INTERNATIONAL JOURNAL OF COMPARATIVE PSYCHOLOGY

2025, 38
Charles I. Abramson
Editor
Peer-reviewed

Performance of African Bush Elephants (*Loxodonta africana*) on a Cooperative Task

Kaitlyn Willgohs[1*], Kayla Fulkerson[1], Kristina Przystawik[2], Christi Reiter[2], Mike Burns[2], Madeline Ketner[1], & Lauren Highfill[1*]

[1] Eckerd College, St. Petersburg, FL, 4200 54th Avenue S, St. Petersburg, FL 33711

[2] ZooTampa at Lowry Park, Tampa, FL, 1101 W Sligh Ave, Tampa, FL 33604

Several species have demonstrated the ability to cooperate with conspecifics in a lab or zoological setting. The present study sought to replicate previous research (Plotnik et al., 2011) in which pairs of Asian elephants (*Elephas maximus*) had to simultaneously pull on the ends of a rope in order to bring food rewards within reach. The initial study was conducted in a free-contact setting with Asian elephants, whereas the present study was conducted under a protected-contact management program with ZooTampa at Lowry Park's herd of six African bush elephants (*Loxodonta africana*). Trials were deemed successful if the sled was pulled to a distance where both elephants were able to access food that was resting on the sled. Overall, 15 different pairings were tested on the rope-pulling cooperative task while released simultaneously (non-delayed trials). All but one pairing quickly learned that a form of cooperation was necessary to complete the task successfully ($p < .05$). After non-delayed trials were complete, trials were run with a five-second delay interval for one of the two elephants to assess the elephants' understanding of the role of a partner in the cooperative task (delayed trials). Four elephants were faced with the decision of waiting for their partner to arrive before pulling their end of the rope, of which two juvenile elephants successfully waited for their partner. This study contributes to the literature of cognition across the elephant taxon.

Keywords: elephant, cognition, cooperation, zoo, enrichment

アフリカゾウ(Loxodonta africana)の協力課題におけるパフォーマンス

いくつかの種において、実験室や動物園の環境で同種個体と協力する能力が実証されてきた。本研究は、アジアゾウ（Elephas maximus）のペアが、餌の報酬を手に入れられる位置まで運ぶために、同時にロープの両端を引く必要があった先行研究（Plotnik et al., 2011）を再現しようと試みたものである。先行研究は、アジアゾウを対象にフリーコンタクト（直接飼育）の環境で行われたのに対して、本研究は、ロウリーパークにあるZooTampaの6頭のアフリカゾウ（Loxodonta africana）の群れを対象に、プロテクテッド・コンタクト（間接飼育）という管理プログラムの下で実施した。各試行は、2 頭のゾウ両方がそりの上のエサに届く距離までそりを引くことができた場合に成功とみなされた。全体として、このロープ引きの協力課題では、15 通りの異なるペアが、同時に放たれる条件下（非遅延試行）でテストされた。1 組を除くすべてのペアは、課題を成功させるためには協力することが必要であることを素早く学習した（$p < .05$）。非遅延試行が完了した後、ゾウたちが協力課題におけるパートナーの役割を理解しているかを評価するため、ペアの一方に対して5秒の遅延を設けた試行（遅延試行）を実施した。4頭のゾウは、ロープを引く前にパートナーが到着するのを待つかどうかの決断を求められ、そのうち 2 頭の若いゾウは、パートナーが来るまで待つことに成功した。この研究は、ゾウという分類群における認知に関する学術文献に貢献するものである。

キーワード：ゾウ、認知、協力、動物園、エンリッチメント

Please send correspondence to Kaitlyn Willgohs (email: kaitlyn.willgohs@gmail.com) and Lauren Highfill (email: highfiLE@eckerd.edu)

Desempeño en una tarea cooperativa de elefantes africanos de sabana (*Loxodonta africana*)

Diversas especies han demostrado capacidad para cooperar con conespecíficos en entornos controlados, como laboratorios o zoológicos. El presente estudio tuvo como objetivo replicar investigaciones previas (Plotnik et al., 2011), en las que parejas de elefantes asiáticos (*Elephas maximus*) debían tirar simultáneamente de los extremos de una cuerda para obtener recompensas alimenticias. El estudio inicial se realizó en un entorno de contacto libre con elefantes asiáticos, mientras que el presente estudio se realizó bajo un programa contacto protegido del ZooTampa con una manada de seis elefantes africanos de sabana (*Loxodonta africana)* del Parque Lowry. Las pruebas se consideraron exitosas si el trineo se tiraba a una distancia donde ambos elefantes podían acceder a la comida que descansaba sobre él. En total, se evaluaron 15 pareamientos diferentes en la tarea cooperativa de tirar de la cuerda mientras eran liberadas simultáneamente (pruebas sin demora). Todas las parejas, excepto una, aprendieron rápidamente que era necesaria alguna forma de cooperación para completar la tarea con éxito ($p < 0,05$). Tras completar los ensayos sin demora, se realizaron ensayos con un intervalo de cinco segundos de demora para uno de los dos elefantes a fin de evaluar su comprensión del rol de un compañero en la tarea cooperativa (ensayos con demora). Cuatro elefantes se enfrentaron a la decisión de esperar a que llegara su compañero antes de tirar de la cuerda, de los cuales dos elefantes jóvenes esperaron exitosamente. Este estudio contribuye a la literatura sobre cognición en el taxón de elefantes.

Palabras clave: elefante, cognición, cooperación, zoológico, enriquecimiento

Evolution of Elephant Species

Examining the phylogenetic family tree of elephants, Asian (*Elephas maximus*) and African elephant (*Loxodonta spp.*) ancestors diverged from a common ancestor, *Primelephas*, during the Pliocene approximately five million years ago (Maglio, 1973). Asian elephants and wooly mammoths (*Mammuthus primigenius*) evolved in one direction, while African elephants evolved in another (Maglio, 1973; Shoshani, 2006). It was not until very recently in 2021 that the International Union for Conservation of Nature (IUCN) recognized two distinct species of African elephants—the African bush elephants (*L. africana*) and African forest elephants (*L, cyclotis*)—despite the fact that these two species diverged approximately two million years ago (Comstock et al., 2002; Eggert et al., 2002; Gobush et al., 2021a, 2021b; Grubb et al., 2000; Roca et al., 2001). Therefore, it is evident we are just breaching the surface of understanding the evolution of cognition in the elephant taxon.

The three extant elephant species are anatomically *similar*—the elephant taxon possesses the largest brains of any terrestrial organism (Hart et al., 2008; Shoshani et al., 2006). Despite inhabiting different ecosystems, the three species exhibit similar behaviors, such as feeding on herbivore diets and living in matriarchal fission-fusion societies populated by adult females and calves while adult males reside in bachelor herds (Archie et al., 2011; Bates et al., 2008a; de Silva & Wittemyer, 2012; Fishlock et al., 2008; Fishlock & Lee, 2013; Lee & Moss, 2012; McComb et al., 2001; McComb et al., 2011; Pool & Granli, 2009; Schulte, 2000; Schuttler et al., 2014; Sukumar, 2006; Wittemyer et al., 2009). Furthermore, the three species face similar anthropogenic challenges, such as poaching for the ivory in their tusks and human-elephant conflict caused by habitat degradation (Campbell-Staton et al., 2021; Chiyo et al., 2012; Compaore et al., 2020; Gobush et al., 2021a, 2021b; Hauenstein et al., 2022; LaDue et al., 2021a, 2021b; Maisels et al., 2013; Mumby & Plotnik, 2018; Riddle et al., 2010; Sitati et al., 2005; Srikrachang & Srikosamatara, 2005; Williams et al., 2020).

Studies of Elephant Cognition

Previous experimental investigations into the cognition of the elephant taxon have often been conducted on Asian elephants (Plotnik & Jacobson, 2022). As a result, we know that Asian elephants possess the capacity for insightful problem-solving (Barrett & Benson-Amram, 2020; Foerder et al., 2011; Hart et al., 2001; Hart & Hart, 1994), innovative problem-solving (Jacobson et al., 2021, 2023), social learning (Barrett & Benson-Amram, 2020), associative learning (Nissani, 2006), spatial memory (Jacobson et al., 2023), behavioral flexibility (Foerder et al., 2011), causality (Mizuno et al., 2016), and cooperation (Li et al., 2021; Plotnik et al., 2011). Related to sensory perception, we know that Asian elephants possess exceptional olfactory discrimination (Arvidsson et al., 2012; Plotnik et al., 2013, 2014, 2019; Polla et al., 2018; Rizvanovic et al., 2013) as well as the ability to discriminate between visual stimuli (Markowitz et al., 1975; Nissani et al., 2005; Polla et al., 2018; Rensch, 1956). Furthermore, Asian elephants have demonstrated abilities believed to be associated with higher-order thinking such as mirror self-recognition (Plotnik et al., 2006, 2010), targeted help (Plotnik & de Waal, 2014), theory of mind (Nissani, 2004), and the ability to recognize themselves as an obstacle to completing a novel task (Dale & Plotnik, 2017).

In contrast, less is known about the cognitive abilities of the African elephant species. We know that they possess exceptional social memory (Bates et al., 2008c; Hoerner et al., 2023; Hörner et al., 2021; McComb et al., 2000, 2001) and spatial memory (Dale, 2008; de Knegt et al., 2011; Moss, 1992; Polansky et al., 2015; Tsalyuk et al., 2019), in addition to olfactory (Bates et al., 2007; Perret, 2017; von Dürckheim et al., 2018), visual (Bates et al., 2007; Smet & Byrne, 2013, 2014), and auditory (McComb et al., 2000, 2001, 2014) discrimination abilities. Furthermore, African elephants have demonstrated the capacity for social (Greco et al., 2013) and vocal learning (Poole et al., 2005).

In the grand scheme of elephant cognition, it is relatively unknown whether cognitive capacities are shared across the elephant taxon. However, a recent comparison of post-mortem Asian and African bush elephant brains found structural differences that could explain variations in cognitive abilities between the species (Shah et al., 2025). Despite their smaller body size, female Asian elephants possess heavier brains and greater cerebral gray matter volume than their African counterparts, suggesting a higher degree of encephalization (Shah et al., 2025). This may be because Asian elephants have an extensive history of human interaction and self-domestication, however further research is warranted (Shah et al., 2025). In contrast, African bush elephants exhibit a relatively larger cerebellum, which could suggest differences in trunk function and sensory processing between species (Shah et al., 2025).

Few studies have attempted to empirically compare the cognitive abilities of the elephant species. When replicating the methodologies of Irie-Sugimoto et al. (2008), Highfill et al. (2016, 2018) found that African bush elephants performed similarly to Asian elephants on means-end tasks that increased in difficulty, suggesting that the two species share similar logic and reasoning abilities as it relates to accessing a food reward. Both the Asian and African bush elephant adults performed successfully at the first two conditions, but neither performed successfully on the third condition, suggesting that the adult elephants were not able to comprehend the concept of connectedness. Contrarily, Highfill et al. (2018) found that juvenile elephants performed successfully across all three conditions, suggesting that younger elephants may be more cognitively flexible than older elephants. These findings align with the results of Irie-Sugimoto et al. (2008), which investigated means-end problem solving in two juvenile Asian elephants and found that the younger of the elephants performed successfully across all conditions. Researchers note that because the third condition contrasted the connectedness of objects that elephants often encounter in their natural habitats (e.g., pulling on branches attached to trees to access leaves), it may have been more challenging for developed elephant brains to comprehend (Highfill et al., 2016, 2018).

Moreover, researchers have observed explicit differences in the cognitive abilities of African and Asian elephants. For example, researchers have explored whether elephants are able to use human social cues to locate food hidden in one of two buckets (Ketchaisri et al., 2019; Plotnik et al., 2013; Smet & Byrne, 2013, 2014). Smet and Byrne (2013, 2014) found evidence that African bush elephants are able to follow human pointing cues to locate hidden food, even when the pointing cues are subtle. Furthermore, Smet and Byrne (2014) found that the elephants were able to generalize the cue when other human body parts (i.e., feet) were used to point toward the hidden food. Contrarily, researchers have not been able to observe the same abilities in Asian elephants. Plotnik et al. (2013) found that Asian elephants used human vocal commands but not pointing cues to locate hidden food. Ketchairsi et al. (2019) later replicated the aims of Plotnik et al. (2013) and found that Asian elephants were able to follow human pointing cues when the experimenter was in close proximity to the correct bucket; therefore, this suggests that Asian elephants might rely on local enhancement rather than human social cues.

Furthermore, some studies have produced conflicting results for cognitive abilities within elephant species (Agrillo & Miletto Petrazzini, 2012). For example, several studies have investigated whether Asian and African elephants can discriminate between quantities in two containers using various sensory cues (Irie-Sugimoto et al., 2009; Irie et al., 2019; Perdue et al., 2012; Plotnik et al., 2019; Snyder et al., 2021). Perdue et al. (2012) examined the performance of zoo-housed African bush elephants on this task, finding that they successfully selected the greater quantity of food above chance in both conditions using visual and auditory cues. Additionally, Perdue et al. (2012) found magnitude effects, such that as the ratio between the two quantities increased, the elephants' ability to discriminate between them decreased. When replicating this methodology with zoo-housed Asian elephants, Snyder et al. (2021) found that, similar to their African bush elephant counterparts, Asian elephants also chose the greater quantity of food significantly above chance using visual and auditory cues. Furthermore, Snyder et al. (2021) also found magnitude effects present in the quantity discrimination abilities of Asian elephants. Similarly, Plotnik et al. (2019) found that elephants could use isolated olfactory cues to discriminate between quantities and observed that as the ratio between the two quantities increased, the elephants' ability to discriminate between them decreased, consistent with magnitude effects. However, the results of these studies contrast the results of a previous study of Asian elephant quantity judgment (Irie-Sugimoto et al., 2009), which found that Asian elephants did not exhibit magnitude effects when presented with two different quantities. Given the limited sample sizes of these studies, a plausible explanation for these results could be that there is individual variation (Hertel et al., 2020; Jacobson et al., 2023) in elephant behavior and cognition, which can be influenced by factors such as personality and previous experiences; therefore, further research is warranted (Agrillo & Miletto Petrazzini, 2012; Perdue et al., 2012; Snyder et al., 2021).

Researchers argue for the replication of methodologies across the elephant taxon and within individual elephant species to increase our understanding of the overall cognitive abilities of elephants (Agrillo & Miletto Petrazzini, 2012; Highfill et al., 2016, 2018; Perdue et al., 2012; Snyder et al., 2021). Furthermore, comparing and contrasting the cognitive abilities of the three elephant species can provide insight into how characteristics have persisted through the evolution of species in different environments and contribute to our understanding of selective pressures on behavior (Bates et al., 2008b; Plotnik & Clayton, 2015).

The present study seeks to investigate whether the ability to understand the role of a partner in a cooperative task is shared across the elephant taxon. While Plotnik et al. (2011) has previously demonstrated this ability in Asian elephants, the present study examines the performance of African bush elephants on a cooperative task.

Present Study

The present study is a systematic replication of Plotnik et al. (2011)'s investigation of elephant cooperation which demonstrated that Asian elephants could understand the role of a partner in a cooperative task. Plotnik et al. (2011) presented elephant pairs with an out-of-reach wooden sled that contained a food reward; to pull the sled within reach, the elephants needed to simultaneously pull each end of a rope that was woven through the sled. The elephants successfully performed the cooperative task when released simultaneously (*non-delayed condition*). Moreover, when the release of their partner was delayed (*delayed condition*)—with the delay interval ranging from one to 45 seconds—the elephants inhibited their pulling response until their partner was released and also arrived at the rope (Plotnik et al., 2011). Additionally, when their partner lacked access to the rope (*no-rope control*), the elephants did not even attempt to pull their end of the rope, suggesting that they understood that they would not be able to complete the task without their partner (Plotnik et al., 2011). The present study adopts a similar methodology by testing African bush elephants under non-delayed and delayed conditions, and seeks to determine whether African bush elephants possess the same ability to understand the role of a partner in a cooperative task as their Asian elephant counterparts.

We hypothesized that the cognitive abilities of the African bush elephant species closely resemble those of the Asian elephant, yet, as demonstrated above, we also acknowledge that there are potential deviations. However, based on observational knowledge of wild African bush elephants, we hypothesized that zoo-housed African bush elephants will be able to comprehend the cooperation paradigm. Cooperation is often observed in herds of wild African bush elephants in the form of allomothering (Lee, 1987; Lee & Moss, 1999; Poole & Granli, 2009; Rapaport & Haight, 1987; Schulte, 2000; Vidya, 2014), as well as locating food/water sources and defending the herd against predators (McComb et al., 2011; Schulte, 2000). Furthermore, previous experimental investigations of cognition in wild African bush elephants suggest that they possess highly intelligent social abilities, such that they can recognize up to 30 family members and their respective locations (Bates et al., 2008c). Therefore, we hypothesized that African bush elephants will perform successfully in the cooperative task, similar to their Asian elephant counterparts. Furthermore, we aim that the present study provides insight into the evolution of cognitive abilities across the elephant taxon.

Method

Ethics Statement

ZooTampa at Lowry Park (ZT), located in Tampa, Florida, USA, is accredited by the Association of Zoos and Aquariums (AZA) and meets the highest standards for animal care and welfare. All research met humane standards and was approved by the ZT research committee (ZT.AB.2.00).

Subjects

In partnership with ZT, the cooperation study was performed on a herd of six (1 male, 5 females) African bush elephants (*Loxodonta africana*) (Table 1; Figure 1). The four adult elephants were wild-born and arrived at ZT in 2003. Specifically, Ellie (E) was born in Namibia before being housed at a number of American zoos prior to joining the ZT herd in 2003. Matjeka (MT), Mbali (MB), and Sdudla (S) were born in South Africa, later transferred to Swaziland, before arriving at ZT in 2003. The two calves, Mavi (MV) and Mpumi (MP) were both born at ZT to mothers MT and MB, respectively, and were both sired by S.

Table 1

Elephant Demographic Information

Elephant	Sex	Age (*years*)	Abbreviation
Sdudla	M	24–28	S
Ellie	F	34–38	E
Matjeka	F	23–27	MT
Mbali	F	24–28	MB
Mavi	F	4–8 (MT/S)	MV
Mpumi	F	4.5–9 (MB/S)	MP

Note. The present study was conducted between June 2017 and November 2021, thus, we have provided the age ranges of the elephants over the course of the study, respectively.

Figure 1

Five Out of Six Members of the ZooTampa African Bush Elephant Herd (Left to Right: Mpumi, Sdudla, Mavi, Matjeka, Mbali). Photo Credit: ZooTampa at Lowry Park

It is important to state the unique hierarchy of the ZT herd; while most elephant herds have a matriarchal hierarchy, as stated in the introduction, the ZT herd has a cyclical hierarchy. E is dominant over MT, MT is dominant over MB, and MB is dominant over E. The calves, MV and MP, have yet to fall in the hierarchy. As an adult male, S also does not fall into the hierarchy. This cyclical hierarchy was determined by zookeepers, hereafter referred to as keepers, based on observations of displacement and aggression, and it has remained stable over time.

For most of their day, the animals socialize as a herd in their outside exhibit areas (two large elephant yards) with free access to food and water. The elephants at ZT are managed using positive reinforcement operant conditioning in a protected-contact management program. The elephants are trained to participate in husbandry and veterinary care, of which they continued while research was being conducted.

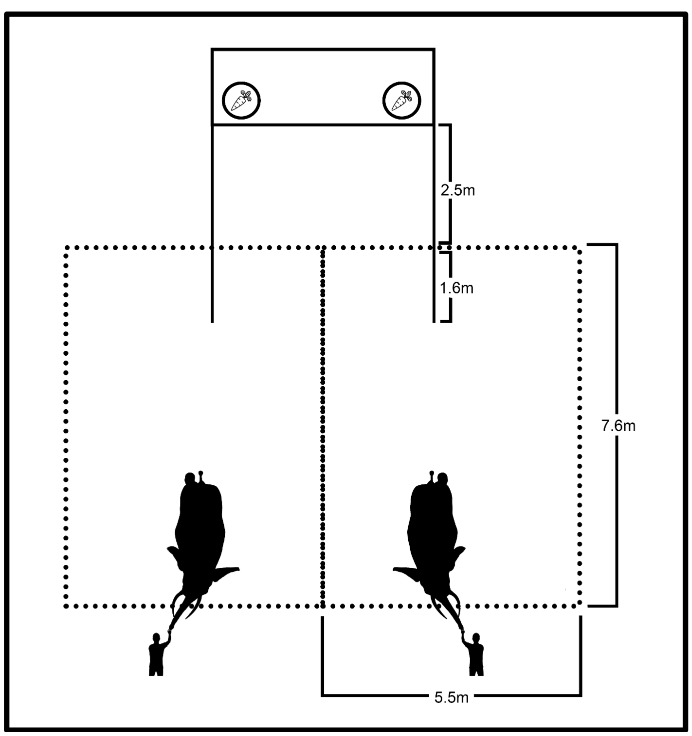
Experimental Set-Up

The cooperation apparatus utilizes a rope-pulling paradigm, in which a rope is threaded through a wooden sled that contains two out-of-reach food rewards. In order to reach the food rewards, each end of the rope must be pulled simultaneously to move the sled forward and bring the food rewards within reach. The rope-pulling paradigm has been employed in a number of studies investigating cooperation in primate species (Chalmeau, 1994; Chalmeau & Gallo, 1996; Chalmeau et al., 1997a; Chalmeau et al., 1997b; Hirata & Fuwa, 2007; Jaeggi et al., 2010; Kappeler & Van Schaik, 2006; Kopsch & Geissman, 2023; Martin et al., 2021; Melis et al., 2006; Suchak et al., 2017). Furthermore, this paradigm has also been adapted to investigate cooperation in other taxons, most commonly in birds (Péron et al., 2011; Seed et al., 2008; Torres Ortiz et al,. 2020) and cetaceans (Bagley et al., 2020; Eskelinen et al., 2016; Jaakkola et al., 2018; Jaakkola et al., 2021; King et al., 2021; Kuczaj et al., 2015; Meier, 2023; Yamamoto et al., 2019), but also in canines (Marshall-Pescini et al., 2018; Martínez et al., 2023; Range et al., 2019a, 2019b), lions (Borrego, 2020), and otters (Schmelz et al., 2017).

The cooperation apparatus used in the present study was built out of wood (2.5 m × 2.3 m × 1 m). Two plastic PVC pipes were installed on the underside of the sled to thread the 10.75m rope through. Two bowls (0.5 m diameter) were baited with food and placed on each end of the sled. The baited sled was located 2.5m outside of the stalls, with 1.6 m of rope located inside of each stall for the elephants to pull, respectively (see Figure 2). All trials took place in the elephant husbandry barn at ZT. The barn is where members of the herd frequently have training sessions with their keepers through a husbandry gate. Testing was conducted in two identical elephant stalls, with one elephant located in stall two (5.5 m × 7.6 m) and the other elephant located in stall three (5.5 m × 7.6 m). The elephants had to travel approximately 6m (including turning their bodies around) to reach the rope.

Figure 2

Sketch of Experimental Set-up



Training Procedure

Prior to the cooperative task, the elephants had never been exposed to a rope. To familiarize the elephants with a rope, keepers threaded a rope through a large boomer ball that was stuffed with food. Keepers then placed the boomer ball 2.5 m outside of the stall (out of reach from the elephants), with 1.6 m of rope placed inside of the elephant stall. Thus, to successfully complete the task, the elephants needed to pick up the rope in their stall and use it to pull the boomer ball within reach.

The elephants tended to be neophobic toward the rope at their first exposure, but quickly grasped the concept by their second exposure (Table 2). Overall, each elephant was exposed to the boomer ball task five times and continued to quickly approach and pull the rope in subsequent exposures. All elephants were able to demonstrate successful rope pulling abilities with the boomer balls; thus, the elephants demonstrated an understanding of rope pulling which was necessary to complete the cooperation task.

Table 2

Boomer Ball Latencies (in Seconds)

Elephant	Exposure #	Latency to Approach Rope	Latency to Pull Rope
	1	36	3
MV	2	9	1
	1	219	6
MP	2	12	4
	1	110	9
E	2	9	5
	1	6	18
MT	2	5	9
	1	60	10
MB	2	5	5
	1	14	8
S	2	5	2

Note. Latency to approach rope refers to how long it took the elephant to pick up the rope while latency to pull rope refers to how long it took the elephant to move the boomer ball (beginning the moment they picked up the rope and ending once the boomer ball was within reach).

Experimental Procedure

Elephant pairings were tested in both non-delayed (simultaneous) and delayed conditions. For the non-delayed trials, all elephants were paired with one another to perform the cooperative task, creating 15 unique combinations. Due to time limitations, only seven pairings were tested under the delayed condition. Pairings were chosen based on suggestions from keepers, as the act of a delay—asking one elephant to wait—created an opportunity for aggression, therefore, keepers suggested pairings with the least likelihood of aggression based on social hierarchy.

For the non-delayed experimental trial condition, elephants were tested across three sessions of ten trials each for a total of 30 non-delayed trials. For the delayed experimental trial condition, elephants were tested across four sessions. To randomize the delayed release in each of the four delayed trial sessions, five of the ten trials were delayed while the other five were non-delayed. This randomization was predetermined to ensure that elephants could not rely on a consistent pattern and instead had to attend to the specific trial context—demonstrating flexible behavioral strategies within a session. Importantly, these intermittent non-delayed trials from the delayed condition were not combined with the earlier non-delayed trials for analysis purposes and were excluded from statistical analyses of the non-delayed experimental trial condition. Overall, the elephants were tested for a total 20 delayed trials across four delayed sessions. Ideally, we would have liked to test the elephants for a total of 30 delayed trials (as we did during the non-delayed trial condition), however, doing so would have required a total of six sessions because of the randomization component. Given limited time and resources, that was not feasible. Overall, the criterion for success of an average success rate of > 70% remained the same between both non-delayed and delayed trial types.

The time between successive sessions within a pairing was dependent on the schedule of the animal care management team (see Table 3 for length of time between trial sessions). The time between non-delayed trials ranged between 1–145 days (mean = 21 days), while the time between delayed trials ranged between 1–204 days (mean = 14 days). The length of time between the end of non-delayed trials and beginning of delayed trials ranged from 67–1116 days (mean = 596 days). Non-delayed trials ran between June 2017 through July 2020. Delayed trials ran between September 2020 and November 2021. The varying lengths of time between successive sessions did not have a significant impact on performance (Pearson correlation coefficient—non-delayed trials: $r(20) = -.99$, $p = .33$; delayed trials: $r(19) = .43$; $p = .68$).

Table 3

Time Between Successive Trial Sessions in Days

Pairing	**Non-Delayed**		**Non-Delayed → Delayed**	**Delayed**		
	ND1 → ND2	***ND2 → ND3***		***D1 → D2***	***D2 → D3***	***D3 → D4***
MP-E	4	1	488	1	6	2
MP-S	4	3	67	3	4	3
MV-MP	4	9	940	204	2	2
MV-MT	8	4	1042	3	1	1
S-MB	44	2	-	-	-	-
S-MT	9	26	1116	6	13	1
S-MV	3	4	80	4	7	14
E-MT	28	38	-	-	-	-
E-MV	54	95	438	3	4	7
E-S	12	8	-	-	-	-
MB-MP	10	37	-	-	-	-
MB-MV	3	4	-	-	-	-
MT-MB	7	21	-	-	-	-
MT-MP	145	2	-	-	-	-

Note. Each non-delayed (ND) session was made up of ten non-delayed trials, therefore, session 1 was made up of non-delayed trials 1–10; session 2 was made up of non-delayed trials 11–20; and session 3 was made up of non-delayed trials 21–30. Each delayed (D) session was made up of five delayed trials and five non-delayed trials to randomize delayed release, therefore, session 1 was made up of delayed trials 1–5; session 2 was made up of delayed trials 6–10; session 3 was made up of delayed trials 11–15; and session 4 was made up of delayed trials 16–20.

To set up for a trial, the elephant pairing would be split up into two side-by-side stalls in the husbandry barn. Elephants were bridged and food-rewarded by keepers when shifting into the holding areas prior to the start of each trial. Outside of the stalls, a sled was baited with produce which consisted of a variety of fruits and vegetables known by keepers to be highly palatable and consistently consumed by all elephants (see Figure 3); however, formal preference testing was not conducted. A rope was woven under the sled and each end was placed in one of the side-by-side stalls (see Figure 4). For each trial, two trainers would stand behind a protective barrier at the far end of each stall where their respective elephants were located. Once all parties were ready for the trial, the keepers would ‘release’ the elephants using the verbal cue “go.” It is important to note that the “go” only released the elephants from the keeper’s station; the “go” cue was not paired with the rope-pulling behavior. Once the “go” cue was given, keepers turned away and moved toward the back wall of the stall area, where they remained quiet. Once released, it was the elephant’s choice whether or not they wanted to approach the rope. Ropes were not cleaned between elephants or sessions due to logistical constraints; we acknowledge this as a limitation and recognize the potential influence of olfactory cues in future replications.

Figure 3

Aerial View of Trial Setup. Photo Credit: ZooTampa at Lowry Park

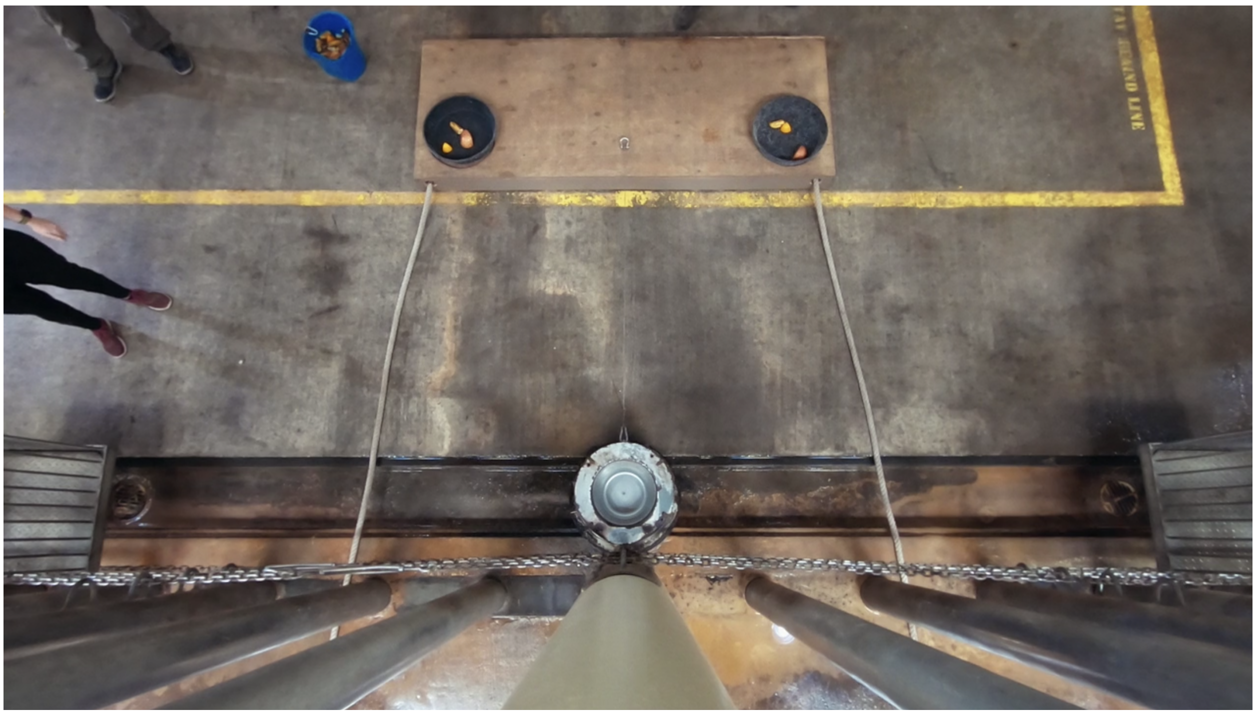
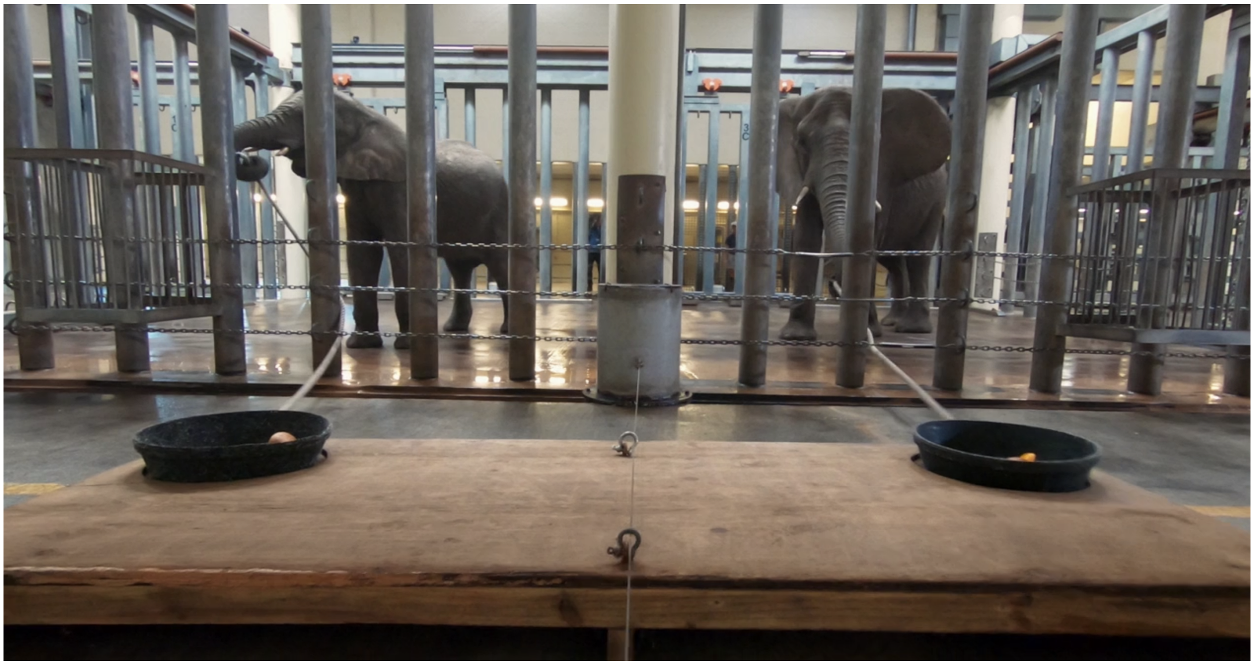


Figure 4

Front/ground View of Trial Setup. Photo Credit: ZooTampa at Lowry Park



To participate in the cooperative task, the elephants had to make their way to the opposite side of the stall where the rope was laying on the ground. If only one elephant pulled the rope, or they pulled at the wrong time, the rope would unravel and the sled would not move. When the sled was pulled as desired, it would move closer, allowing the elephants to access the food rewards. Trials were deemed successful if the sled was pulled to a distance where both elephants were able to access the food. Trials were deemed a failure if there was any other outcome and elephants were not food rewarded. Trials were filmed from the front by either a researcher or ZT staff member using an iPad, beginning a couple of seconds before the keepers released the elephants, and ending once the cooperative task was accomplished or it was clear that it would not be completed at all (i.e., when one elephant pulled the rope through, unthreading the rope from the sled, making the cooperative task impossible to complete).

The only difference in methodology between the non-delayed and delayed trials was the release of the elephants. For the non-delayed trials, both elephants were released simultaneously. During the delay trials, one elephant (predetermined by keepers to minimize the likelihood of aggression based on social hierarchy) was released, then, after a five-second delay interval, the other elephant was released. Although the five-second delay interval was decided upon based on Plotnik et al. (2011)'s methodology, following the completion of the non-delayed trials, we calculated the latencies for the time it took each of the elephants to arrive at the rope once they were released. This calculation was important to ensure that during the delayed trials, a five-second delay interval would allow for the elephant released first to arrive at the rope prior to the 'release' of their partner and require that they decide whether to wait for their partner to arrive before pulling their end of the rope, providing insight into if the elephant understands the role of a partner in the cooperative task. The average latencies for all six elephants were under five seconds (MV = 3.64 s; MP = 3.04 s; E = 4.62 s; MT = 3.33 s; MB = 3.18 s; S = 4.29 s).

It is important to note that not all pairings were able to participate in the task due to the elephant social hierarchy, as described above. It is also important to note that to control for social learning of the cooperative task, the elephants that were not actively participating in a trial were outside in one of two elephant yards; therefore, they could not learn about the cooperative task through observation.

Data Analysis

Once the videos were collected, they were uploaded onto Google Drive for analysis. Researchers analyzed the following: (a) trial success, (b) latency to approach rope, and (c) latency to pull rope. Trial success was coded on the basis of success (the sled was pulled to a distance where both elephants were able to access the food) or failure (any other outcome). Latency to approach rope was calculated as the time, in seconds, from when the elephant was ‘released’ from their keeper to when the elephant first made contact with the rope. Latency to pull rope was calculated as the time, in seconds, from when the elephant first made contact with the rope to when they pulled the rope. Interrater reliability was assessed using Cronbach’s alpha across three raters ($\alpha = .981$). Note, although the majority of trials were recorded for analysis, a few trials were not filmed for various reasons, including staffing and other factors. Consequently, our data are missing some latency measurements; however, we are confident in the available data.

Statistical Analyses

To determine whether the elephants performed successfully above chance, we utilized binomial cutoffs based on success or failure outcomes. A cumulative success rate of greater than chance was defined by the minimum number of successes required to reach statistical significance at $p < .05$, based on the exact binomial distribution. For 30-trial sessions (non-delayed condition), this threshold was 21 successful trials (70%); for 20-trial sessions (delayed condition), the threshold was 15 successful trials (75%). These thresholds were derived using the Vassar Statistics Exact Binomial Probability Calculator (Lowry, 1988). Microsoft Excel was used to calculate the raw percentage of successful trials per elephant pairing.

To investigate whether the elephants modified their rope-pulling behavior to account for the delayed release of their partner, we employed a series of Welch’s *t*-tests using the *base* package in R (R Core Team, 2023) to compare differences in latency to pull the rope between the non-delayed and delayed conditions for the four elephants (MP, MV, S, E) that faced a delay in the release of their partner.

Results

Non-Delayed

Out of 15 total pairings of elephants, 14 pairs successfully reached the criterion of an average success rate of > 70% over 30 trials (mean ± SD across the elephant pairings = 87.61 ± 8.92%) (Table 4). The one unsuccessful pair, E-MB, was discontinued after MB showed signs of displacement toward E resulting in E choosing to not participate in the session (see discussion for further details). With three sessions of 10 trials per pairing, all duos reached the criterion of an average success rate of > 70% (successful completion of at least 21/30 trials; $p < .05$). Two pairings of elephants (S-MV and MB-MP) were successful 100% of the time (30/30 trials). The lowest average success rates were both 73.3% (E-S and E-MT).

Table 4

Elephant Success Across Non-delayed Trials

Elephant Pairing	Trial Performance	Success Rate	*p*-value
MP-E	28/30	93.3%	$p < .01$*
MP-S	26/30	86.7%	$p < .01$*
MV-MP	26/30	86.7%	$p < .01$*
MV-MT	27/30	90.0%	$p < .01$*
S-MB	28/30	93.3%	$p < .01$*
S-MT	25/30	83.3%	$p < .01$*
S-MV	30/30	100.0%	$p < .01$*
E-MT	22/30	73.3%	$p < .01$*
E-MV	29/30	96.7%	$p < .01$*
E-S	22/30	73.3%	$p < .01$*
MB-MP	30/30	100.0%	$p < .01$*
MB-MV	27/30	90.0%	$p < .01$*
MT-MB	23/30	76.7%	$p < .01$*
MT-MP	25/30	83.3%	$p < .01$*

Note. Asterisks (*) denotes significance ($p < .05$). Criterion for success > 70%.

Delayed

As mentioned above, only seven elephant pairings were tested under the delayed condition due to time limitations. Furthermore, across those seven pairings, only four elephants (MP, MV, S, E) experienced being released first and faced the decision of waiting for their partner to arrive before pulling their end of the rope (MP: $n = 40$, mean ± SD = .95 ± .221%; MV: $n = 40$, mean ± SD = .9 ± .304%; S: $n = 40$, mean ± SD = .725 ± .452%; E: $n = 20$, mean ± SD = .7 ± .47%). Five of the seven pairings successfully reached the criterion of an average success rate of > 70% (successful completion of at least 15/20 trials; $p < .05$) over 20 trials during the delayed condition (mean ± SD across the seven elephant pairings = 82.86 ± 12.54%) (Table 5).

Table 5

Elephant Success Across Delayed Trials

Elephant Pairing		Trial Performance	Success Rate	*p*-value
Released first	***Released second***			
MP	S	19/20	95.0%	$p < .01$*
MP	E	19/20	95.0%	$p < .01$*
MV	MP	18/20	90.0%	$p < .01$*
MV	MT	18/20	90.0%	$p < .01$*
S	MV	13/20	65.0%	$p = .13$
S	MT	15/20	75.0%	$p = .02$*
E	MV	14/20	70.0%	$p = .06$

Note. Asterisks (*) denotes significance ($p < .05$). Criterion for success > 70%. As a reminder, the elephants that were released first faced the decision of waiting for their partner to arrive before pulling their end of the rope.

Performance of MP

The daughter-father pairing of MP and S—where MP was released first and S was delayed—had a 95% success rate and failed only one trial (delayed session 1–trial 1). It is important to note that the failed trial was the pairing's first delayed trial. Additionally, the reason the pairing failed was not an issue of the delay interval, but instead of the cooperation paradigm itself. MP waited for S to be released, but when S arrived at the rope, he pulled it so forcefully that MP lost hold of the rope.

The pairing of MP and E—where MP was released first and E was delayed—also had a 95% success rate, failing only one trial (delayed session 1–trial 2). Upon a delayed release, E returned to her keeper unprompted. Despite E's return to her keeper, MP continued to wait for 20 seconds before pulling the rope.

Performance of MV

The calf-calf pairing of MV and MP—where MV was released first and MP was delayed—had a 90% success rate, failing only two trials (delayed session 1–trial 1; delayed session 1–trial 4. During the first failed trial, though MV waited, MP grabbed but did not pull the rope when she arrived, therefore preventing the pair from performing a successful trial. The reason for the second failed trial was also not attributed to the delay interval, as MV waited for MP, however, MP dropped the rope while MV continued to pull, so the rope unraveled from under the sled.

The daughter-mother pairing of MV and MT—where MV was released first and MT was delayed—had a 90% success rate, failing only two trials (delayed session 3–trial 3; delayed session 4–trial 5). In both failed trials, MV pulled the rope before MT arrived.

Performance of S

The father-daughter pairing of S-MV—where S was released first and MV was delayed—had a 65% success rate on the delayed task, falling short of criterion. They failed a total of seven trials (delayed session 1–trial 1; delayed session 1–trial 2; delayed session 2–trial 1; delayed session 3–trial 1; delayed session 3–trial 3; delayed session 4–trial 3; delayed session 4–trial 5), which were all due to S pulling the rope before MV arrived.

The pairing of S-MT—where S was released first and MT was delayed—had a 75% success rate. They failed five trials (delayed session 1–trial 2; delayed session 1–trial 4; delayed session 3–trial 1; delayed session 3–trial 2; delayed session 3–trial 3), which were all due to S pulling the rope before MT arrived.

Performance of E

The pairing of E-MV—where E was released first and MV was delayed—had a 70% success rate on the delayed task, falling just short of criterion. They failed six trials (delayed session 1–trial 1; delayed session 1–trial 2; delayed session 1–trial 3; delayed session 3–trial 2; delayed session 3–trial 5; delayed session 4–trial 1), which were all due to E pulling the rope before MV arrived. Though they had some failures within the first, third, and fourth delayed trial sessions, it is worth mentioning that this pairing had a 100% success rate during their second session.

Latency to Pull Rope

A series of Welch's *t*-tests were employed to compare differences in latency to pull the rope between non-delayed and delayed trials for the four elephants (MP, MV, S, E) that faced a delay in the release of their partner (Table 6). There was a statistically significant difference in latency to pull the rope between non-delayed and delayed trials for MP ($p < .0001$) and MV ($p < .0001$), suggesting that MP and MV inhibited their pulling responses when the release of their partner was delayed. This change in behavior provides evidence that the calves, MP and MV, understood the role of a partner in the cooperative task. The difference in latency to pull the rope between non-delayed and delayed trials were not significant for S and E, suggesting that they did not understand the role of a partner in the cooperative task.

Table 6

Differences in Latency to Pull the Rope Between Non-delayed and Delayed Conditions

Elephant	Condition	*n*	Mean	SD	df	*t*	*p*-value
MP	Non-Delayed	87	.805	1.22	44.64	-17.55	$p < .0001$*
	Delayed	40	9.7	3.10			
MV	Non-Delayed	108	1.23	1.57	51.79	-14.05	$p < .0001$*
	Delayed	38	6.55	2.14			
S	Non-Delayed	145	.08	.3	38.74	-1.89	$p = .07$
	Delayed	39	.56	1.59			
E	Non-Delayed	24	.08	.28	21.55	-2.02	$p = .06$
	Delayed	20	.55	.1			

Note. Asterisks (*) denotes significance ($p < .05$).

Discussion

Performance of African Bush Elephants on a Cooperative Task

When released simultaneously to complete the cooperative task, 14 out of 15 African bush elephant pairings performed successfully (see a non-delayed trial video here), demonstrating proficient use of the cooperation apparatus. Two pairings, S-MV and MB-MP, performed successfully 100% of the time. The one unsuccessful pairing of E-MB was discontinued halfway through the second non-delayed session after MB displayed displacement behavior toward E by trumpeting and charging toward the bollard barrier that separated them within adjacent stalls. Although physical contact was not possible, researchers and keepers decided to discontinue this pairing to prioritize E's welfare. Researchers and keepers suggest that this act was due to MB being dominant over E as discussed in the subjects section. Additionally, researchers and keepers suggest that social relationships impacted the performances of other pairings as well; though E-MT and E-S both performed above chance with a 73.3% success rate, these were the lowest average success rates across all 15 pairings. In the case of E-MT, E is dominant over MT. In the case of E-S, although S does not have a place within the cyclical hierarchy of the herd, there have been previous incidents of aggression between E and S. Because of this, E and S cannot be housed together without a barrier in between them. Therefore, researchers and keepers suggest that this social dynamic influenced the performance of E and S when paired together. Overall, the success of the 14 pairings suggests that African bush elephants are able to understand the concept of the cooperation apparatus.

When a delayed release was added to the task, five out of seven elephant pairings performed successfully (see a delayed trial video here). As stated previously, because of time limitations, not all pairings could be tested under the delayed condition; pairings were created based on keeper suggestions as to minimize the likelihood for aggression. Because of this, only four out of the six elephants (MP, MV, S, and E) experienced a delay in the release of their partner. The two calves, MP and MV, demonstrated that they understood the role of a partner in a cooperative task, as they successfully waited for their partner above chance in each of their two delayed pairings. Furthermore, MP and MV exhibited significant changes in their rope-pulling behavior between non-delayed and delayed conditions, demonstrating that they actively altered their behavior to account for the delayed release of their partner. Moreover, another potential explanatory factor is that the two calves, MP and MV, were born under human care, unlike the adults who were wild-born. Early rearing environments can influence behavioral development and familiarity with human-mediated tasks, which may have contributed to their increased success (Bachevalier et al., 1991; Highfill et al., 2018; Milgram et al., 1994). Further research is warranted to disentangle the roles of age, cognitive flexibility, and rearing history in cooperative performance.

We infer that S understood the cooperation paradigm, but not the role of the partner in a cooperative task. There was no significant change in latency to pull the rope upon arriving at the apparatus between non-delayed and delayed conditions, suggesting that, overall, S did not alter his behavior to account for the delayed release of his partner despite performing above chance in one pairing (S-MT) but not the other (S-MV). However, it is worth mentioning that in one non-delayed S-MB learning trial, S pulled his rope, stepped on it to anchor it, then reached into the stall where MB was and pulled her end of the rope, thus completing the task on his own. This example of insightful problem-solving suggests that S understood the criteria of the cooperation task. Notably, similar behavior was observed by Plotnik et al. (2011), where one elephant learned to stand on the rope to enable their partner to do all the pulling. This parallel further supports the notion that elephants can creatively manipulate the task structure to achieve success.

E was the only adult female elephant who experienced a delay in the release of her partner, as neither MB or MT were chosen for a delayed pairing based on keeper suggestions of pairings with the least likelihood for aggression. Though the pairing of E-MV fell just short of criterion, E displayed no significant change in latency to pull the rope upon arriving at the apparatus between non-delayed and delayed conditions, suggesting that E did not understand the role of a partner in a cooperative task. It is important to note that E was housed in a different social setting at a number of American zoos prior to joining the ZT herd; because of this, keepers note that E lacks typical social skills since she was raised individually and therefore likely lacked the motivation to participate. Further research is warranted on the performance of adult female African bush elephants on the cooperative task.

Overall, given the success of the juvenile elephants, the present study suggests that, like their Asian elephant counterparts, African bush elephants are capable of understanding both the cooperation paradigm and the role of a partner in a cooperative task.

Waiting Behavior

While MV was silent when waiting for her partner to be released, which is not uncommon for elephants (Plotnik et al., 2011; Poole & Granli, 2011), we observed that MP often offered rumbles and what keepers referred to as “frog noises”—a low, gurgling, throaty vocalization somewhat reminiscent of a frog’s call. Future replications of this study could investigate elephant vocalizations during the cooperative task to examine communication, as other researchers have done with cetacean cooperation studies (Eskelinen et al., 2016; Jaakkola et al., 2021; King et al., 2021; Meier, 2023). Additionally, though challenging for such a large animal, it would be interesting to collect eye tracking data as the elephants are moving toward the rope and/or waiting. We do, however, recognize that elephants tend to rely on olfactory and auditory sensory modalities more often than visual (Ball et al., 2022; Jacobson & Plotnik, 2020b).

In addition to the differences in vocalization, MV and MP differed in their waiting behavior as it pertained to grabbing the rope. When waiting for her partner, MV would wrap her trunk around the rope to remove any slack, and then pull the rope when her partner arrived. MP on the other hand, would grab the rope with her trunk (sometimes pulling the slack out of it by lifting it up high), shift her weight, and then wait for her partner to arrive before pulling the rope.

General Limitations

The present study took over three years to complete, and though we would have liked to test the elephants at longer delay intervals and under a no-rope control condition—where the delayed elephant lacks access to the rope—as Plotnik et al. (2011) did, the project was deemed unsustainable after the first delay interval due to several (understandable) factors at ZT. Since we were limited by time and trials, we had to choose elephant pairings for the delayed trials, though ideally we would have liked to test all pairing combinations and at longer delays. Despite the shorter distance in the present study compared to Plotnik et al. (2011), our elephants still had to travel to access the rope. Notably, because they were initially positioned facing away from the apparatus, they also had to turn around and orient themselves before engaging with the task—introducing an additional attentional and motor component. In contrast, the elephants in Plotnik et al. (2011)'s study were positioned facing the cooperative apparatus.

We acknowledge that since we replicated this study in a protected-contact setting, the distance that our elephants had to travel from where they were released to where they could access the rope (~6m) was shorter than the distance that their Asian elephant counterparts experienced (10m) in Plotnik et al. (2011). Despite the distance constraints of the present study, the elephants still had to travel to access the rope—they were not able to access it by simply turning around and reaching for it.

Each trial typically required the involvement of at least four people: two keepers on the back side (one per elephant) and one keeper to manage the elephants on the sled-side. And an additional individual (an intern, researcher, or keeper) to assist with setup and video recording. While unrelated to personnel needs, the small sample sizes in most zoological facilities—due to inherently small herd sizes—highlight the importance of replication across institutions to expand the dataset. The challenge of gaining access to large sample sizes is not new to the field of comparative cognition, but one that should be acknowledged and supported through replication and collaboration (Agrillo & Miletto Petrazzini, 2012; Beran et al., 2014; Highfill et al., 2016, 2018; Many Primates et al., 2019; O'Connor & Barrett, 2023; Perdue et al., 2012; Snyder et al., 2021; Stevens, 2010, 2023). We encourage other researchers to collaborate with their respective zoological facilities and continue to replicate this study with additional delays to build our knowledge of elephant cooperation and cognition at large.

Implications

Though elephants are often marveled at for their intelligence, the scientific literature on both elephant and non-primate cognition in general is limited (Byrne et al., 2009; Jacobson & Plotnik, 2020a; Plotnik et al., 2011; Plotnik & Jacobson, 2022). Furthermore, as discussed in the introduction, knowledge of the evolution of cognitive abilities across the elephant taxon is lacking. Therefore, the goal of the present study was to investigate if the concept of understanding the role of a partner in a cooperative task—an ability demonstrated in Asian elephants by Plotnik et al. (2011)—was shared in African bush elephants. Our results indicate that African bush elephants are capable of understanding the role of a partner in a cooperative task, as was evident by the successful performances of our calves, MV and MP, across all of their delayed condition pairings when released first and faced with the decision of waiting for their partner to arrive before pulling their end of the rope. As discussed previously, further research is warranted into the performance of adult African bush elephants on this cooperative task since, as neither S nor E demonstrated that they understood the role of a partner in the cooperative task. As stated previously, neither MT nor MB were released first during the delayed condition—a decision that was made by the ZT team to minimize the likelihood of aggression within the delayed condition pairings given that the delay could create conflict—therefore, MT and MB were not presented with an opportunity to demonstrate an understanding of the role of a partner in the cooperative task. Overall, this study contributes to the literature on African bush elephant cognition as well as supports the idea that cooperative capacities are shared across the elephant taxon.

Additionally, while Plotnik et al. (2011) took just five months to complete the Asian elephant cooperation study, the present study took three and a half years to complete. Despite the varying lengths of time between successive sessions—which was sometimes several months at a time—the elephants were able to retain their knowledge of the cooperative task. Furthermore, as discussed in the method section, the varying lengths of time between successive sessions had no significant impacts on the performances of the elephants. Therefore, this could act as evidence for long-term memory capacities in African bush elephants, however, more research is warranted on this topic (Hope et al., 2025).

We would be remiss not to mention the plight of African bush elephants; African bush elephants are currently listed on the International Union for Conservation of Nature (IUCN)'s red list as an endangered species (Gobush et al., 2021a). Experts estimate that the wild population of African bush elephants has declined by more than half in the last several decades (Gobush et al., 2021a). While African bush elephants are threatened by habitat degradation—though not nearly as severely as their Asian elephant counterparts (Williams et al., 2020)—more notably, the imminent threat to African bush elephant populations is poaching for the ivory in their tusks (Chase et al., 2016; Gobush et al., 2021a). Unfortunately, African forest elephant populations face the same threats from poaching (Gobush et al., 2021b; Maisels et al., 2013). However, given that the present study investigates the socio-cognitive abilities of elephants, it our hope that it can be used to evoke empathy and bring awareness to the plight of elephants, as experts argue that highlighting cognitive abilities in elephants that are regarded as similar to those in humans can aid in engaging the public in conservation efforts (Jacobson & Plotnik, 2020a; MacDonald & Ritvo, 2016; Makecha et al., 2022; Makecha & Ghosal, 2017). Furthermore, experts also argue that knowledge of elephant cognition—and thus, knowledge of how elephants perceive and interact with their respective environments—can aid in developing tailored conservation strategies for all three elephant species (Barrett et al., 2019; Barrett & Benson-Amram, 2021; Greggor et al., 2014; Jacobson et al., 2023; Jacobson & Plotnik, 2020a; MacDonald & Ritvo, 2016; Marzluff & Swift, 2017; Mumby & Plotnik, 2018; Plotnik & Jacobson, 2022; Ball et al., 2022).

The present study supports the notion that zoological facilities are conducive for cognitive research experiments, as these facilities provide unique close-up opportunities given the relationships between the animals and their keepers/caretakers (O'Connor & Barrett, 2023). Additionally, it is important to note that participating in cognitive research is mentally stimulating and acts as a form of enrichment for the animals (Barrett & Benson-Amram, 2021; Clark, 2013, 2017; Herrelko et al., 2012; MacDonald & Ritvo, 2016; Puppe et al., 2007).

Conclusion

The present study provides evidence that African bush elephants are able to understand both the cooperation paradigm and the role of a partner in a cooperative task, similar to their Asian elephant counterparts. However, we acknowledge that more research is warranted on the cooperative abilities of the African elephant species given that juvenile but not adult African bush elephants were successful at understanding the role of a partner in this study. Overall, this study contributes to the literature of cognition across the elephant taxon.

Author Contributions

K. Willgohs: Formal Analysis, Investigation, Data Curation, Writing - Original Draft, Writing - Review & Editing, Supervision. **K. Fulkerson:** Data Curation, Writing - Original Draft. **K. Przystawik:** Conceptualization, Investigation, Project Administration. **C. Reiter:** Conceptualization, Investigation, Project Administration. **M. Burns:** Conceptualization, Investigation, Project Administration. **M. Ketner:** Writing - Original Draft. **L. Highfill:** Conceptualization, Methodology, Validation, Formal Analysis, Writing - Review & Editing, Supervision.

Acknowledgements

We extend our sincere gratitude to ZooTampa at Lowry Park and their African bush elephant team for their enthusiasm and logistical support of this project. We also extend our gratitude to Ryan Tracy of the Graduate Center, City University of New York, for his statistical expertise.

Data Availability Statement

The data that support the findings of this study are available on request from the corresponding author.

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Financial conflict of interest: No stated conflicts.
Conflict of interest: No stated conflicts.

Submitted: *May 2nd, 2025*
Resubmitted: *July 11th, 2025*
Accepted: *July 14th, 2025*