

# Advanced cognitive abilities in elephants? - does the African Elephant (*Loxodonta africana*) show cognitive flexibility?

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# Advanced cognitive abilities in elephants – does the African Elephant (*Loxodonta africana*) show cognitive flexibility?

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## Abstract

Cognitive flexibility allows an animal to adapt their behaviour in response to a changing stimulus outcome. It is tested by first training an individual to make an association between a stimulus and a reward. Once they have learned this association the reward is swapped, and the animal is trained to associate the previously non-rewarding scent with a reward instead. It is classified as an advanced cognitive ability as it activates a different reward centre in the brain as the animal must exert inhibitory control. The aim of the present study was to investigate whether African elephants (*Loxodonta africana*) show cognitive flexibility through a reversal learning test. The study subjects in this experiment were four elephants at the Knysna Elephant Park, South Africa. They were presented with a two-choice olfactory discrimination test. Elephants rely primarily on their sense of smell to navigate their world, so this sensory modality was chosen due to its ecological relevance. The results showed that as a group (N=4), the elephants performed above chance in most trials, however, they did not learn the association across sessions. Only one individual reached the learning criterion for the associative learning phase and proceeded to the reversal learning phase where she was trained to associate the previously non-rewarding scent with a reward. This elephant passed the reversal phase also. The results of this study are discussed in the context of other cognitive experiments in elephants, focusing on how the choice of a relevant sensory modality can affect performance, with interesting findings surrounding the cognitive capabilities of African and Asian elephants (*Elephas maximus*) alike.

### **Keywords**

Cognition, elephants, cognitive flexibility, reversal learning.

# Popular summary

Cognitive flexibility is a process that allows animals to adapt their behaviour in response to changing environmental conditions. It can be measured through a reversal learning test. This involves an initial associative learning phase where the animal is taught to associate a particular stimulus with a reward. When the animal has made this association, the next step is to swap which option is rewarded. By doing this, the animal has to essentially forget the association it has made previously and create a new association. It is understood that this activates a different region of their brain to inhibit the automatic reaction of what they learned in the first step to create a new association, which may indicate higher cognitive abilities. Elephants are a long-lived species, and they have complex social structure with strict hierarchies. They are considered to a highly intelligent species. However, they are facing rapid changes to their environment and are frequently coming into contact with humans, creating a conflict. Cognitive flexibility would therefore allow elephants to adapt their behaviour in response to unstable and unpredictable conditions. In this study, four African elephants were presented with a reversal learning test to test cognitive flexibility. The elephants had to make an association between two different scents, as they rely primarily on their sense of smell to navigate their world. The results showed that as a group the elephants did not learn the association. However, one elephant passed the reversal learning test, providing support for cognitive flexibility in this species.

## Ethical and social aspects

Elephants are referred to as a keystone species as they act as ecosystem engineers, providing and maintaining habitats for other species in the ecosystem. They are considered to be highly intelligent and emotional animals. However, elephants are currently facing rapid and unpredictable changes to their environment, and they are frequently coming into contact with humans, leading to negative human-elephant interactions. Studying cognitive abilities in elephants, and by focusing on ecologically relevant sensory modalities and tests will provide us with an understanding about how these animals can respond to the challenges of living in complex environments. Taking the elephants perspective into account when designing experiments is critical.

All research followed ethical regulations in South Africa and was approved by the African Elephant Research Unit (AERU). The elephants have been habituated to stand behind a low metal barrier during feeding experiences, so this set-up was the most suitable way to conduct the experiment. Experienced elephant guides were present at all times to ensure the safety of everyone involved. The elephants choice to participate in the experiment was voluntary, they were never forced to participate and the upmost attention to their welfare was taken into consideration. No deprivation of food or any other punishment occurred in case of refusal to participate or the use of an alternative strategy during the experiment.

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# Introduction

Associative learning is an important process in which animals obtain information about connections between events or entities in their environment. Associative learning is expressed when an animal modifies existing behaviours or develops novel behaviours and behaviour modifications can result from associative learning when an outcome has a positive or negative consequence (Pearce 2013; Christian 2010). This can be triggered by aversive stimuli, enabling the organism to avoid a negative outcome, or by attractive stimuli, which will increase the chance of receiving a reward (Christian, 2010). Reversal learning, on the other hand, is when the organism has been trained to discriminate between two opposing options but the option which was previously rewarded is reversed (Izquierdo *et al.*, 2017). While associative learning may be a conscious or unconscious process, reversal learning measures the ability to actively suppress the original reward-related response, which is linked to a more controlled decision-making process (Christian, 2010). This encourages the animal to exert inhibitory control over the more rapid automatic response system that they previously learned (Izquierdo and Jentsch, 2011). Because of this, reversal learning tests are commonly used to test cognitive flexibility in many different taxa. It has been tested in many different animals such as seals (Niesterok *et al.*, 2022), dogs (Lazarowski *et al.*, 2014), birds (Aljadeff and Lotem, 2021; Cauchoix *et al.*, 2017), mice (Rochais *et al.*, 2021), rats (Brushfield *et al.*, 2008), octopus (Bublitz *et al.*, 2021), fish (Vega-Trejo *et al.*, 2020), toads (Jenkin and Laberge, 2010), and insects (Liedtke and Schneider, 2014). A high degree of flexibility in behavioural responses is often advantageous when animals are required to cope with instability in their environment and unpredictable resources (Bublitz *et al.*, 2021). Worth noting in this context is that the location of vital resources such as food, shelter, and finding a mate, rarely remain constant over an animal's lifetime or between generations (Pearce, 2013). Given the extreme changes and alterations that humans have brought about to environments worldwide It is more important than ever to consider how animals will react to this instability (Wong and Candolin, 2015).

Elephants have long been considered a highly intelligent species. There is a lot of anecdotal evidence as well as long-term studies of wild elephants exhibiting higher cognitive abilities (Bates *et al.*, 2008). For example, there have been many instances where elephants have been seen paying particular interest to the bones of deceased elephants (Mc Comb *et al.*, 2005), potentially indicating a sense of self-awareness and theory of mind. There are also numerous examples of elephants helping conspecifics in distress (Hart *et al.*, 2008). Elephants are also known to possess an extraordinary memory, especially when it comes to social situations. They are able to recognise up to 100 individuals of their own species, as well as recognising familiar and unfamiliar elephants through acoustic information (Mc Comb *et al.*, 2003). Furthermore, it has been shown that they can keep track of the location of family members in the herd in relation to themselves through olfactory cues (Bates *et al.*, 2007b). Not only are they able to recognise individuals of their own species but they are also able to discriminate between human tribes based on olfactory and visual cues (Bates *et al.*, 2007a). It has also been shown that they can discriminate between the languages spoken by the members of these tribes and adjust their behaviour accordingly (Mc Comb *et al.*, 2014) Despite this evidence, however, elephants do not fare so well in formal cognitive tests even though they should be able to at least anatomically and physiologically. For example, elephants possess the largest absolute brain size of all terrestrial animals, weighing up to 5kg (Herculano-Houzel *et al.*, 2014). They have a large cerebral cortex and temporal lobe which have been linked to complex learning and behavioural

functions in humans. They also possess a large neocortex which is associated with higher intelligence and cognitive abilities in many species including humans, apes, and dolphins (von Dürckheim *et al.*, 2018). However, there may be differences within the neural architecture in the brain between elephants and great apes or humans that explain why elephants perform well in studies linked to memory, social awareness and self-awareness but display a poorer performance in other conventional tests investigating cognitive ability (Hart *et al.*, 2008; Hart and Hart 2007). For example, the majority of the neurons in the elephant brain are found in the cerebellum which is responsible for the control and movement of this large animal (Herculano-Houzel *et al.*, 2014). Furthermore, while their cerebral cortex is much larger than other species, they have much fewer neurons than great apes or humans (Herculano-Houzel *et al.*, 2014; Hart *et al.*, 2008). Another possible reason why elephants are performing poorer in formal cognitive tests may be because many of these tests have been done primarily in the visual realm which are more commonly designed for non-human primates and birds (Jacobson and Plotnik, 2020). While vision is an important sensory modality for elephants, it is mainly used to complement more dominant senses such as scent, tactile and auditory information (Plotnik *et al.*, 2019; Barrett and Bensom-Amram 2020). Cognitive ability and perceptual experiences often differ based on what is ecologically relevant for a species (Birch *et al.*, 2020) and this may be affecting how elephants perceive their environment and cognitive tests. Elephants rely heavily on olfaction for survival in many aspects of their lives such as foraging, reproduction and social interaction (von Dürckheim *et al.*, 2018). When tests have been redesigned or modified to be more ecologically relevant for the species such as measuring olfactory methods (Jacobson and Plotnik, 2020; Plotnik *et al.*, 2019; Schmitt *et al.*, 2018; von Dürckheim *et al.*, 2018) or using more than one type of perception in one study such as auditory, visual and olfactory (Plotnik *et al.*, 2014; Polla *et al.*, 2018) elephants appear to be performing better in these experiments when more relevant sensory modalities are used to test cognitive ability when compared to visual tests (Nissani *et al.*, 2005; Savage *et al.*, 1994; Nisani 2006; Plotnik *et al.*, 2006; Mac Lean *et al.*, 2014).

This study set out to investigate whether African elephants (*Loxodonta africana*) show cognitive flexibility through reversal learning tests which to my knowledge, has not been demonstrated using this type of test. I hypothesised that as a long-lived, group-living species, with high emotional intelligence (Hart *et al.*, 2008) elephants should show cognitive flexibility to some degree. I tested this using scent as the sensory modality, i.e., testing of the olfactory senses of elephants in a reversal learning context as this is the most important sensory modality in this species (von Dürckheim *et al.*, 2018). A reversal learning test was also performed using an auditory stimulus on one elephant after she passed the reversal learning test using an olfactory stimulus. In addition, to provide a recently updated synopsis on the current knowledge about elephant cognition, I compiled a summary of existing literature and I discuss my empirical results in the context of other cognitive experiments.

# Methods

## Subjects

The study took place at Knysna Elephant Park (KEP), with the assistance of the African Elephant Research Unit (AERU) which is located on site from the 3<sup>rd</sup> October 2022 to 16<sup>th</sup> December 2022. KEP is a private reserve located in the Western Cape region of South Africa. The park is comprised of a fenced area of approximately 60ha is open daily to the public who

come for feeding and walking experiences with the elephants. The elephants are able to roam freely during the day between these experiences. At the end of the day, they are brought to an enclosed area with a boma to sleep in, but they have access to both indoor and outdoor areas throughout the night. The resident herd and study subjects in this project consisted of five female African elephants (*Loxodonta africana*). Sally (33) was the first elephant to arrive at Knysna Elephant Park in 1994 at approximately five years old, after being rescued from Kruger National Park when her family was culled. As the oldest member of the herd, Sally is the self-appointed matriarch and leader of the herd. In a natural elephant herd, in addition to being the oldest female, a matriarch is generally chosen by her family by displaying great leadership skills and is trusted with important decision-making (Poole, 2019). At KEP however, the resident herd arrived much later than Sally and have learned to respect and accept her status (AERU personal communication). Nandi (29) arrived at the park in 2002 when she was nine years old. Nandi was pregnant when she arrived and gave birth to her daughter Thandi in 2003. Due to her mother's close bond with the matriarch, Thandi (19), has a high rank within the herd. Keisha (19) arrived at the park in 2004 in very poor health after she had been orphaned and suffered extensive wounds and psychological trauma. She is the lowest-ranked individual in the herd. Thato (14) arrived at the park in 2008, orphaned at one year old. Thato has a close bond with Keisha, but she also spends a large proportion of her time with Thandi and the higher-ranked individuals and therefore has a higher status within the herd than Keisha (Table 1). The elephants in this study have been involved in behavioural studies before but have not been involved in any cognitive tests.

### Experimental procedure

The elephants stood behind a low metal barrier during the experiment as this was something that they have already been habituated to do when they receive food from park guests (Figure 1a). Experimental sessions were held from Monday to Friday between 7-8 am, before tourists arrived at the park. An AERU staff member wore a pair of disposable gloves and extended their arms towards the elephants to introduce them to the olfactory stimuli (Figure 1b). The chosen olfactory stimuli during associative and reversal learning were garlic and ginger which are known to be aversive and highly salient scents to African elephant (Gross *et al.*, 2016; Tiller *et al.*, 2022), these scents were also unfamiliar to the study subjects. The gloves were prepared in advance with fresh ginger or garlic which was cut and then rubbed onto both sides of the gloves and stored separately in an airtight container until use. A different pair of gloves was used for each session, to avoid any additional scent cues from the previous session or elephant.

*Table 1: Background information and experimental stage reached of each elephant within the present study.*

Elephant	Sex	Arrival to Park and approximate age	Age during experiment	Origin	Position within the herd	Experimental Stage reached within study
Sally	Female	1994 (5 years old)	33 years (Adult)	Kruger National Park	Matriarch	Associative learning
Nandi	Female	2002 (9 years old)	29 years (Adult)	Thabazimbi Game Reserve	Thandi's mother	Reversal learning
Thandi	Female	2003 (Born at Park)	19 years (Young Adult)	Born at Knysna Elephant Park	Nandi's daughter	Training
Keisha	Female	2004 (1 year old)	19 years (Young Adult)	Kruger National Park	Low ranking female	Associative learning
Thato	Female	2008 (1 year old)	14 years (Young Adult)	Madikwe National Park	Youngest member	Associative learning

#### (a) Pre-training

One pre-training session per elephant was conducted. Here the elephants were simply rewarded for their participation during this phase allowing them to become familiar with the process and to the olfactory stimuli presented to them on the gloves. They received pellets as a food reward from their guide when they reached out their trunk to touch the gloved hand of the experimenter. The sessions were set at two minutes per elephant as this was the optimal time for them to remain focused as per the advice of the experienced elephant guides and the AERU researchers who work with the elephants on a daily basis. The guides were present at all times to ensure that the elephants were comfortable during the experiment and to ensure the safety of those working with them.

#### (b) Training

After the pre-training phase, the elephants had six training sessions. One touch of their trunk to the gloved hand marked one trial within a session. They received a food reward if they touched the gloved hand that had the correct scent (A+). The elephants were not rewarded touching the incorrect scent (B-). If they made a correct choice (A+), an AERU team member would call “reward” and the elephant guide would give the elephant pellets to reward a correct choice. If the elephant made an incorrect choice (B-) the AERU team member would say “no”, the experimenter would take a step back and the elephant would not receive a reward. Then, the experimenter would approach the elephant again and lift their hands back up marking the beginning of another trial. The rewarding scent (garlic or ginger) was chosen at random by an AERU team member before the training sessions began. The elephant guide would try to remain in a neutral position behind the experimenter so as to avoid any accidental cueing to the elephant (Chu *et al.*, 2023). It is important to note that the elephants were never punished for an incorrect choice (B-), as positive reinforcement techniques were used throughout the experiment and the elephant’s welfare was considered at every step.

#### (c) Associative learning

Four out of the five elephants moved on to the associative learning phase. One elephant failed to reach the criteria for the associative learning stage as she did not participate well in previous pre-training sessions and was therefore removed from further testing (see Table 1). The procedure remained the same as the training phase with one addition. The gloves were swapped between the experimenters’ hands after one minute, increasing the difficulty for the elephants. The rewarding scent remained the same but the side in which it was on was changed for the second minute of the session. To pass this stage the elephants had to meet a learning criterion of selecting the correct stimulus (A+) in 80% of the trials for two consecutive sessions. The order in which the elephants were chosen to participate each morning was at random. The order in which the rewarding scent (A+) was first placed on the right or left hand of the experimenter was also chosen at random.

#### (d) Reversal learning

One of the elephants passed the criterion for the associative learning phase (see results) and moved on to the reversal learning phase of the experiment testing cognitive flexibility (Table 1). To reiterate, this is believed to be more difficult as the elephant needs to withhold what they were initially trained in the associative learning phase and regard the association as useless (Izquierdo *et al.*, 2017). They are essentially required to forget the association they previously learned, while the association still remains temporarily dominant due to the training history and prior reinforcement. In this case, A+ will no longer be rewarded and instead becomes A-. This



means that B- in the associative learning phase will become the correct choice (B+) and will now be rewarded. Again, the criteria for the elephant to pass this phase was when they selected B+ in 80% of trials for two consecutive sessions.

(e) Auditory test

The elephant that passed both associative and reversal learning phases of the experiment using olfactory stimuli began the process again with another sensory modality. Here, an auditory stimulus was introduced using a clicker. The experimental setup remained the same as before, the experimenter wore gloves and extended their arms towards the elephant, but the gloves remained unscented. The elephant was asked to make a choice and after her choice, she would hear one click or two clicks from the clicker depending on which hand (left or right) was rewarding for this trial. The gloves were swapped one minute into the session to increase the difficulty for the elephant. For the associative learning phase of the auditory learning, the sound of two clicks was arbitrarily chosen to be correct (A+), and one click was (B-). As the information was presented to the elephant after the trial (clicking sound), rather than during as was the case with the olfactory stimulus, the elephant was given two trials before the official session started to be able to hear what the rewarding sound was. Again, the criteria for the elephant to learn this association was when they selected A+ in 80% of trials in two consecutive sessions. The elephant passed this association using auditory cues and moved on to the reversal learning phase where the rewarding sound (B+) this time was one click, and two clicks was non-rewarding (A-).



*Figure 1a: Experimental set-up. Elephant stood behind metal barrier. Experimenter stands with their gloved hand outstretched towards elephant. Elephant guide stands behind experimenter.*



*Figure 1b: Elephant making a choice between the olfactory stimuli on the gloves. The other elephants are provided pellets scattered on the ground while focal elephant is being tested to avoid interruption.*

## Compilation of elephant studies

To complement this experiment, a review of existing studies on elephant cognition was conducted to provide a summary of the present understanding of elephant cognition. The review was broadly divided into two main categories: “Standard learning” (N=15) and “Advanced learning” (N=25). Standard learning in this case includes studies that investigate discrimination learning (N=7), memory (N=3) and how elephants respond to social cues from humans (N=5) (Table 4). Advanced learning in this case includes studies that explore higher cognitive abilities in elephants such as relative quantity judgement (RQJ) (N=4), theory of mind (N=4), causal reasoning (N=3), innovation and tool use (N=7), social learning and cooperation (N=6), and self-control (N=1) (Barrett and Benson-Amram 2020) (Table 5). The studies are highlighted in bold and with an Asterix (\*) had more than one task or test for the elephants. For example, those that tested more than one sensory modality or had more than one way of presenting the test to the elephants (see S1). This created a more accurate picture of what tasks the elephants passed and failed on individual tasks and differences are outlined in more detail in the Table 4 and Table 5. The studies have been categorised by sensory modality and whether the elephants passed or failed the tasks presented to them. Studies using captive and wild elephants were included as well as taking into consideration both African and Asian elephants (*Elephas maximus*).

## Statistical analysis

The data was analysed using R statistical software version 4.1.2. Generalized Linear Models (GLM) and Generalized Linear Mixed Models (GLMM) were used to determine statistical significance with a binomial distribution (0= incorrect response, 1= correct response) using the *lme4* package in R (R Core Team, 2021). Associative learning ability was tested during phase two of the experiment where the elephants learn to discriminate between the two olfactory stimuli presented to them. To study if session number had a significant effect on the results of the learning phase, we built a GLMM with discrimination score (0 or 1) as the response variable, and session number, and the hand the elephants choose as fixed effects. Experimenter ID and elephant ID were included as random factors. To test if there was a difference in the performance between elephants a GLMM was built with discrimination score as the response variable (0 or 1), the interaction between session number and elephant ID and hand were fixed effects. Experimenter ID was included as a random factor. To assess if the hand the elephant chose had an effect on the score a GLM was built with discrimination score (0 or 1) as the response variable, the interaction between the hand chosen and elephant as fixed effects. A GLM was built to investigate whether the swapping of the gloves within a session affected learning. Success after the swap (0 or 1) was the response variable to test whether this was different from the performance before and elephant ID as fixed effects. A GLM was built to test how the elephants learned within each session. Discrimination score (0 or 1) was the response variable and the interaction between trial and elephant were fixed effects. As only one elephant passed the associative learning test, a separate GLM was built to investigate her performance separately for the associative learning phase, with discrimination score (0 or 1) as the response variable and session number, trial number and the hand the elephant chose as fixed effects. Cognitive flexibility and therefore reversal learning was tested during phase three of the experiment when the rewarding stimuli was swapped. This was done by building a GLM with discrimination score (0 or 1) as the response variable and session number, trial number and hand as fixed effects. Two similar GLMs were built to investigate auditory associative learning and auditory reversal learning for this individual. All models were selected by comparing the AIC and choosing the model with the lower AIC value, or in the case of the same AIC, choosing the simplest model. All pairwise post hoc multiple comparisons were done using

the package *emmeans* and *multcomp* in R. Due to the low sample sizes and therefore low statistical power results from these tests must be taken with caution.

# Results

## Olfactory associative learning

Table 2 depicts the number of sessions for each elephant in the olfactory stage of the experiment. Each elephant had a total of 6 training sessions at the beginning to become familiar with the procedure. Thandi had a very low number of trials (<10 trials) throughout the training phase and did not perform any trials in the first session of the associative learning phase so was removed from further testing. Thato had the lowest average performance in terms of proportion of correct choices across all sessions with 65.7% and the highest number of errors across sessions (6.29). The elephant with the highest average performance across sessions was Nandi with 70.7%. She had the fewest number of errors across sessions compared to all other elephants at 1.91 errors per session. She reached the set criteria for learning (scoring over 80% in two consecutive sessions: 11/11 and 15/15 correct trials in sessions 10 and 11 respectively) and performed 76 trials across 11 sessions. The other three elephants did not reach the learning criteria within the experimental phase even though they completed 24 sessions each. Within the 24 sessions, Sally had 472 trials which was the highest number for all elephants. Keisha performed 439 trials and Thato performed 395 trials (Table 2).

*Table 2: Breakdown of olfactory associative and reversal learning sessions for each elephant.*

Elephant	Experimental Stage reached within study	Training		Associative learning				Reversal learning			
		Total Sessions	Total Trials	Total Sessions	Total Trials	Average % correct across sessions	Average no. errors across sessions	Total Sessions	Total Trials	Average % across sessions	Average no. errors across sessions
Sally	Associative learning	6	62	24	472	68.60%	6.17	NA	NA	NA	NA
Nandi	Reversal learning	6	28	11	76	70.70%	1.91	3	46	78.30%	3.33
Thandi	Training	6	9	1	0	NA	NA	NA	NA	NA	NA
Keisha	Associative learning	6	16	24	439	69.10%	5.08	NA	NA	NA	NA
Thato	Associative learning	6	46	24	395	65.70%	6.29	NA	NA	NA	NA

Initially, A GLMM was created to test whether there was any evidence of learning across the sessions overall. As expected, the results showed no significant difference in learning when the elephants were compared as a group ( $p=0.5506$ ). A second GLMM was run to investigate whether there was any variation in learning for each individual elephant. Post hoc tests revealed that there was no evidence of learning across individuals, as the elephants all had similar scores across sessions, Sally ( $p=0.6637$ ), Nandi ( $p=0.1430$ ), Keisha ( $p=0.5930$ ) and Thato ( $p=0.8071$ ) (Figure 2). It is worth noting that despite this, Nandi reached the learning criterion for the associative learning test (see details below).

The models showed that the elephants were impacted by which hand the rewarding stimulus was on. Results from a GLM showed that the elephants were negatively affected when the

rewarding stimulus was on the right hand ( $p=0.0305$ , Figure 3). Post hoc tests revealed significant differences for Sally ( $p=0.0097$ ), Keisha ( $p=0.0305$ ), and Thato ( $p<0.001$ ). In contrast, there was no significant difference whether the rewarding stimulus was on the right hand or the left hand for Nandi ( $p=0.1064$ ).

Figure 3 shows that there was a strong preference for choosing the right hand, regardless of whether it was rewarding or not, resulting in significantly more wrong choices in the right hand ( $p=0.0305$ , Figure 3). One of the designs of this study was that the gloves were swapped one minute into the session. This meant that the hand that was previously rewarding became unrewarding and vice-versa to avoid the elephants simply adopting a strategy of choosing the previously rewarding hand, instead of investigating the two olfactory stimuli presented to them on the gloves. A GLM was created to test if there was a difference in their performance in the trial after the swap compared to the trial before the swap. It was found that the elephants performed significantly worse in the trial after the swap ( $p=0.0085$ ). A GLM was run to test whether the success after the swap improved over sessions, but this was not significant ( $p=0.474$ ), thus showing no improvement or learning when the gloves were swapped to the other hand across sessions when the elephants were compared as a group. Each session consisted of approximately 15-20 trials for Sally, Keisha, and Thato. However, Nandi performed a much fewer number of trials within each session (Figure 4). A GLM was created to test whether score improved within a session (i.e., as trial number increased in each session). It was found that the performance did not improve with trial number in sessions when the elephants were compared as a group ( $p=0.5706$ ). However, when running post hoc tests to look at each individual elephant, it was found that Nandi's performance improved within each session as trial number increased ( $p=0.0222$ ), but this was not the case for Sally ( $p=0.8258$ ), Keisha ( $p=0.5706$ ), or Thato ( $p=0.8497$ ).

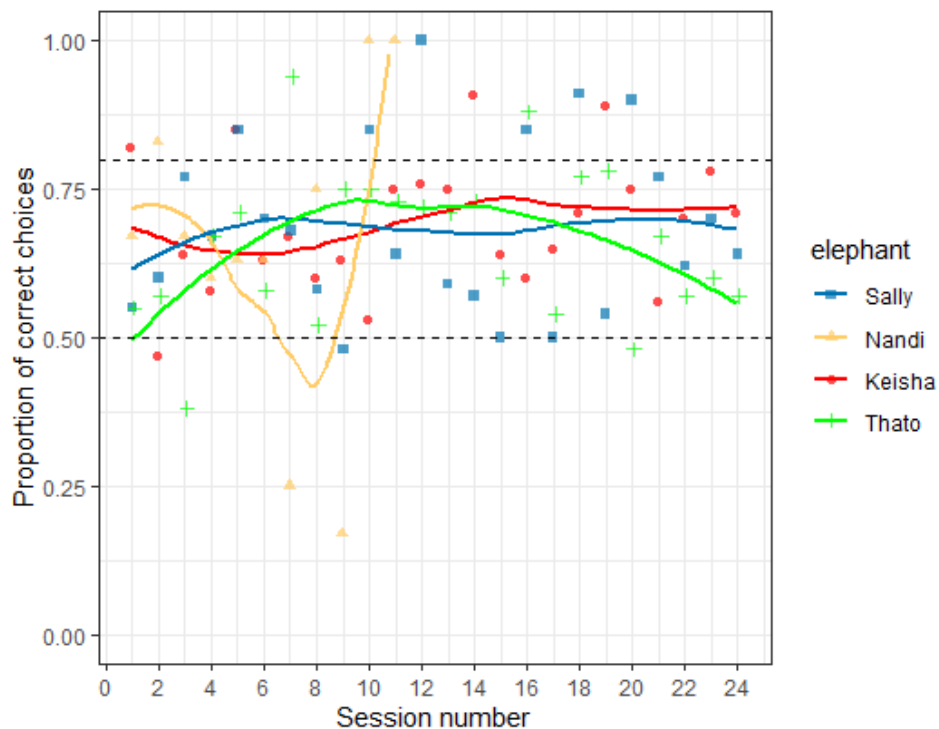


Figure 2: Proportion of correct choices for each elephant in the olfactory associative learning phase. Sally, Keisha, and Thato ( $N=24$  sessions), Nandi ( $N=11$  sessions). Points are the mean proportion of correct choices in each session.

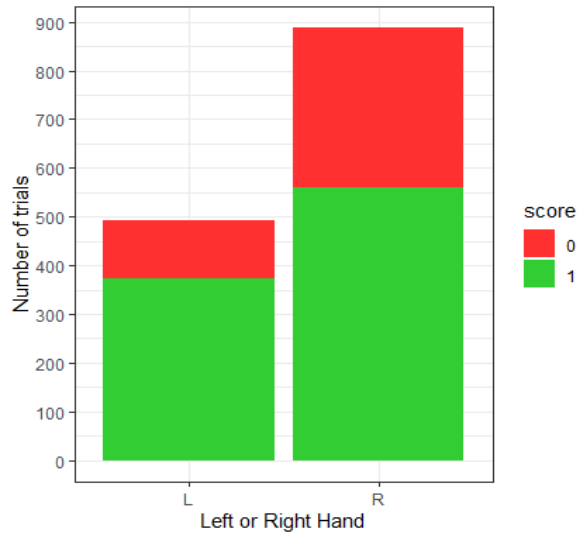


Figure 3: The number of trials where the left or right hand was chosen for all elephants combined.

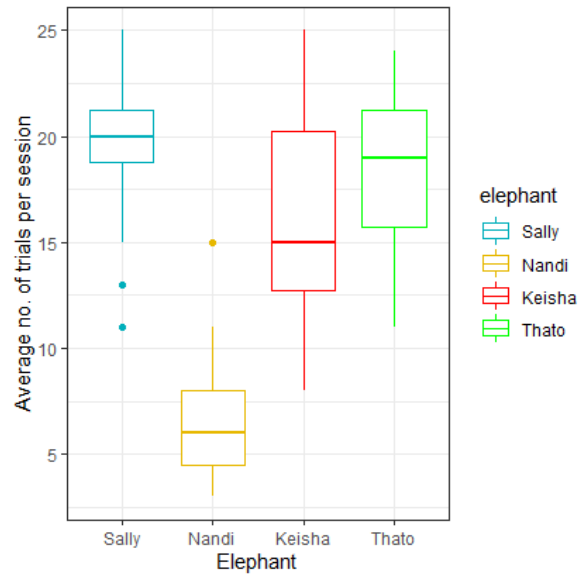


Figure 4: Average number of trials per session for each elephant.

Separate statistical analysis was run for on the olfactory associative learning phase for Nandi, as she was the only individual to reach the set learning criterion for the associative learning phase as she scored 80% or above in two consecutive sessions (Figure 5). However, there was a strong variation in her performance across the 11 sessions in relation to her score and the number of trials she performed within each session. Nandi performed an average of 5.2 trials per session in the first nine sessions in the associative learning phase while in sessions 10 and 11, she had a perfect score of 100% and performed 11 and 15 trials respectively. A GLM was run separately to investigate whether there was any evidence of learning across sessions, but this was not significant ( $p=0.7802$ ). While there was no significant difference in the mean proportion of correct choices across sessions, her performance improved within each session as trial number increased ( $p=0.0232$ ). This result is similar to what was obtained for Nandi in the post-hoc analysis, when a GLM was built to test the elephants together as a group ( $p=0.0222$ ).

### Olfactory reversal learning

As this elephant had reached the set learning criteria for associative learning using an olfactory stimulus, she moved on to the reversal learning phase. Here she completed 3 sessions with a total of 46 trials. Her overall average performance across sessions was 78.3% and had an average of 3.33 errors per session (Table 2). In the first session of the reversal learning, Nandi performed around chance level, with a proportion of correct choices of 53%. This is expected, as the animal should perform worse during this first session if they have learned the association in the previous stage of the experiment. By the second session the following day, she scored 82% and the following session she reached 100% (Figure 6). Again, meeting the set criteria for learning the association and thus completing the reversal learning phase of the experiment within 3 sessions. From the results of a GLM, it was found that her score significantly increased across the three sessions ( $p=0.00947$ , Figure 6). There was no significant difference in her success based on which hand the rewarding stimulus was on and performance before the swap was not significantly different when compared to the trial directly after the swap ( $p=0.748$ ),

which may indicate that Nandi was not choosing the previously rewarded hand but was in fact focusing on the olfactory stimulus.

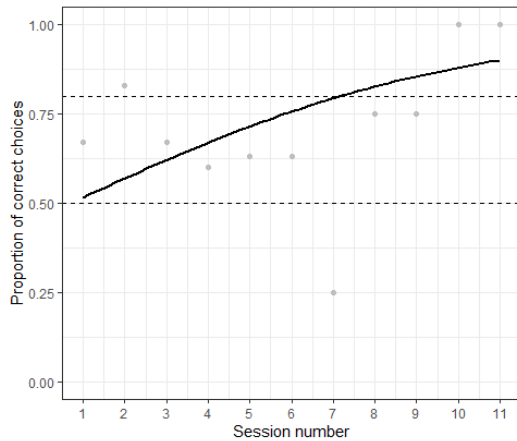


Figure 5: Proportion of correct choices for Nandi in the olfactory associative learning phase. Points are the mean proportion of correct choices at each session. Solid line is the GLM predictions for the learning curves.

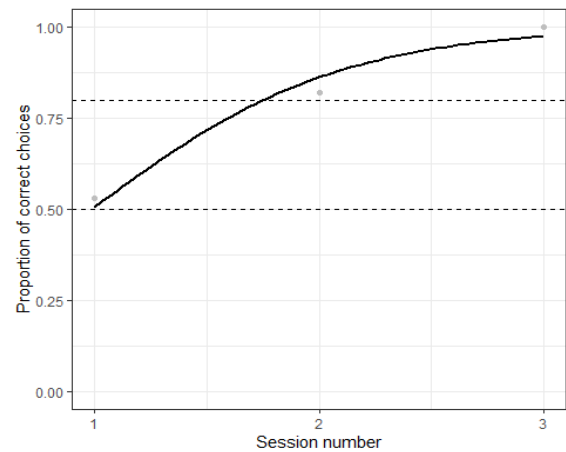


Figure 6: Proportion of correct choices for Nandi in the olfactory reversal learning phase. Points are the mean proportion of correct choices at each session. Solid line is the GLM predictions for the learning curves.

### Auditory associative learning

As Nandi passed the reversal learning task using an olfactory stimulus, the experiment was repeated using an auditory stimulus (see Methods part (e)). She completed 91 trials over four sessions during the auditory associative learning phase. She had an average proportion of 84.5% correct choices across all sessions and an average of three errors per session (Table 3). There was no significant increase in success across sessions ( $p=0.2375$ , Figure 7). This can be explained by the fact that this elephant scored very high in each of the four sessions (between 71-94%, Figure 7). However, there was an increase in success within sessions ( $p=0.0364$ , Figure 7).

### Auditory reversal learning

She reached the learning criteria (see Methods) for the associative learning phase with an auditory stimulus after four sessions moved on to the reversal learning phase. Here, Nandi completed 63 trials in total across 3 sessions. Her average proportion of correct choices was 74.67% and had a greater average number of errors per session 4.33 than the associative learning phase (Table 3). Unfortunately, due to time constraints we were unable to continue this experiment with Nandi. No evidence of learning was found within sessions ( $p=0.252$ , Figure 8) or across sessions ( $p=0.107$ , Figure 8).

Table 3: Breakdown of auditory associative and reversal learning sessions for Nandi.

Elephant	Experimental Stage	Associative learning				Reversal learning			
		Total Sessions	Total Trials	Average % correct across sessions	Average no. errors across sessions	Total Sessions	Total Trials	Average % correct across sessions	Average no. errors across sessions
Nandi	Reversal learning	4	91	84.50%	3	3	63	74.67%	4.33

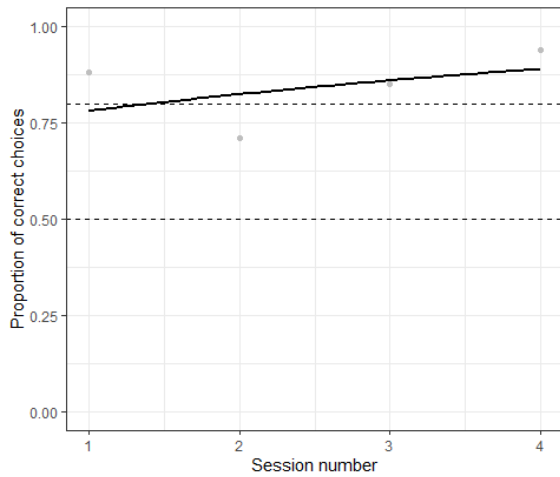


Figure 7: Proportion of correct choices for Nandi in the auditory associative learning phase. Points are the mean proportion of correct choices at each session. Solid line is the GLM predictions for the learning curves.

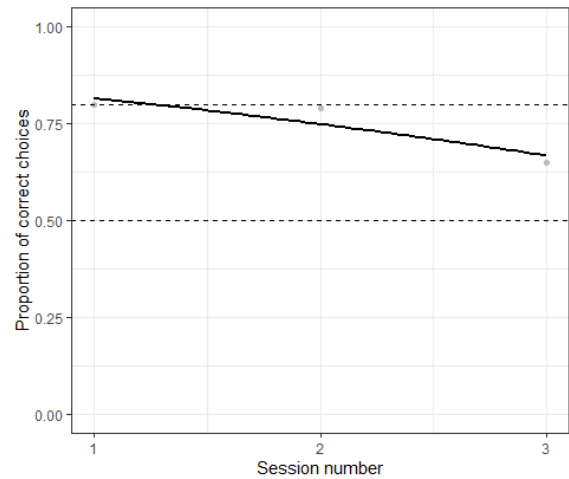


Figure 8: Proportion of correct choices for Nandi in the auditory reversal learning phase. Points are the mean proportion of correct choices at each session. Solid line is the GLM predictions for the learning curves.

### Compilation of elephant studies

A total of 40 studies are presented together in Table 4 and Table 5. 65% of these studies tested Asian elephants and 35% tested African elephants with one study including both species of elephant. Table 4 outlines studies that investigated standard learning abilities in elephants (N=15). Table 5 outlines studies that investigated advanced learning abilities in elephants (N=25). There were a number of studies that presented more than one experiment to the elephants. For example, those that used more than one sensory modality to test to the elephant's cognitive ability or by including more than one way to test the elephants in a given situation or including testing the elephants at a later stage after an original discrimination learning task testing memory. There were seven such cases presenting two or more tasks to the elephants in the standard learning studies. So instead of 15 total studies, I refer to 26 individual tasks that the elephants were tested on. There were also seven such cases in the advanced learning studies increasing the number of individual tests to 35. All tasks were then categorised in terms of pass and fail. Figure 8 shows an overview of the proportion of pass and fail from the elephants between standard learning and advanced learning with the adjusted number of studies.

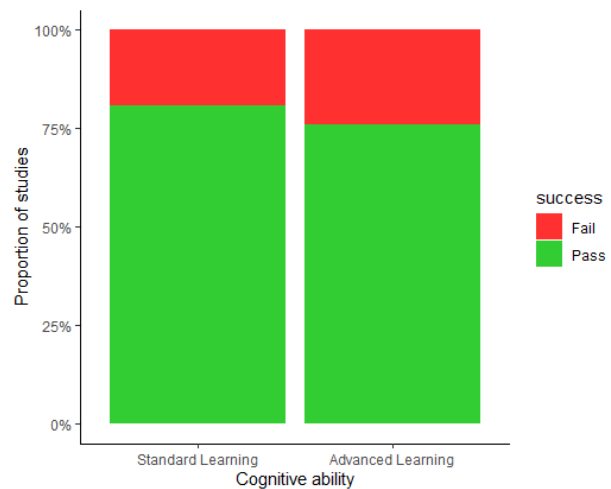


Figure 9: Proportion of studies investigating standard learning (N=26) and advanced learning abilities in elephants (N=35).

In the standard learning category, the elephants passed 80% of these tasks and failed 20%. In the advanced learning category, the elephants passed 77% of the tasks and failed 23% (Figure 9). Figure 10 shows a breakdown of the sensory modalities tested within the standard learning

category. 50% of these cognitive tests required the elephants to solve the task relying on their vision as the main sensory modality and they solved the majority of these tests. The remaining tests required the elephants to rely on olfactory cues (30%) or auditory cues (20%). The elephants passed all of the standard learning tests that required learning via olfactory cues while they failed some tasks using auditory cues. Figure 11 shows a breakdown of the sensory modalities tested within the advanced learning category. Similar to the standard learning tests, the largest proportion of studies investigating advanced learning abilities in elephants were designed requiring visual cues to solve a task (32%). While the elephants did relatively well in the visual tests for standard learning, there is a much higher proportion of fails when it comes to more advanced learning. Surprisingly, there was only one test investigating advanced learning abilities using olfaction as the primary sensory modality and the elephants passed this test. 11% of the studies required elephants to solve tasks using auditory cues as a primary sensory modality and the elephants passed each one. The last two categories in Figure 11 are “tactile” and “other”. When investigating some advanced cognitive abilities, there is not one particular sensory modality in particular that can be tested. For example, there was a large proportion of experiments (17%) where the elephants were able to touch and/or manipulate a novel object for example during a task. While this was usually to retrieve a food reward, in cannot be said that the tasks are solved relying on one particular sensory modality. The elephants passed all of these tasks except one. Similarly for some tasks investigating tool use and social learning there is no particular sensory modality being tested in this case and these instances were classified into the “other” category. This category accounted for over 30% of the studies.

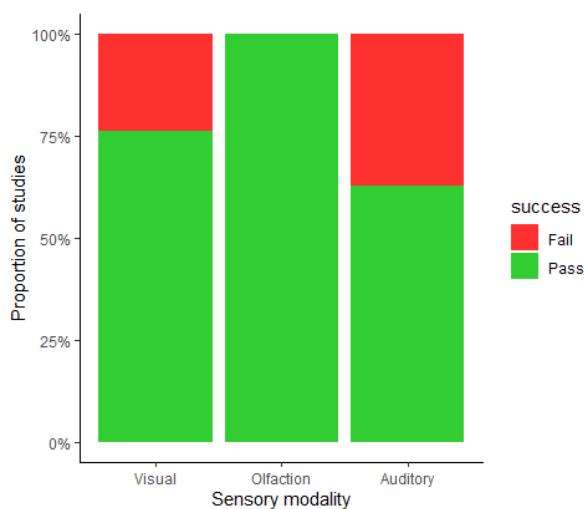


Figure 10: Proportion of pass or fail of studies testing elephants in the standard learning category using visual, olfactory, or auditory cues.

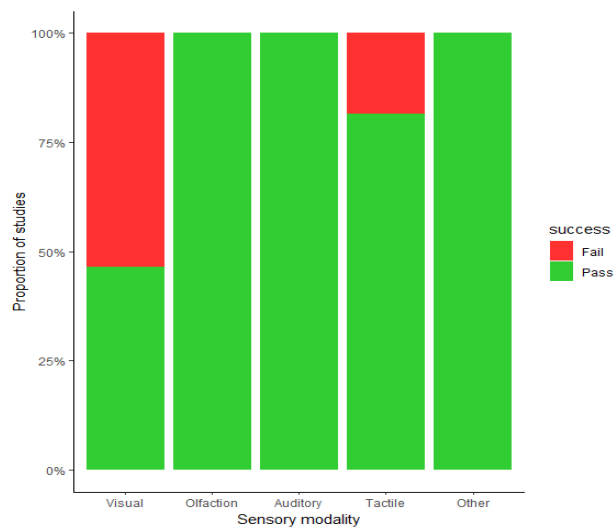


Figure 11: Proportion of pass or fail of studies testing elephants in the advanced learning category using visual, olfactory, auditory, tactile, or other cues.



Table 4: Studies that investigate standard learning abilities in elephants (N=15). Those highlighted and marked with (\*) indicate studies that have more than one task presented to the elephants.

Standard Learning							
Species	No. of Elephants	Captive or Wild	Modality	Test	Pass/Fail	Comments	Author
African	3	Captive	Visual	Discrimination	Pass	Required many more trials than seals	Savage <i>et al.</i> , 1994
Asian	14	Captive	Visual	Discrimination	Pass	Passed task but took many trials and there was a surprising age effect	<b>Nissani <i>et al.</i>, 2005*</b>
African	36 families	Wild	Olfaction	Discrimination	Pass	Kept track of up to 30 out of sight family members using olfactory cues	Bates <i>et al.</i> , 2007b
African	3	Captive	Olfaction	Discrimination	Pass	Discriminated between related and unrelated humans with remarkable accuracy	von Dürckheim <i>et al.</i> , 2018
African	5	Semi-wild	Olfaction	Discrimination	Pass	Identified plant odours on small and large spatial scales	Schmitt <i>et al.</i> , 2018
Asian	9	Captive	Olfaction & Auditory	Discrimination	Pass	Located food using olfactory senses but not auditory stimuli	<b>Plotnik <i>et al.</i>, 2014*</b>
Asian	2	Captive	Visual, Auditory & Olfaction	Discrimination	Pass	Discriminated between familiar and unfamiliar humans using visual and olfactory cues but not auditory cues	<b>Polla <i>et al.</i>, 2018*</b>
Asian	1	Captive	Visual & Auditory	Discrimination and Memory	Pass	Discriminated between patterns and sounds and required a large number of trials but retained information after 1 year	<b>Rensch 1957*</b>
African	3	Captive	Visual	Discrimination and Memory	Pass	Discriminated between 22 pattern pairs after a large number of trials and retained information after 7 months	<b>Hyatt 2013*</b>
African	5	Captive	Olfaction	Spatial memory	Pass	Biased towards picking scents in front of them but retained information after 6 months	<b>Dale 2008*</b>
Asian	7	Captive	Visual	Social cues from human	Fail	Did not follow visual cues unless a more salient cue (experimenter location) was beside the correct choice	Ketchaisri <i>et al.</i> , 2019
Asian	7	Captive	Visual & Auditory	Social cues from human	Pass	Visual cues alone were not sufficient to find food but were able to follow vocal commands	<b>Plotnik <i>et al.</i>, 2013*</b>
African	10	Captive	Visual	Social cues from human	Pass	Understood the importance of visual attention for effective communication	Smet and Byrne 2014a
African	8	Captive	Visual	Social cues from human	Pass	Understood the importance of visual attention for effective communication	Smet and Byrne 2014b
African	11	Captive	Visual	Social cues from human	Pass	Followed human pointing to find food	Smet and Byrne 2013

Table 5: Studies that investigate advanced learning abilities in elephants (N=25). Those highlighted and marked with (\*) indicate studies that have more than one task presented to the elephants. (RQJ= Relative Quantity Judgment).

Advanced Learning							
Species	No. of Elephants	Captive or Wild	Modality	Test	Pass/Fail	Comments	Author
African	2	Captive	Visual and Auditory	RQJ	Pass	Ratio effects were seen in RQJ	<b>Perdue et al., 2012*</b>
Asian	2	Captive	Visual and Auditory	RQJ	Pass	Passed both visual and auditory RQJ tasks with ratio effects	<b>Synder et al., 2021*</b>
Asian	5	Captive	Visual and Auditory	RQJ	Pass	Passed both visual and auditory RQJ tasks but ratio effects were not seen	<b>Irie-Sugimoto et al., 2009*</b>
Asian	6	Captive	Olfaction	RQJ	Pass	Passed olfactory RQJ task with ratio effects	Plotnik et al., 2019
Asian	2	Captive	Visual	Theory of mind	Fail	Failed task but used mirror to spontaneously look for food	Povinelli 1989
Asian	2	Captive	Visual	Theory of mind	Fail	Feather attached to elephants' head as a more conspicuous item than a mark but showed no interest in the mirror	Nissani & Hoefler-Nissani 2007
Asian	3	Captive	Visual	Theory of mind	Pass	One out of three elephants showed self-recognition in a mirror test	Plotnik et al., 2006
Asian	12	Captive	Other	Theory of mind	Pass	Moved their body from the mat they were standing on showing self awareness	Dale & Plotnik 2017
Asian	2	Captive	Visual	Causal reasoning	Pass	One out of two elephants showed means-end behaviour	Irie-Sugimoto et al., 2008
Asian	6	Captive	Visual	Causal reasoning	Fail	Did not show means-end behaviour in a protected contact setting (tool use)	Highfill et al., 2016
Asian	15 (4, 11)	Captive	Visual	Causal reasoning	Fail	Results open to interpretation but it appears that it is more likely associative learning than causal reasoning (tool use)	<b>Nissani 2006*</b>
Asian	6	Captive	Visual	Self control	Fail	Failed the A not B task in object permanency	MacLean et al., 2014

Table 5 (ctd): Studies that investigate advanced learning abilities in elephants (N=25). Those highlighted and marked with (\*) indicate studies that have more than one task presented to the elephants. (RQJ= Relative Quantity Judgment).

Advanced Learning (Ctd)							
Species	No. of Elephants	Captive or Wild	Modality	Test	Pass/Fail	Comments	Author
Asian	3	Captive	Other	Innovation	Pass	Insightful problem solving seen in one out of three individuals (tool use)	Foerder <i>et al.</i> , 2011
Asian	2	Captive	Other	Innovation	Pass	Aquired inaccessible food by blowing (tool use)	Mizuno <i>et al.</i> , 2016
Asian	14	Captive	Tactile	Innovation	Pass	Majority of elephants solved novel multi-access box	Jacobson <i>et al.</i> , 2021
Both	18	Captive	Tactile	Innovation	Pass	Majority of elephants were capable of solving all three tasks presented to them	<b>Barrett &amp; Benson-Amram 2021*</b>
Asian	15	Captive	Other	Tool use	Pass	Evidence of tool use and modification	Hart & Hart, 1994
Asian	47	Both	Other	Tool use	Pass	Similar tool construction and use in both wild and captive elephants	Hart <i>et al.</i> , 2001
African	1	Wild	Other	Tool use	Pass	Evidence of tool use in wild elephant	Wickler & Seibt, 1997
Asian	12	Captive	Other	Social learning	Pass	Spontaneous problem solving by one elephant (tool use). Others solved through social learning via social enhancement	<b>Barrett &amp; Benson-Amram 2020*</b>
Asian	26	Captive	Other	Social learning	Pass	Reassured other elephants in distress through vocalisations and physical touch	Plotnik & de Waal 2014
Asian	12	Captive	Other	Social learning	Pass	Evidence of coordination and cooperation	Plotnik <i>et al.</i> , 2011
Asian	9	Semi wild	Other	Social learning & Cooperation	Pass	Showed cooperation when food was plentiful but exhibited competitive behaviour when resources were less abundant	Li <i>et al.</i> , 2021
African	6	Captive	Tactile	Social learning	Pass	Showed improved efficiency of learning through social enhancement but did not engage in imitative social learning	<b>Greco <i>et al.</i>, 2013*</b>
African	2	Captive	Auditory	Social learning	Pass	Elephants imitated different sounds	Poole <i>et al.</i> , 2005

# Discussion

This study set out to investigate cognitive flexibility in the African elephant through a reversal learning experiment. It is complemented by a review of existing literature to further explore and understand the cognitive capabilities of elephants. In the experiment, one elephant (Nandi) was able to pass a reversal learning task using olfactory cues as the sensory modality. This elephant passed the set criterion for learning. While she showed a large amount of variation in performance across sessions in the initial associative learning phase, it was found that Nandi's score improved as trial number increased with each session. This may indicate that she was learning during the day within each session but by the next day there was a decrease in her performance. This could indicate that this elephant had to re-learn the association each day she was being tested rather than remembering the association from the previous day (Martina *et al.*, 2020). However, by session 10 and 11 where she scored 100%, it could be that the elephant showed a rapid understanding of the task. Her performance decreased back down to chance level in the first session of the reversal learning phase which supports the idea that this elephant may have learned the previous association. A lower performance after the reversal is expected as it is difficult to forget the previously rewarding stimulus after having learnt the association (Izquierdo *et al.*, 2017; Vega-Trejo *et al.*, 2020; Cauchoix *et al.*, 2017). However, in contrast to reversal learning studies in other animals, this elephant required fewer sessions to reach the criteria during reversal than in the original discrimination phase (Lazarowski *et al.*, 2014; Brushfield *et al.*, 2008). While it can be argued that the reversal learning phase is more difficult and a larger number of sessions would be expected to complete it, there was a remarkable increase in this elephant's motivation to participate towards the end of the initial association phase, as she performed many more trials within a session. This increase in participation continued throughout the rest of the experiment. Such an increase in motivation could indicate that she began to understand the task, and beginning to solve the tasks faster and faster could be support for "learning rules" in elephants. Evidence of this type of learning where animals progressively improve their performance over time when presented with a similar task, has been seen in reversal learning experiments for instance in seals (Niesterok *et al.*, 2022), and octopus (Bublitz *et al.*, 2011), but not in guppies (Boussard *et al.*, 2020). Rensch (1957) also found that the elephant in his study required fewer trials to discriminate between visual patterns after she had learned the first association reporting that she had gained an understanding of what was "right" and "wrong" in each pattern sequence (Rensch 1957).

It came as a surprise that the other three elephants were not able to pass the initial association phase using olfactory cues as this is the primary sensory modality for elephants (von Dürckheim *et al.*, 2018; Jacobson and Plotnik, 2020). However, it has been shown in many visual discrimination tasks that elephants require a large number of sessions and trials to understand an association (Savage *et al.*, 1994; Nissani *et al.*, 2005; Rensch 1957; Hyatt 2013). It remains unclear if the three elephants would have needed more sessions to have learnt the association or if they were focusing on the olfactory cues at all. There are number of potential reasons why the elephants may not have been focusing on the olfactory cues presented to them. Firstly, it was found that there was a clear difference in their performance when the rewarding stimulus was on the right hand versus the left hand. There was an extreme disproportion in how often Sally, Keisha and Thato chose the right hand over the left hand even when it was unrewarding. This led to a lower success on the right hand than the left hand regardless of the olfactory stimuli on the gloves. It is not uncommon for animals to exhibit a side preference in discrimination experiments such as this one (Bublitz *et al.*, 2021; Niesterok *et al.*, 2022; Plotnik *et al.*, 2013;

Dale 2008). This could be explained by cerebral laterization, which is a preference to use either left or right in a certain situation and it is widespread throughout the animal kingdom (Camerlink *et al.*, 2018). Laterization is found in paired organs such as hands and limbs, but it also found in trunk movements in elephants (Haakonsson and Semple, 2009). It has been observed mainly at the individual level in elephants and they show different side preferences depending on the context (Lefeuvre *et al.*, 2021). It has been shown that the strength of a side preference is higher in feeding contexts when compared to non-feeding contexts (Haakonsson and Semple, 2009). However, it is also plausible that the bias in this study may derive from feeding experiences from park guests (AERU-personal communication). The experiment was set up in a similar manner to feeding experiences at KEP where guests buy a small bucket of fruit and present one piece of food at a time to the elephants. It was observed that an overwhelming number of guests feed the elephants with their right hand. The elephants may thus be conditioned by this experience as this type of interaction occurs daily, usually in 30-minute intervals and the elephants have experienced this type of interaction from a very young age. This may have impacted the elephant's ability to focus on the olfactory stimulus that was presented to them. This was not something we anticipated in this study and from reflecting on this experiment, testing if there were any pre-existing preferences for the left or right hand could have been done during the pre-training phase. This may have given the opportunity during the associative learning phase to test the elephants first on their least preferred side to investigate whether this impacted *et* their learning of the association. Nevertheless, this is an interesting observation, and it may give support to how life history and previous reinforcement may play a role in elephant behaviour and performance (Nissani 2006). Another explanation for this potential side bias is that the elephants were simply not paying attention to the olfactory stimuli and were adopting a different strategy of "choosing one hand and sticking to it" (Plotnik *et al.*, 2013). This strategy would have been highly effective if the gloves were not swapped half-way into a session. This can be a common strategy and is seen in many cognitive experiments where animals try to maximise perceived success (Plotnik *et al.*, 2013; Niesterok *et al.*, 2022; Erdsack *et al.*, 2022).

A second possible confounding factor that could have affected the elephants focus on the olfactory stimuli was the presence of humans involved in the experiment. It is often necessary in captive settings to have handlers and staff present while experiments are being held for the safety of everyone involved as studies with large animals such as elephants do not come without risks (Chu *et al.*, 2023; Nissani *et al.*, 2005; Highfill *et al.*, 2016). However, it is no secret that humans can unintentionally and accidentally give cues to animals in experiments (Miklösi *et al.*, 1998). Animals who live closely among humans can become very aware of their intentions from subtle body language and gazing (Watters and Krebs 2019). Elephants can follow cues from their handlers in various contexts (Plotnik *et al.*, 2013; Smet and Byrne 2013). Measures were put in place to reduce potential cueing in this experiment. The guides remained in a neutral position behind the experimenter when possible, but oftentimes they would have to move around to either side of the elephant to deliver the reward or they would have to give a command to their elephant. Furthermore, when working with such a charismatic animal, strong bonds can form over time and the elephants in this study are no exception (Chu *et al.*, 2023; Rossman *et al.*, 2017). Therefore, it is plausible that the elephants may have been paying attention to their guides (and other humans) rather than the olfactory stimulus at certain times during the experiment.

Lastly, it is possible that the elephants were not always motivated to engage in the experiment. While the sessions took place early in the morning before the elephants got their breakfast to increase the likelihood of high food motivation, their breakfast bowls were positioned in front

of them during the sessions. Additionally, pellets were chosen as a highly rewarding reinforcer however, due to the nature of the setup, all elephants stood in a line together and waited as the focal elephant was being tested. Thus, pellets were scattered on the ground before and after their sessions to keep the elephants occupied which may have decreased the value of this reward. Furthermore, while sessions were kept short at two minutes each, the elephants displayed behaviours indicative of lack of interest or frustration (AERU observations). The most frequently observed behaviours included walking away from the experimental area, trying to sleep, or turning around and scratching their bodies on the barrier. These behaviours were especially seen in Keisha and Thato. Sally remained the most focused throughout the experiment but would occasionally try to slap the experimenter with her trunk. Interestingly Nandi performed a high number of these behaviours during the training phase and for the first nine sessions during the associative learning phase. However, there was a dramatic shift where her focus and motivation appeared to increase in session 10, which continued for the rest of the experiment. Life history and previous experiences as well as personality traits may also have the potential to affect how individuals react to experiments and cognitive tests (Nissani, 2006; Barrett and Benson-Amram, 2021). This was not investigated in this study, but it could be worthwhile to include this in future studies as a method to potentially address the variation that is seen across elephant performances.

From reviewing the literature on the cognitive abilities of elephants it was found that they are capable of passing many types of standard and advanced cognitive tasks. However, the modality in which they were tested seemed to have an effect on their performance. It was found that while the elephants were able to pass the majority of visual tasks in the standard learning category, the elephants had more difficulty solving tasks in the advanced learning category when relying on their vision. These studies investigated theory of mind (Povinelli 1989; Nissani and Hoefler-Nissani 2007; but see Plotnik *et al.*, 2006) self-control (MacLean *et al.*, 2014), and causal reasoning (Nissani 2006; Highfill *et al.*, 2016; but see Irie-Sugimoto *et al.*, 2018). These types of visual tests are more commonly designed for investigating higher cognitive abilities in non-human primates and birds as this their primary sensory modality (Jacobson and Plotnik 2020). It is possible that elephants have a better chance at passing more advanced cognitive tasks when studies are designed to be more species specific, for example, by testing a dominant sensory modality or allowing the elephant to use their trunk (Erdsack *et al.*, 202; Jacobson and Plotnik, 2020; Lefeuve *et al.*, 2021). There was a relatively low number of studies that tested elephants using olfactory cues, the majority tested standard cognitive abilities such as the discrimination abilities of elephants (Bates *et al.*, 2007b; von Dürckheim *et al.*, 2018; Schmitt *et al.*, 2018, Plotnik *et al.*, 2014) and their spatial memory (Dale 2008). There was only one study in the advanced learning category investigating relative quantity judgement in elephants through scent (Plotnik *et al.*, 2019). The elephants passed all of these tests which emphasises the importance of this sensory modality in elephants, but more tests should be done, especially testing the more advanced cognitive abilities of elephants to be able to draw stronger comparisons. There were multiple studies that used more than one sensory modality to test certain cognitive abilities which provides us with a deeper understanding on how we should design cognitive experiments to be ecologically relevant for this species. For example, in the standard learning category it was found that elephants could locate food using olfactory cues but not auditory cues (Plotnik *et al.*, 2014). Elephants were also able to discriminate between familiar and unfamiliar humans using visual and olfactory cues but not auditory cues (Polla *et al.*, 2018). However, elephants were able to discriminate between six different sounds and remember them one and a half years later (Rensch 1957), and Asian elephants were able to find food by following vocal commands (Plotnik *et al.*, 2013). In terms of advanced learning abilities elephants were able to pass relative quantity judgement tests using visual and/or auditory cues

(Perdue *et al.*, 2012; Synder *et al.*, 2021; Irie-Sugimoto *et al.*, 2019). The use of multiple sensory modalities within a study creates a clearer picture of what elephants are capable of achieving and can highlight the strengths and weaknesses of different sensory modalities in various contexts (Jacobson and Plotnik, 2020).

Another way that experiments have been designed to be more species specific is allowing for the use of the trunk, a highly specialised appendage for which elephants rely on daily (Lefeuve *et al.*, 2021; Foerder *et al.*, 2011). Examples of tasks where elephants were able to explore their environment or manipulate a novel object demonstrated advanced cognitive capabilities in elephants such as innovation, social learning, and the ability to use tools (Table 5). The elephants also displayed innovative behaviour by tactile means (Jacobson *et al.*, 2021; Barrett and Benson-Amram 2021), as well as an improved efficiency of learning through social enhancement (Greco *et al.*, 2013). Furthermore, evidence of theory of mind in elephants was seen when given a non-visual task where they had to move their body from a mat they were standing on, showing self-awareness (Dale and Plotnik, 2017).

This study has highlighted that there can be strong variation in individual performance. In this experiment, only one individual passed the reversal learning test using olfactory cues while the others showed no evidence of learning. After reviewing the literature, I found there are also other reports of only one elephant from a group passing a test. For example, one out of three elephants passed the visual mirror test demonstrated by Plotnik *et al.* (2006) and one elephant in Nissani and Hoefler-Nissani (2007) did not demonstrate theory of mind with the mirror test but instead used the mirror to find hidden food showing innovative behaviour and one out of two elephants showed means-end behaviour using vision (Irie-Sugimoto *et al.*, 2018). This is not surprising, especially in the case of insightful or spontaneous behaviour as not all individuals will react the same to a stimulus or they account for opportunistic events. Such variation in individual performance can also be linked to personality (Barrett and Benson-Amram, 2021). These individual differences are amplified in studies where sample sizes are low. Almost 50% of the studies reviewed here have a sample size between 1-5 elephants. This reflects the difficulty of studying such large animals. As is the case with this reversal learning experiment, the majority of studies are conducted in captive settings where the number of elephants are generally low (Plotnik and Jacobson, 2022). Therefore, replication of these studies is important to be able to conclude with any certainty on the results as it is difficult to draw any strong conclusions.

At present, formal studies in elephant cognition are sparse and are divided across many different topics highlighting that the field is still relatively new (Plotnik and Jacobson, 2022). This study provides an overview on how elephants perform in cognitive experiments, focusing on which sensory modality is being tested and how tasks are designed or modified to suit this species. An increased understanding in elephant cognition, and by extension what cues they are paying the most attention to, will facilitate in creating solutions on how to deal with the current problems that elephants are facing today. A major concern is the extreme and rapid changes to their environment, brought about by human expansion on their habitat (Wong and Candolin 2015; Plotnik and Jacobson, 2022). This leads to an increase in human-elephant conflict, which describe the negative interactions between humans and elephants (Mumby and Plotnik, 2018). Finding evidence of advanced cognitive abilities in elephants such as theory of mind, innovation, causal reasoning, and tool use may allow these animals to adapt in the face of human altered environments and reduce negative human-elephant interactions (Mumby and Plotnik, 2018). Furthermore, cognitive flexibility measured by a reversal learning as demonstrated in this study allows an animal to adapt their behaviour in response to a changing stimulus outcome

(Izquierdo *et al.*, 2017). This flexibility reduces the cost of relearning new reward contingencies when a new solution is presented. It is highly advantageous in situations where food resources are unpredictable and is strongly associated with highly social animals that exhibit fluctuations in status and individual behaviour (Buechel *et al.*, 2018, Bond *et al.*, 2007). Wild elephants have been reported adjusting their behaviour to avoid human conflict by changing the timing of their movements by entering crop fields at night or using roads that are less active to avoid direct contact with people (Gaynor *et al.*, 2018). While it is difficult to draw conclusions based on one individual's performance, if it is the case that elephants can show cognitive flexibility, it would allow elephants to adapt their behaviour to respond to these challenges.

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