

Elephants know when they need a helping trunk in a cooperative task

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Elephants are widely assumed to be among the most cognitively advanced animals, even though systematic evidence is lacking. This void in knowledge is mainly due to the danger and difficulty of submitting the largest land animal to behavioral experiments. In an attempt to change this situation, a classical 1930s cooperation paradigm commonly tested on monkeys and apes was modified by using a procedure originally designed for chimpanzees (*Pan troglodytes*) to measure the reactions of Asian elephants (*Elephas maximus*). This paradigm explores the cognition underlying coordination toward a shared goal. What do animals know or learn about the benefits of cooperation? Can they learn critical elements of a partner's role in cooperation? Whereas observations in nature suggest such understanding in nonhuman primates, experimental results have been mixed, and little evidence exists with regards to nonprimates. Here, we show that elephants can learn to coordinate with a partner in a task requiring two individuals to simultaneously pull two ends of the same rope to obtain a reward. Not only did the elephants act together, they inhibited the pulling response for up to 45 s if the arrival of a partner was delayed. They also grasped that there was no point to pulling if the partner lacked access to the rope. Such results have been interpreted as demonstrating an understanding of cooperation. Through convergent evolution, elephants may have reached a cooperative skill level on a par with that of chimpanzees.

animal behavior | comparative cognition | problem solving

The last decade has seen increased attention to the cognitive complexity of animal cooperation. Ethological observations suggest that nonhuman primates have some understanding of how cooperation works (1, 2), but experimental research has produced mixed results. Some investigators have ascribed successful cooperation to random coaction (3, 4), whereas others report deliberate coordination to attain a goal (5–8). Cooperation is tested experimentally by gauging the reactions of animals to a partner's presence or absence, specific behavior, and motivation (or lack thereof) in a context requiring interindividual coordination (9, 10). Apart from a few studies (11–15), little experimental evidence exists with regards to the cooperative abilities of nonprimates. Although much research explores the cognitive bases for complex sociality and cooperation in various animals, including primates (16, 17), corvids (18), and cetaceans (19), elephants have rarely been subjected to cognitive tasks of any kind (see refs. 20–23 for reviews). However, these animals are well-known for their complex sociality in nature (24–30) and their relatively large and complex brains (e.g., refs. 31–35). African (the genus *Loxodonta*) and Asian elephants (24–30, 36) live in closely bonded, female-centric family groups and display a wide range of other-directed, often cooperative behaviors that may be supported by specialized cognitive mechanisms (37, 38). For example, elephants often act as allomothers toward each other's calves (39), assist distressed or immobilized family members by pulling or pushing them out of prostrate or otherwise dangerous positions (40, 41), and form close, multi-individual coalitions to protect calves against predation (39, 40). In addition, elephants are natural problem solvers and use their trunks to carefully and me-

thodically manipulate objects (e.g., refs. 23–26, 35, 40, 42, and 43), suggesting that they would make good candidates for experimental tasks that exploit these abilities and their cooperative tendencies. This study investigated the cooperative abilities of elephants at the Thai Elephant Conservation Center (TECC) in Lampang, Thailand—assisted by each of the elephant's caretakers, or “mahouts”—through the adaptation of a paradigm designed by Hirata and Fuwa (5; also see ref. 7) for chimpanzees.

Results and Discussion

In traditional captive elephant management throughout South-east Asia virtually every animal is assigned their own individual mahout (i.e., an elephant caretaker responsible for the daily care of the animal), a close relationship that enables the safe conduction of controlled experiments (44). Using mahouts does, however, require some deviations from primate-centric protocols. Our study elephants were docile and in most novel situations responded only to mahout commands. Because this study required spontaneous problem solving, some initial, preliminary training was necessary. Twelve elephants first learned to pull a single rope attached to the center of an out-of-reach sliding table with a food bowl attached at each end. Pulling the table brought the food within the elephants' reach, a task reliably accomplished by all subjects within 1 d of training them to pull the rope with their trunks (Table S1 and *Materials and Methods*).

The 12 elephants were then grouped into six unique pairs to participate in a task that required coordinated pulling. A classical, 1930s cooperation paradigm (45) used a counterweight so heavy that it required two chimpanzees to pull together, but we used a variation with a single rope, thus precluding the need for a counterweight (5). A single rope was threaded around the apparatus such that pulling on one end would only move the rope, not the sliding table, making the other end of the rope unavailable to a partner. Only if both rope ends were pulled at the same time could the table be moved (5). Each rope end was placed in the center of two separate, fenced lanes into which each elephant was released for testing. If one elephant arrived before the other and pulled the rope without waiting, the opportunity for collective pulling was lost and the table stayed in place (Fig. 1). The pairs were tested sequentially under the following three primary conditions:

Simultaneous Release. Both elephants were released together from 10 m back by their respective mahouts. From then on, the mahouts remained silent, turned their backs to or looked away

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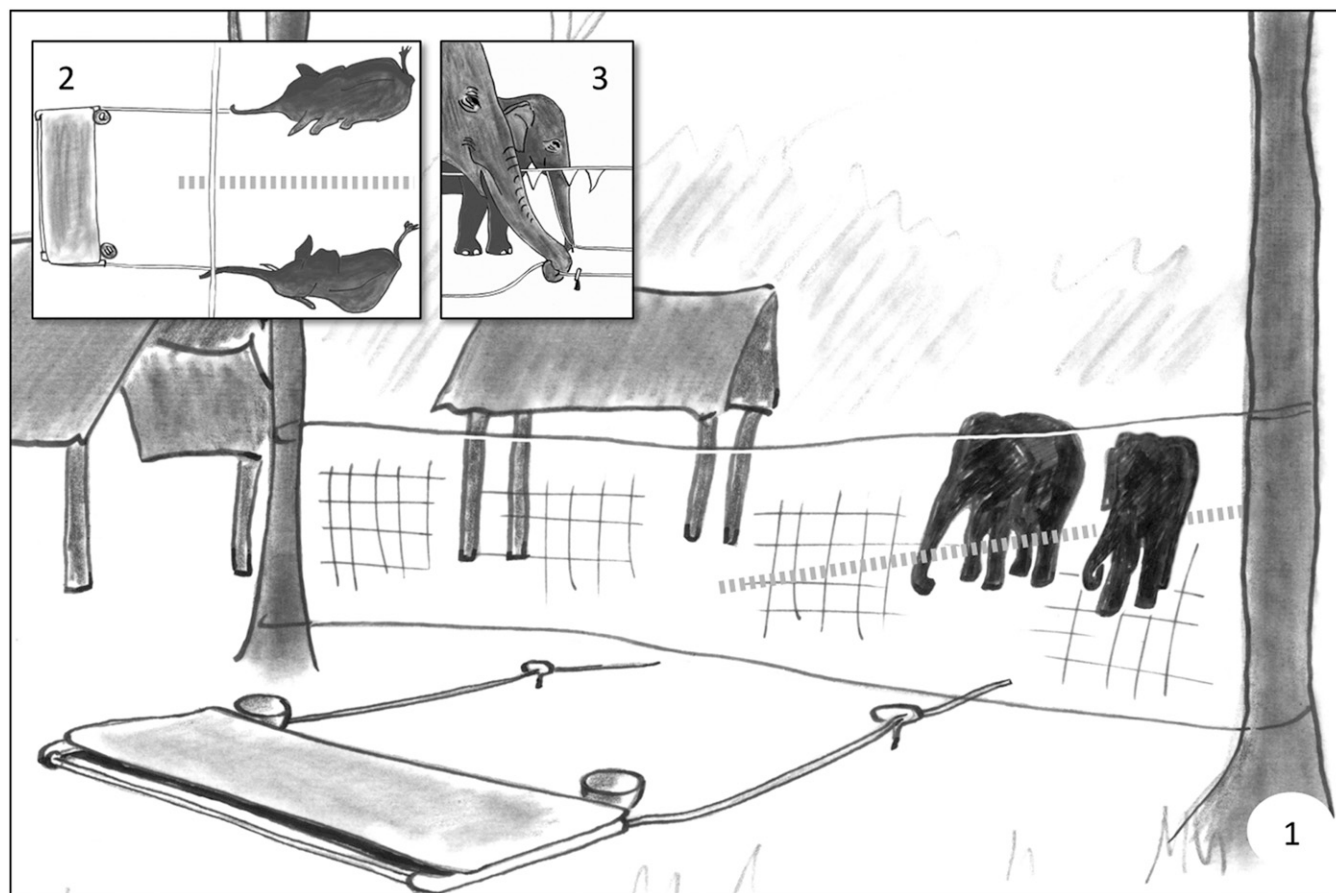


Fig. 1. A multiview diagram of the elephant cooperation apparatus. View 1 pictures a ground view from beyond the table. In test and control trials, the two elephants, lined up at the release point, walked down two separate, roped-off lanes (presented here in views 1 and 2 as a dashed line) from a point 10 m behind the apparatus. The apparatus, a sliding table, could be moved by grasping rope ends fed through metal rings set in the ground. These rings were positioned under a stout but transparent barrier (a volleyball net and wire ropes) needed to prevent the elephants from physically approaching the table and attached food bowls. Upon release, the elephants were free to approach the rope ends and to pull. The catch was that only coordinated pulling of both rope ends at the same time would bring the table toward the elephants so that they could retrieve the food in the bowls. Any pulling of one rope end without the other would result in the rope becoming unthreaded, thereby denying pulling access to the second elephant. View 2 mirrors that of the bird's-eye video footage in the supporting information taken from above the elephants. View 3 shows a side view from the base of the barrier. Drawings from video stills by F.B.M.d.W.

from the elephants, and did not interfere with the behavior of the animals. The elephants were tested in 20 trials per day for 2 d. All pairs reached the criterion of at least eight successful pulls in the final 10 trials (Table S1 and Movie S1). Although this phase tells us little about coordination because the elephants could, after having reached the rope ends at the same time, simply have used a “see the rope, pull the rope” strategy based on previous training, the simultaneous release phase was necessary before progressing to the next condition.

Delayed Release. Using the same apparatus, the release times of the elephants were staggered. Now, for the elephants to retrieve the table, the first released individual had to learn to wait for the partner before pulling their own rope end. One elephant in each pair was selected to be the first released, and the release order was not switched until completion of the entire testing protocol. Each lead elephant was initially released 5 s before the partner until the pair successfully pulled in the table in three consecutive trials, upon which the interval was increased to 10 s until the same criterion was reached. This shaping procedure, adapted and modified from one used with chimpanzees (7), was followed in added 5-s increments through 25 s. The first elephants tested in each of the six pairs all reached this criterion in 30 trials or less (the fastest way possible to accomplish all criteria is in 15 trials if

no errors are made), and each elephant made fewer than a total of 12 errors (Table S1 for raw data). The range of errors across all six elephants was 3–12 [compared with 0–28 for chimpanzees in a similar procedure (7)]. The same elephant subjects were then tested for 3 d with 20 randomized trials per day including 10 trials of release intervals between 1 and 25 s and 10 trials of longer release intervals, not previously experienced, between 26 and 45 s (see Table S2 for details on interval lengths).

All six elephants were highly successful in waiting for their partners across the 60 trials, which they did between 88% and 97% of the time (mean \pm SD across the six elephants = $93.33 \pm 3.72\%$). The success of the elephants in longer delay trials increased significantly after the first test day, suggesting they quickly learned the waiting contingency of the task regardless of the length of waiting time (Fig. 2 for a combined analysis across all elephants, and Table S2 for raw data by elephant).

When comparing pulling rates, each trial was divided into two time intervals. Interval 1 began when the first elephant arrived at one rope end and ended with the arrival of the second elephant to within reach of the other rope end. Interval 2 began with the arrival of the second elephant and ended when either the table was retrieved or the rope became unthreaded. The first-released elephant's rope pulling rate in each time interval was calculated to determine whether success was due to their ability to wait for

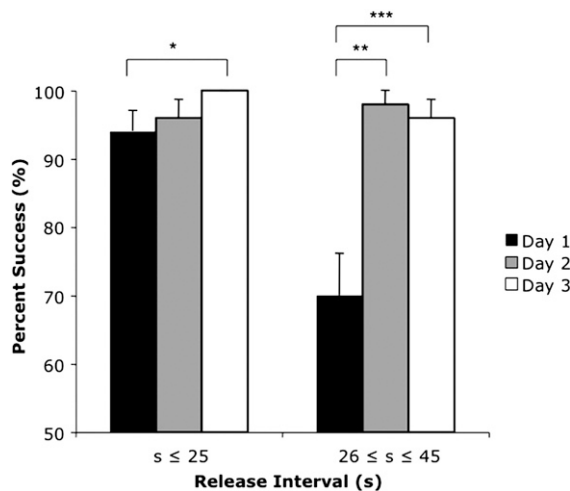


Fig. 2. Success rate per day of delayed release testing in previously trained ($s \leq 25$) and untrained ($26 \leq s \leq 45$) delay intervals. Elephants were given 10 trials of each type per day randomized across the session. As would be predicted based on their previous training, elephants performed at a high success rate on the first day of testing in trained interval lengths, and improved significantly by day 3 (94–100%; $t = -1.96$, $df = 9$, $*P = 0.041$, paired-samples t test, one-tailed). In untrained interval lengths (i.e., delay intervals exceeding those experienced in previous training), the elephants' success improved significantly from day 1 to day 2 (70–98%; $t = -4.12$, $df = 9$, $**P = 0.002$) and remained high in the final day of testing (day 1 to day 3: 70–96%; $t = -4.99$, $df = 9$, $***P < 0.001$; day 2 to day 3: 96–98%; $t = 0.56$, $df = 9$, $P =$ not significant). Error bars represent \pm SEM.

their partners before pulling. One of the six elephants (NU) was excluded from all of these analyses because of an alternative, successful strategy (see below). Interrater reliability of pulling rates was assessed through a Pearson's correlation between two raters' reported frequency per trial, which was highly significant (Interval 1: $r = 0.96$, $n = 67$, $P < 0.001$; Interval 2: $r = 0.87$, $n = 67$, $P < 0.001$). All five elephants (excluding NU as the sixth) pulled significantly more during interval 2, following the arrival of their partner, than during interval 1 as shown by analyzing each subject (identified by their two-letter initials) with Wilcoxon signed-ranks tests: SS: $z = -4.97$, $n = 51$, $P < 0.001$, two-tailed; PT: $z = -5.03$, $n = 56$, $P < 0.001$; WL: $z = -6.65$, $n = 60$, $P < 0.001$; UP: $z = -5.20$, $n = 59$, $P < 0.001$; PP: $z = -4.70$, $n = 53$, $P < 0.001$ (Fig. 3A). Four of the five elephants, in a significant number of trials, did not pull the rope at all until their partner arrived [sign test for a significant number of trials with pulls in interval 2 and no pulls in interval 1, two-tailed: SS: $n = 51$, $P = 0.453$ (binomial P value), PT: $z = -5.40$, $n = 56$, $P < 0.001$; WL: $z = -6.29$, $n = 60$, $P < 0.001$; UP: $z = -4.58$, $n = 59$, $P < 0.001$; PP: $z = -3.01$, $n = 53$, $P = 0.003$]. Although the elephants clearly waited for their partners before pulling (Movies S2 and S3), one possible explanation for their behavior is that they had learned to coordinate their pulling with the arrival of their partner, rather than how their partner's actions contributed to success. Thus, to further test what the elephants had learned or understood about cooperation, we instituted a third condition directly after delayed release.

No-Rope Control. Only the rope end of the first-released elephant was available; the partner's rope was coiled at the base of the table but out of reach, thus making retrieval of the table impossible. Elephants were released simultaneously, and control trials alternated in a random order with an equal number of simultaneous release trials (described earlier). Except for the pair of SS and KW, which received five trials of each type due to unforeseen husbandry issues, all other pairs received 10 trials of

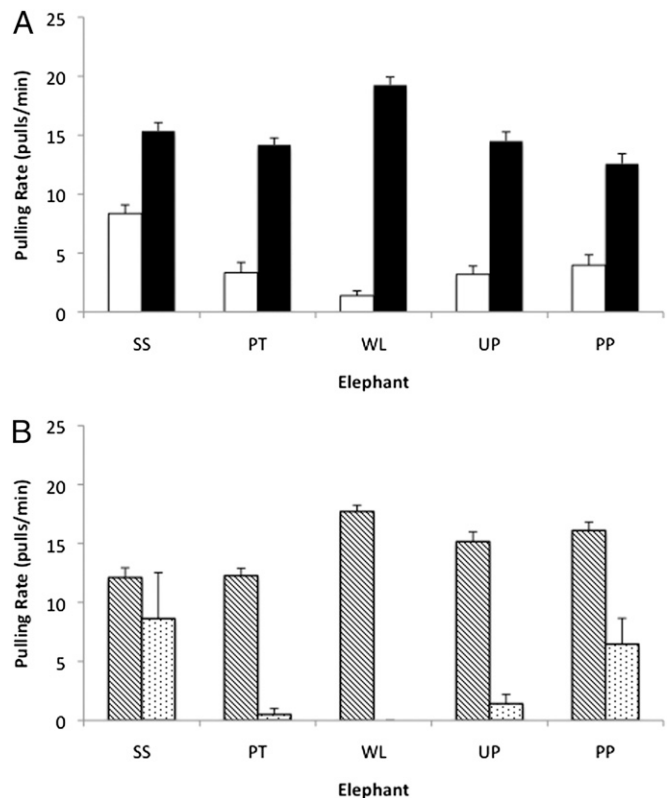


Fig. 3. Pulling rates in the delayed release and no-rope control conditions. (A) Pulling rate per minute of each individual elephant (two-letter designation on x axis, full names in Table S1) across all delayed release trials. Open bars represent the pulling rates in interval 1, before arrival of the second elephant at the rope ends, whereas filled bars represent the pulling rates in interval 2, when both elephants had reached the rope ends. Error bars represent \pm SEM. (B) Pulling rate per minute of each individual elephant across the control condition. Dotted bars represent the pulling rates in control trials where the lead elephant had access to the rope but the partner's rope was placed out of reach. Diagonally hatched bars represent the simultaneous release trials (in which both individuals had access to the rope) that were randomized with control trials. Error bars represent \pm SEM. See also Table S1.

each on 1 d of control testing. Four of five elephants—the data for the fifth, SS, demonstrated a trend but was not significant—pulled significantly more often in trials when their partner had access to and pulled at the rope than when the partner lacked access to the rope and stood idle [Two-sample Kolmogorov–Smirnov (K-S) Test per subject, with a K-S z value reported: SS: $z = 1.27$, $n = 10$, $P = 0.082$, two-tailed; PT: $z = 2.24$, $n = 20$, $P < 0.001$; WL: $z = 2.24$, $n = 20$, $P < 0.001$; UP: $z = 2.24$, $n = 20$, $P < 0.001$; PP: $z = 1.80$, $n = 20$, $P = 0.003$; Fig. 3B and Movie S4]. One elephant (WL) never pulled in trials in which the partner did not have access to the rope, and one elephant (PT) only pulled once (in the very first control trial). All six pairs completed simultaneous release trials with 100% success during these control tests. These data indicate pulling rates close to (for UP, PP, and PT) or at zero (for WL) when a partner's rope was unavailable, but normal pulling rates until success when the partner had access to the rope. The elephants thus demonstrated both a propensity to wait for partners before pulling in a cooperative task and recognition that success requires not only the partner's presence, but also its access to and handling of the rope. However, their behavior could still be explained in terms of a learned contingency related to the rope, specifically as it relates to feeling the rope tense when their partner grabs or pulls it.

Although PT regularly picked up and held the rope only after her partner was released (she did this in 95% of trials on the last 2 d of delayed release testing), thus suggesting her recognition that the partner at least caused the tension, all other elephants regularly held the rope—without pulling—until the partner arrived. Even so, in control trials, in which the partner's rope was out of reach, four elephants retreated (i.e., returned to the starting point without prompting and thus before being recalled by their mahout) either before or soon after (<15 s) their partners did in more trials than would be expected if these elephants were merely waiting for tension in the rope [observed values were PT: 100% of trials soon after, WL: 50% soon after, UP: 20% before and 30% soon after, and PP: 30% before and 60% soon after (see Table S3 for data)]. Expected values would be 0%, because one would expect the elephants to retreat only when recalled by their mahouts at the end of each trial. Thus, if these elephants had simply learned to pull the rope when it tensed, regardless of the partner's contribution, they should not have responded to their partner's retreat (or the partner's lack of rope access) by retreating themselves, and should have waited instead for their mahout's end-of-trial command. WL and UP retreated >15 s after their no-rope partners in 5/10 control trials, but both elephants progressed from a long latency to retreat in their first three control trials, to all short (soon after) latencies in their last three, suggesting they may have been learning during the no-rope control session about their partner's role.

It is important to note here that the ability of the elephants to learn the task contingencies as well as the role of their partners neither implies nor requires that they understood how the rope and the apparatus itself worked. Our experiment concerned itself entirely with the social aspect of cooperation. We would assume that if the elephants had an understanding of the workings of the apparatus, they would have always retreated as soon as they realized their partners did not have access to the rope. Their behavior would have then been independent of partner presence, because it would have been based solely on whether they could physically see if the partner's rope was available upon approach. Unfortunately, this was not testable in this experiment, nor to date has the acuity of elephant eyesight been given sufficient attention (46). Thus, the elephants' retreat immediately after their partner's hints at a learned contingency based on partner presence, i.e., without knowing why their partner was retreating, the elephants may have retreated solely because their partners did. This behavior, in conjunction with the aforementioned finding that pulling rates were zero or close to zero when the partner lacked rope access (and that one elephant never pulled in these control trials), suggests the elephants had learned—independent of our training—that the partner's presence and behavior mattered to complete the task.

The results of this experiment only concern 6 of the 12 elephants, and only the first elephant tested in each pair. Because of constraints at the elephant facility, we could only work with one pair at a time for 3 wk. To ensure that at least one individual per pair had sufficient time to learn the task, the second individual was not tested (i.e., released first in a trial) until the first elephant's testing was completed. Unfortunately, after testing the first individual in each pair, we were always left with insufficient time to test the second elephant under the three primary conditions, except for one (JO discussed below).

Alternative Strategies. It speaks to the flexibility of elephant behavior that two highly successful individuals could not be included in the pulling rate analysis because of their unconventional solutions to the task. One young elephant, NU, reached 97% success in test trials by approaching her rope end and firmly placing one foot on it, thus preventing the rope from being pulled away when her partner arrived and pulled. This technique had the advantage of forcing her partner to do all of the work to retrieve the table

(Movie S5). A seventh elephant, JO, reached 83% success on test trials, but did so by waiting for his partner's (WL) release at the release point rather than close to the table. There was thus no interval 1 for JO, precluding his inclusion in our pulling rate analysis. It also means that JO may have learned a different contingency between the partner's presence and success at the apparatus than the other focal elephants. The fact that three distinct strategies—(i) approach, wait, then pull ($n = 5$), (ii) stand on rope and wait ($n = 1$), and (iii) wait, approach, and then pull ($n = 1$)—were used by seven different subjects suggests a greater understanding of the partner's role in the task than might be suggested by a uniform learned task performance. If the elephants had all learned a mere contingency between a partner's presence at the apparatus and rope pulling for a reward, we would not have expected to see all of the following: (i) consistent inhibition of rope pulling when the partner was present at the apparatus but lacked rope access, (ii) three different strategies—including one that did not involve rope-pulling at all—following a uniform training procedure, and (iii) strikingly fast learning of multiple task contingencies across three different test and control conditions (Tables S1 and S2).

Because chimpanzees (*Pan troglodytes*) perform better in cooperation tasks when paired with tolerant partners (47), and bonobos (*P. paniscus*) perform better than chimpanzees overall (48), in part because of their sexual ways of resolving conflict (49), we attempted in a final set of “tolerance trials” to further assess cooperative tendencies by determining whether the degree of elephant cooperation varied with available food. In these simultaneous release trials, we varied whether one or both of the food bowls was baited and how much food was provided (see *Materials and Methods* for details). In all trials across all elephants in this condition, however, there was never a failed cooperation attempt or an incidence of aggression between both individuals. We never could be sure whether elephants would recognize before a trial began if food was available because of their general reliance on scent and sound over sight (24–27, 46, 50, 51).

We were also unable to pair potentially intolerant partners because of safety and husbandry concerns, but the absence of aggression suggests high tolerance between the selected individuals. Although open conflict is relatively common in chimpanzee groups (2), it is relatively rare among elephants (24–27), suggesting greater tolerance within the latter's social relationships. It is important to note that elephants never conspicuously vocalized or glanced at their partners during trials; elephants are considered sophisticated vocal communicators (24–27, 29, 50), but in this task, it is most likely elephants used other auditory and olfactory cues—especially the sound and smell of the partner's approach—to successfully coordinate their behavior. In addition, silent, waiting behavior is relatively common in wild elephants (51) and occurs most often when elephants are waiting for family members to arrive or “catch-up,” so the elephants' behavior in our task fits natural behavior.

In similar studies conducted on both nonprimates and primates, the animals' understanding of cooperation varied markedly. Rooks (*Corvus frugilegus*) pulled the cooperation apparatus' two rope ends as a pair when the ends were presented simultaneously (11, 52), but failed to wait for each other in the delayed release condition (11). Unlike in our study and that of Melis et al. on chimpanzees (7), the rooks were not given initial training in the delayed release condition. Instead, the birds were presented with a choice between two apparatuses (one that could be manipulated alone and another that required a partner's help but provided more food). The birds never successfully pulled in the latter apparatus when paired, and most of them did not prefer one apparatus over the other when released alone. In our no-rope control, which is a different way to measure what the animals have learned about the need for a partner, the elephants

failed to pull if their partner lacked access to the rope, and sometimes withdrew from the apparatus before or soon after the partner. Although our study provided training and the rook study did not, the elephants seem to have learned more about their partner's role than the rooks. Recent experiments with hyenas (*Crocuta crocuta*) (12) and capuchin monkeys (*Cebus apella*) (6) used variations on the cooperative pulling task and found that both species learned the need for a partner, but it was unclear whether they understood their partners' behavioral contribution. Chimpanzees, on the other hand, have demonstrated clear knowledge of both a partner's role and contribution (5, 7, 47, 48). Our own study shows that elephants not only (i) cooperate successfully in a coordinated pulling task but also (ii) recognize the need for a partner by waiting if the partner is delayed. Elephants perhaps also (iii) recognize the necessity of their partner's actions, given that they discriminate between a partner with or without rope access. As with humans and other primates, it is hard to draw a line between learning and understanding, however. The least we can conclude is that the elephants demonstrated cooperative behavior in this experiment with attention to their partner's presence and actions, thus showing a well-developed propensity toward partner-oriented, deliberate cooperation. These results put elephants, at least in terms of how quickly they learn the critical contingencies of cooperation, on a par with apes.

Materials and Methods

Elephants. The study included four female-female pairs, one male-female pair, and one male-male pair (12 elephants, six unique pairings—see Table S1 for demographics). As far as the TECC records indicate, none of the 12 elephants were related to one another. We selected pairs based on their docility and the quality of the elephants' relationships, as dictated by the mahouts. We did not have an adequate sample size to compare an equal number of same-sex and different-sex pairings in this study, but this type of comparison would be more relevant in studies that focus specifically on tolerance. Four of these animals (KW, PT, WL, and AL) were born at the TECC and the rest were "rescued" elephants gifted by other government agencies or private donors. By regulation, all of these animals will spend the rest of their lives at the TECC.

All of the study elephants were highly trained and performed in daily shows for visitors and tourists, including a demonstration of traditional logging techniques, painting, and making music. All training and work is humane and under the supervision of experts, including two of the authors (R.L. and W.S.). KW and SS were trained to coordinate log-carrying as a pair, but only with their mounted mahouts giving constant commands (no other elephants in this experiment had such previous training). None of these elephants had ever been trained for work similar to the task in this study, nor had the elephants ever been given an opportunity to transfer their training to a novel task without additional training.

General Setup of the Experimental Apparatus. The table apparatus was comprised of two pieces of plywood painted and bolted to a rectangular PVC pipe frame 3.3 m wide and 1.2 m deep. The table was placed 4 m beyond two trees, and three wooden planks set in the ground ensured smooth movement of the table. A 7-m-wide volleyball net was strung between the two trees, anchored by two strong, taut wire ropes, forming a transparent but impassable barrier between the elephants and the table. In training trials, a single piece of rope, ≈ 6 m in length, was clipped to the front of the table and fed through a metal ring set in the ground beneath the net. Elephants could approach this rope and pull, drawing the table toward them. A wooden post embedded in the ground (replete with rubber shock absorber made from old tires) served as a stopper that prevented the table from advancing past the net. To keep the table centered as it was pulled in, a ≈ 2.5 -cm-thick wire rope—running perpendicular to the volleyball net—was strung from the buried table stopper, through the central PVC pipe of the table's frame, and then fixed to a tree on the central axis beyond the table. This rigid guide cable prevented any skewing of the table and thus eliminated incongruities in food availability. Two red food bowls were attached to wooden boards, 50 cm in length, one on each side of the table; as the table reached the stop point, the two bowls became available to the elephant just under the net. In test trials, a single piece of 16.5-m-long, 1-cm-thick hemp rope was threaded through guides and around the back and two

sides of the PVC frame so that the loose ends appeared out of two openings on either side of the front of the table. Each side's rope end was then threaded through a metal ring set in the ground underneath the net, leaving 1.6 m of rope available to each elephant upon approach.

To demarcate the test area, from each of the two central trees was strung a single, flagged green rope ≈ 1.5 m above the ground and reaching back 10 m behind the net to the release point. During testing and control trials, a third flagged rope was strung down the center of the test area, dividing it into two equally wide lanes (3.5 m); thus, each elephant was released into a single lane and had access only to a single rope end. These two lanes are similar to the separation between subjects in some previous studies (6), but not others, in which subjects were allowed to move around (e.g., refs. 5, 7, and 11). Because of the sheer size of the elephants and their regular, free-contact interaction with the experimenters and mahouts between trials, these lanes were necessary for safety reasons, whereas they did not prevent the elephants from reaching over to their partner or their partner's food bowl. The lanes did not seem to compromise the elephant's ability to learn the experimental task contingencies.

All data were coded from two video cameras. A Panasonic PV-GS500 miniDV camera was fixed to a metal mount on a 7-m-long bamboo ladder, which was hoisted on pulleys between the two trees to a height ≈ 8 m above the ground. This camera's view was monitored on the ground via closed-circuit television. A second camera, a Canon HV20, was placed on a tripod beyond the table, providing a heads-on view of the elephants.

Procedure. In training trials, a mahout would walk with his elephant to the single available rope end and train his animal to pick up and pull the rope by using vocal commands. Rope-pulling strategies were ultimately at the discretion of the elephant, but all elephants had earlier, as part of the facility's routine, been trained to pull chains. In testing trials, the two mahouts stood at the release point with their elephants and restrained them by touching the ear or front leg. When signaled by the experimenters—who were positioned 10 m to the side and back from the setup—elephants were released down their respective lanes. Upon release, mahouts turned away from the elephants and remained silent to minimize chances for cuing, and in position behind the elephants for safety. Trials began when the mahouts gave release commands—they released their hold on the elephant and gave a single word, "go" command once so that it was up to the elephant whether to proceed—and ended when the rope became unthreaded from the drawer, or when all of the food had been eaten (at which point a simple "stop" command was given by the experimenters and the elephants were recalled). During simultaneous and delayed release trials, each of the two food bowls on the table contained two halves of a full ear of corn, a highly desirable but rarely used food reward at the elephant facility. During the final tolerance condition, two trials each of the following were randomized over six trials: (i) each bowl was baited as in test trials, with two half-ears of corn, (ii) one (or the other) bowl was baited with six half-ears of corn. In between all trials, mahouts gave elephants pieces of banana and sugarcane to ensure they remained relaxed. Commands were never given during trials, and mahouts were cued to release their elephants with a hand signal that was not visible to the subjects. The interval between trials was 30 s, and elephant pairs never received >30 trials a day. Testing occurred between January and May 2009. Depending on prior obligations at the facility, elephants were tested in the early morning or early afternoon and were often hosed down with water on exceptionally hot days.

Data Coding. All coding was done from tape from the bird's-eye video camera and supplemented with the ground video footage when appropriate. Each trial was divided into two time intervals as described in *Results and Discussion*. Although elephants used multiple pulling techniques, a pull always involved initially grasping the rope with the trunk and moving the trunk toward the body (some elephants kept the rope end in their mouths while doing this, whereas others grasped the end itself in their trunks). Other techniques that did not involve active pulling could not be coded. Any trials where there was either no interval 1 or 2 were excluded from statistical analyses—regardless of whether they were successful—because they precluded an unbiased comparison of pulling rates within the given trial. SS's *P* value in the pull vs. no-pull sign test analysis is calculated from a binomial distribution (and lacks a sign test *z* value) because of a small number ($n < 35$) of trials in which SS either pulled in interval 1 or 2 but not both (53). For analysis of control trials, a K-S test was chosen over a rank-order non-parametric statistic because of the uniformity of each sample and, thus, the large number of tied scores. J.M.P. coded all sessions, whereas J. Hua coded a randomly selected 20% of trials for interrater reliability.

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