found that the parrots collectively failed to wait and instead started to pull the string alone. During this control condition, the parrots exhibited much more frustration-related behaviours (i.e., destructive behaviours) compared with the other two conditions and finally stopped pulling altogether. While this failure to wait might indicate that the parrots did not understand the task's contingencies (i.e., the need for a partner), they might also be explained by a lack of inhibition, as the parrots need to refrain from pulling the string, a behaviour that had been strongly reinforced during previous sessions. Similarly, the two previously tested African grey parrots (Péron et al., 2011) solved the cooperative loose-string test condition but displayed limited sensitivity to the partner's role

and failed in delay controls. For kea, the only other parrot species tested so far, mixed findings have been reported (Heaney et al., 2017; Schwing et al., 2016). The kea tested by Schwing et al., (2016) did not demonstrate sensitivity to the need of a human "partner," as they continued to pull even when the human experimenter was absent or oriented away; nonetheless, training improved their success (i.e., waiting for a delayed partner; Schwing et al., this issue). On the contrary, kea tested by Heaney et al., (2017) could wait for a conspecific partner up to 65 s, which is longer than previously been shown for any nonhuman species. However, as the authors stated, this waiting behaviour might have been facilitated by the partner's behaviour in the delay test. The second bird was frequently shaking the door to get into the test compartment, which possibly distracted the subject making it easier to wait for such long periods (Heaney et al., 2017). Furthermore, differences in training criteria and thus experience with the task affect cooperative success (Schwing et al., this issue). While the birds in Heaney et al.'s study had extensive experience, as they had to reach a 25 s delay criteria before actually being tested, the kea in Schwing et al., (2016) did not receive any explicit training. The macaws in our study did receive some training prior to starting the experiment; however, unlike the kea in Heaney et al., (2017), they were not required to reach a criterion for commencing with the delayed control. Apart from too little experience with the task, a lack of inhibitory control might overrule appropriate behaviours in the delayed control. Indeed, findings on inhibitory skills in parrots are mixed. Some species tested with the delayed gratification paradigm could refrain from consuming a food item, which could be exchanged against better food at a later point in time for considerably longer periods than the 5 s required by our delayed test (Auersperg, Laumer, & Bugnyar, 2013; Koepke, Gray, & Pepperberg, 2015; Schwing, Weber, & Bugnyar, 2017). However, in other experimental situations, parrots, including the blue-throated macaws from our study, have exhibited limited inhibition abilities (Kabadayi et al., 2017; Péron et al., 2011). Accordingly, this suggests that a lack of inhibitory control is possibly not a general factor explaining failures in the delayed controls, but rather a limited understanding of the tasks' contingencies.

Contrary to our predictions, we found no effect of relationship quality (as measured with the CSI) or food tolerance on dyadic cooperative success. This is in contrast to the findings in kea (Schwing et al., 2016, but see Schwing et al., this issue), ravens (Massen et al., 2015), chimpanzees (Melis et al., 2006b), rooks (Seed et al., 2008) and wolves (Marshall-Pescini et al., 2017), in which the affiliation between the partners was positively related to successful cooperation. This lack of an effect of any social parameters might, however, be explained by the experimental setup. The transparent barrier in between birds prevented them from monopolizing the apparatus thus buffering the competition over food; however, it also prevented free interactions between partners. These restrictions might have eliminated any effects of social parameters on cooperative success (see e.g., Asakawa-Haas et al., 2016), consequently, our results need to be treated cautiously.

To date, there are only very few studies on and only mixed evidence of cooperative behaviours of parrots in experimental settings

(see Lambert, Jacobs, Osvath, & Bayern, 2018 for review). While corvids have successfully demonstrated their capacity for cooperation (e.g., Asakawa-Haas et al., 2016), most parrots failed to show sensitivity to the partner's role in the task (although they might learn to pay attention to their partner with sufficient training; Heaney et al., 2017, Schwing et al. this issue). Parrots and corvids both face complex social situations during which they must cooperate, for instance during bi-parental care (Péron et al., 2011; Schwing et al., 2016). Also, parrots live in complex social groups and exhibit extractive foraging behaviours in the wild (Bouzat & Strem, 2012; Herrera, Vargas, Sandoval, Perskin, & Redón, 2007; Yamashita & Machado de Barros, 1997). Consequently, those similar socio-ecological pressures between corvids and parrots should have shaped the capacity for cooperation also in parrots. Indeed, it is difficult to assess whether a lack of self-control compromises parrots' cooperative abilities in the loose-string paradigm. Accordingly, it would be interesting to test parrots in a different setup that allows disentangling their poor inhibition from their cooperative abilities, potentially by making the action for receiving the reward more costly (e.g., pulling action more effortful by increasing distance to string) or by eliminating food rewards altogether (e.g., replacing them by social rewards). Alternatively, it might be possible that the parrots would have shown an enhanced understanding if they would have received more training or were exposed to the task for more sessions. Experience enhances task understanding (e.g., Asakawa-Haas et al., 2016; Hirata & Fuwa, 2007; Schwing et al. this issue) and, in comparison to other studies (e.g. 5 training steps in Ostojic & Clayton, 2014; 3 training steps in Seed et al., 2008), the parrots received relatively little training.

The results from the current study need careful interpretation. The low sample size and consequently the need to test the same individuals with different partners in order to obtain more test dyads might have resulted in interfering learning effects. Despite controlling for individual multiple testing, it remains difficult to disentangle the effect of experience on dyadic success. Secondly, the changes in study design in the course of the study (i.e., the change from an initially vertical to a horizontal setup or the change of the procedures for the delayed test control) might have had an effect on the results. Nonetheless, we feel confident that the data from the current study constitute a valuable pilot study that provides first insights into macaws' ability to solve string-pulling problems in a social setup.

5 | CONCLUSION

In conclusion, we could demonstrate that blue-throated macaws are able to solve the loose-string paradigm; however, they seem to solve the task by following an associatively learnt rule of pulling as fast as possible/pull when hearing a partner, instead of actively coordinating their actions with each other relying on visual or vocal feedback. Future studies need to assess whether the lack of coordination between cooperation partners is due to a lack of an underlying mechanism for cooperation in macaws or rather due

to the experimental setup, in particular, the need for high levels of inhibitory control.

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CONFLICT OF INTEREST

We declare we have no competing interests.

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