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Do elephants *really* never forget? What we know about elephant memory and a call for further investigation

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Abstract

Despite popular culture's promotion of the elephant's ability to "never forget," there is remarkably limited empirical research on the memory capacities of any living elephant species (Asian, *Elephas maximus*; African savanna, *Loxodonta africana*; African forest, *Loxodonta cyclotis*). A growing body of literature on elephant cognition and behavioral ecology has provided insight into the elephant's ability to behave flexibly in changing physical and social environments, but little direct evidence of how memory might relate to this flexibility exists. In this paper, we review and discuss the potential relationships between what we know about elephant cognition and behavior and the elephants' memory for the world around them as they navigate their physical, social, and spatial environments. We also discuss future directions for investigating elephant memory and implications for such research on elephant conservation and human–elephant conflict mitigation.

Keywords Memory · Cognition · Spatial · Episodic · Elephant · *Elephas maximus* · *Loxodonta africana* · *Loxodonta cyclotis*

Introduction

The idea that an elephant—represented by the three living elephant species (Asian, *Elephas maximus*; African savanna, *Loxodonta africana*; African forest, *Loxodonta cyclotis*)—"never forgets" is likely the result of a complement of factors. These include persistent media products about elephants that feature in cartoons and popular culture, as well as scientific data from long-term research field sites that have shown the elephant's capacity for complex sociality and cognitive flexibility (Moss, 1988; Plotnik & Jacobson, 2022; Poole & Moss, 2008). While we still have much to learn about elephant behavior and cognition, much of what we know already points to a taxon with a rich physical and social experience.

Elephants have large brains with a neuron density three times that of humans (257 billion neurons; Hart et al., 2008; Herculano-Houzel et al., 2014; Shoshani et al., 2006), exhibit complex social behaviors such as allomothering (Bates et al., 2008a; Lee, 1987; Schulte, 2000; Vidya, 2014), targeted helping (Bates et al., 2008a; Douglas-Hamilton et al., 2006; Sharma et al., 2020), and reassurance of others in distress (Plotnik & de Waal, 2014), and have demonstrated a capacity for body- and self-awareness (Dale & Plotnik, 2017; Plotnik et al., 2006, 2010) and perspective taking (Nissani, 2004). Although social structures differ between elephant species (de Silva & Wittemyer, 2012), all species live in fission–fusion societies (Archie et al., 2011; Buss & Smith, 1966; de Silva & Wittemyer, 2012; Fishlock & Lee, 2013; Schuttler et al., 2014), where individuals can experience extended periods of time between subsequent social interactions with certain conspecifics (Hörner et al., 2021; Moss, 1981, 1988, 1992; Poole & Moss, 2008). This means that it is likely necessary for elephants to be able to discriminate between familiar and unfamiliar individuals and

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remember previous social interactions, so that they can account for them in future interactions with the same individual (Gokcekus et al., 2021; Wiley, 2013). Furthermore, elephants migrate long distances in search of resources that are distributed in patches throughout the environment (de Knegt et al., 2011; Moss, 1992; Polansky et al., 2015; Tsalyuk et al., 2019), and thus it is likely important for them to remember spatial information related to the location of resources and the routes by which to reach them. Habitat fragmentation and an increase in anthropogenic landscapes has changed distribution of food resources (Leimgruber et al., 2003) and, to acquire food, some elephants have begun to enter crop fields to forage on high-calorie crops (Barrett et al., 2019; Fernando et al., 2008; Mumby & Plotnik, 2018; Shaffer et al., 2019). To do this, elephants have been observed overcoming barriers to access and forage on crop fields (Fernando et al., 2008; Kioko et al., 2008; Mutinda et al., 2014). For example, some elephants learn to use their tusks, which do not conduct electricity, as a way to manipulate and break electric fences (Mutinda et al., 2014). The way in which certain elephants figure out how to surpass human-built barriers may demonstrate their cognitive flexibility and a capacity for solving novel problems (Plotnik & Jacobson, 2022).

Remarkably, well-controlled experimental tasks to test elephant cognition and memory are limited. Here, we will discuss much of what we know about elephant cognition and the behavior of elephants as they navigate their physical, social, and spatial environments, and what existing research tells us about if, how, and for how long they remember different information. We discuss support for short-term, working, and long-term memory. Short-term memory involves encoding, storing, and retrieving information during short periods of time (e.g., 30 s to a few minutes: Cowan, 2008; Shuell & Giglio, 1973), working memory involves actively maintaining knowledge in short-term memory to use it while performing cognitive tasks (Cowan, 2008), and long-term memory involves the retention of information for extended periods of time (i.e., a few min to years: Cowan, 2008; Meeter & Murre, 2004). We give particular attention to studies that examined elephant long-term memory over the course of weeks to years. We also discuss priority areas for future research directions, as well as broader applications of elephant cognition and memory science to conservation and human health. We acknowledge that there are differences in biology and ecology among the three extant elephant species, and we specify the species of focus whenever possible. However, when making general statements, we focus on the elephant taxon as a whole because there is not currently sufficient evidence to compare and contrast between the three species.

Physical cognition and memory

Sensory perception

Like all animals, the sensory perception of elephants shapes the way in which they view and interact with their environment (reviewed in Jacobson & Plotnik, 2020), and thus it is heavily involved in their cognition and memory. Although vision is likely less important for elephants than olfaction and audition (Jacobson & Plotnik, 2020; Shoshani et al., 2006), elephants are still able to use visual cues in discrimination tasks. For example, when presented with object-choice experiments (i.e., tasks requiring animals to select between two or more choices), Asian elephants have been able to learn which is the rewarded response between black versus white and large versus small objects (Nissani et al., 2005), light versus dark (Markowitz et al., 1975), and different patterns (Rensch, 1956, 1957). In these tasks, elephants must learn about and retain knowledge of the correct visual cue (e.g., black or white) and use this knowledge when making their choice, which suggests a certain level of short-term and working memory. Rensch (1956, 1957) found that, when one Asian elephant who had learned to discriminate between pairs of cards with different patterns was presented with 13 pairs 1 year later, she was able to remember which card was the correct choice with 73%–100% accuracy for 12 of the pairs and 67% accuracy for the last pair. In addition, Markowitz et al. (1975) found that when one Asian elephant who had learned a light versus dark discrimination task was tested again 8 years later, she reached criteria (20 consecutive correct responses) in 6 min with only two errors (out of 43 trials), suggesting long-term retention of the discrimination criteria. However, two other elephants, who were later found to have deficiencies in their vision, did not perform well after 8 years (Markowitz et al., 1975).

In contrast to vision, elephants rely heavily on olfaction to perceive their environments (Jacobson & Plotnik, 2020), and chemical signalling appears to be an integral part of elephant communication (Rasmussen & Krishnamurthy, 2000). Elephants have an enlarged olfactory bulb, in comparison with brain regions for other senses (Shoshani et al., 2006), suggesting that it is one of their strongest sensory modalities. Accordingly, elephants appear to be proficient at using odor cues to discriminate between options in object-choice tasks. For example, Asian elephants can use olfactory cues to determine where food is present and where it is not (Plotnik et al., 2014) and to discrimate between dung from females based on reproductive state (Ghosal et al., 2012). African savanna elephants can use olfactory cues to discriminate between preferred and nonpreferred plants (Schmitt et al., 2018), between fruits with different sugar levels (Nevo et al., 2020), and between odors of closely related human family members, including sibling pairs (in a match-to-sample task; von Dürckheim et al., 2018). Both Asian and African savanna elephants can also choose a container based on the presence of a target odor (Schmitt et al., 2023). In these experiments, elephants must retain information about olfactory cues in working memory in order to make the correct choice (e.g., container with food or correct match). Furthermore, Asian elephants can learn to discriminate between structurally related chemical odorants in object-choice tasks (Arvidsson et al., 2012; Rizvanovic et al., 2013), including chemical structures that only differ by one carbon (Rizvanovic et al., 2013). They also retain knowledge of which odors were rewarded and maintain accuracy when tested after 2, 4, 8, and 16 weeks (Arvidsson et al., 2012) and, in another study, after 3 weeks and 1 year (Rizvanovic, 2012). Together, these studies suggest that elephants can store knowledge of odors in both short- and long-term memory.

Audition is also an important sensory modality for elephants (Jacobson & Plotnik, 2020). The size and structure of elephant ears allow for adept localization of sound, and elephants can hear low-frequency sounds that are below the range of human hearing (Heffner & Heffner, 1982; Heffner et al., 1982). There is also evidence that elephants can discriminate between different sounds. For example, a recent study showed that African savanna elephants can be trained to reliably respond to up to seven different human verbal commands with seven different types of vocalizations (Stoeger & Baotic, 2021). This suggests that elephants can retain information about an association between a specific auditory cue and the correct vocal response, although the length of time that elephants could retain this association was not specifically tested. Rensch (1957) investigated the long-term retention of auditory discrimination in elephants and found that one Asian elephant could learn to discriminate between 12 tones, and after 1 year, demonstrated that she remembered the meaning (i.e., correct or incorrect) of each tone. However, it appears that auditory discrimination performance in elephants may depend on the context of the cue. For example, Plotnik et al. (2014) found that, while Asian elephants could find which container contained food in an object-choice test using olfactory cues, they were not able to correctly choose based on auditory cues (i.e., shaken buckets of sunflower seeds). Importantly, the authors noted that elephants might not be expected to use auditory cues in a foraging context, considering that they likely do not use auditory cues to forage on vegetation in the wild.

Quantity discrimination

The ability of elephants to use different sensory modalities to correctly discriminate between different quantities has informed our understanding of how elephants perceive numerosity. For example, both Asian and African savanna elephants can discriminate between different quantities of food using both or either visual and/or auditory cues (when baits were dropped into a container; Irie-Sugimoto et al., 2009; Perdue et al., 2012; Snyder et al., 2021). Furthermore, Irie and Hasegawa (2012) found that when different quantities of bait were dropped into two containers in two different rounds, Asian elephants chose the container with the greatest total amount of bait, suggesting that elephants were able to count and then add the quantities dropped into each container. In addition, Asian elephants have demonstrated the ability to discriminate between different quantities of food using only olfactory cues (Plotnik et al., 2019). In order to complete quantity discrimination tasks using either olfactory or auditory cues, elephants must first listen or smell, remember both choices and decide which one is greater, and then use that information when subsequently making their choice. This suggests that elephants can perceive and remember small differences in quantity, at least in the short-term, and hold this information in their working memory.

Irie-Sugimoto et al. (2009) and Irie and Hasegawa (2012) found that the performance of Asian elephants when discriminating between quantities of food remained consistent even when differences between the two quantities were small and when overall quantities were large. Most animals represent quantities through approximations (i.e., accumulator model: Gallistel & Gelman, 2000), and succumb to *disparity* (Irie-Sugimoto et al., 2009) or *distance* (Moyer & Landauer, 1967) effects—or decreased performance in quantity discrimination as the difference between two quantities decreases—and *magnitude* (Irie-Sugimoto et al., 2009) or *size* (Moyer & Landauer, 1967) effects—or decreased performance when quantities are large. Thus, the lack of disparity/distance or magnitude/size effects found by both Irie-Sugimoto et al. (2009) and Irie and Hasegawa (2012) led the authors to conclude that elephants may not represent numbers as approximations (i.e., accumulator model) but instead as separate memory files (i.e., object-file model; Kahneman et al., 1992). Interestingly, the object-file model suggests that animals can only store up to four memory files simultaneously. Elephants in these studies performed well on quantities as high as six or seven, suggesting that they may have a uniquely large object-file capacity, which would suggest they have a uniquely large short-term memory capacity (Irie & Hasegawa, 2012; Irie-Sugimoto et al., 2009). Another more recent study showed that one Asian elephant was able to discriminate between numbers 1–10, based only on visual cues (number of pictures on a touch screen) that were not confounded by the quantity of a food reward (Irie et al., 2019). The authors again found no magnitude/size or disparity/distance effects, providing more evidence that elephants may have a very large short-term memory capacity, and that they may even be able to count numbers—similar to humans—instead of simply estimating quantities (Irie et al., 2019).

However, other studies on elephant quantity discrimination have found different results, which were consistent with the accumulator model (Perdue et al., 2012; Plotnik et al., 2019; Snyder et al., 2021). For example, Perdue et al. (2012) and Snyder et al. (2021) replicated the methods of Irie-Sugimoto et al. (2009) with African savanna and Asian elephants, respectively, but with important modifications. Specifically, Irie-Sugimoto et al. (2009) used open containers to test whether elephants could use solely auditory cues (i.e., sequentially dropping food) to discriminate between quantities; however, this does not exclude the possibilities that the elephants could see into the containers and use visual cues. When Perdue et al. (2012) and Snyder et al. (2021) used closed-top containers that controlled for visual cues, they found that elephants were still able to choose the greater quantity, but that accuracy decreased as the difference between the two choices decreased (i.e., disparity/distance effects), which is consistent with the accumulator model (Gallistel & Gelman, 2000). Note that in the above three studies, olfactory information was also available to the elephants (Irie-Sugimoto et al., 2009; Perdue et al., 2012; Snyder et al., 2021). In addition, Plotnik et al. (2019) found that, when only given olfactory information, Asian elephants could discriminate between different quantities, but their accuracy also decreased as the difference between the two choices decreased—again, consistent with the accumulator model (Gallistel & Gelman, 2000). Thus, although some studies suggest that elephants may have a uniquely large capacity to remember numbers in the short-term, the conflicting results of subsequent studies suggest that more work is needed to determine how elephants represent, store, and recall knowledge about numbers and quantities. No study to date has recorded the capacity of elephants to store quantity information in the long-term.

Problem-solving and tool use

In the wild, elephants have demonstrated their ability to find solutions to novel problems when they determine how to overcome barriers, such as electric fences, to enter crop fields to forage (Fernando et al., 2008; Kioko et al., 2008; Mutinda et al., 2014). Experimental studies have also demonstrated the ability of elephants to problem-solve. Both captive Asian and African savanna (Barrett & Benson-Amram, 2021; Greco et al., 2013; Jacobson et al., 2022) and wild Asian (Jacobson et al., 2023) elephants are able to innovate to solve novel foraging problems. For example, both captive (Jacobson et al., 2022) and wild (Jacobson et al., 2023) Asian elephants were presented with a novel multiaccess puzzle box with three compartments, each with a door that required a different method to open (i.e., push, pull, slide) in order to access a food reward. Five out of 44 wild elephants who interacted with the box solved all three door types (Jacobson et al., 2023), and eight out of 13 captive elephants solved all three door types (Jacobson et al., 2022), which provides evidence that elephants can innovate to find solutions to a novel problem. Asian elephants are also able to problem-solve by either using their trunks to blow air on the far side of a food item so that it moves within reach (Mizuno et al., 2016) or by sucking or blowing through their trunks into a tube to obtain a food reward placed in the center of the tube (Nissani, 2004). In addition, Asian elephants have demonstrated an understanding of the role of a partner in a cooperative problem-solving task (Li et al., 2021; Plotnik et al., 2011). In these studies, when faced with the delayed release of a partner (Plotnik et al., 2011), or the need to wait for a partner or mitigate the arrival of a competitor (Li et al., 2021) in a task requiring that two ends of the same rope are pulled together to obtain an out-of-reach food reward, elephants will wait to pull until their partner cooperator can pull with them. For all of the above tasks, elephants must retain information about the end goal (i.e., obtaining the food) while also trying to determine the solution to the problem, which uses working memory. If elephants use trial-and-error to solve problems (e.g., to open a particular door of a puzzle box; Jacobson et al., 2022, 2023), then they must also store and recall the knowledge of the outcomes of previous attempts. Additionally, if elephants are free to choose partners when solving a cooperative task (Li et al., 2021), they must recall knowledge of which elephants are cooperators or competitors.

Problem-solving studies may also provide evidence for memory of solutions. Once a solution is learned, if the knowledge of how to perform the task is stored in memory (e.g., procedural memory), task performance should increase over time because there is no need to relearn. In the first phase of the study, when Jacobson et al. (2022) presented Asian elephants with a puzzle box with three of the same door types (three push doors) in two different sessions that were 2-13 days apart, they found that the latency to solve the first door was shorter in the second compared with the first session, which suggests that elephants likely remembered how to push open the door. Jacobson et al. (2023) also found that the latency to open any puzzle box door type decreased in wild elephants over multiple interactions, suggesting that elephants likely learned that they could gain access to food from the box. However, latency to open did not decrease for particular door types, suggesting that elephants may not have retained knowledge of how to open a specific door. In another study, African savanna elephants were able to retain knowledge of a cooperative problem-solving task with no performance deficit despite varying lengths of time between successive sessions, which ranged between a few days to several months (unpublished data, Willgohs et al.).

In addition, Nissani (2006) found that once Asian elephants learned to remove a lid to access a food reward, they continued to remove the lid in subsequent trials where the lid was adjacent, even though this step was no longer necessary. Although there were issues with the methodology of this study—which aimed to demonstrate causal reasoning but instead illustrated the complicated nature of studying cognition in heavily trained logging elephants—the results still suggest that elephants can store problem solutions, which in this case was removing or flipping a lid. These studies suggest that elephants can retain memory for solutions over a relatively short period of time; however, it is unknown whether this information would be stored over the long-term.

Elephants can also use tools to solve problems. In the wild, both African and Asian elephants have been observed using tools (Chevalier-Skolnikoff & Liska, 1993; Hart & Hart, 1994). For example, Asian elephants use and modify branches to swat flies off their backs (Hart et al., 2001; Hart & Hart, 1994). There is also anecdotal evidence of an African savanna elephant throwing mud and vegetation to deter a rhino (Wickler & Seibt, 1997). In captivity, both Asian and African savanna elephants show a potential means–end understanding for the use of a tray when attempting to obtain out of reach food items; when presented with a choice of a tray with food on it (but out of reach) and a tray with food next to it, they chose to pull the tray with food on it more often, to successfully obtain the food (Highfill et al., 2016, 2018; Irie-Sugimoto et al., 2008). Furthermore, Asian elephants have demonstrated that they can use water as a tool (Barrett & Benson-Amram, 2020) and stand on objects to access out-of-reach food items (Foerder et al., 2011). For all of these examples, elephants must retain knowledge of the end goal (i.e., deterring flies/predator, accessing food) while finding a solution, which uses working memory. In addition, using the same tool repeatedly on different occasions over months/years (e.g., branch to deter flies) may also suggest that elephants retain long-term knowledge of the purpose of certain tools. Interestingly, Foerder et al. (2011) showed that one Asian elephant used insightful problem-solving by spontaneously employing a large plastic cube as a tool on which he could stand to reach food above his head. There was no evidence in this study for trial-and-error learning. Insightful problem-solving would require recalling knowledge from previous experience (i.e., semantic memory) when attempting to solve a novel problem.

Similar to non-tool-related problem-solving, if knowledge of how to use a tool is stored in memory, task performance should increase over time. Consistent with this, Barrett and Benson-Amram (2020) found that once an elephant learned that water could be added to a tube to bring an out-of-reach floating food reward within reach, the latency to solve the task significantly decreased over trials. Furthermore, Foerder et al. (2011) observed that after an initial instance of spontaneous problem-solving—an elephant moved and stood on a large plastic cube to acquire an out-of-reach food item—the latency to use the cube as a tool decreased in successive trials. Additionally, when presented with other objects instead of the plastic cube, the elephant generalized his use of tools to other large objects and even manipulated smaller objects in an attempt to acquire the food. This improvement in task performance in these studies suggests that elephants store information about tool use, although more work needs to be done to determine for how long elephants may be able to remember this information.

Social cognition and memory

Social behaviors in the wild

Elephants exhibit complex social behaviors, form tight social bonds, and live in fission–fusion societies (Archie et al., 2011; Buss & Smith, 1966; de Silva & Wittemyer, 2012; Fishlock & Lee, 2013; Schuttler et al., 2014). Thus, it is likely important for elephants to be able to perceive and remember differences among individuals. Indeed, Pardo et al. (2024) recently found evidence that wild African savanna elephants use name-like calls—which were specific to the receiver but did not imitate the receiver's vocalizations—to individually address conspecifics. This suggests that elephants can remember the identity of certain elephants and, potentially, their corresponding "names." Recognition of individuals is important for elephants when interacting with relatives or based on their previous interactions with others. For example, when reuniting with familiar conspecifics, African elephants have been observed engaging in "greeting ceremonies" in the wild (Moss, 1981, 1988; Poole & Moss, 2008), where elephants seem to remember familiar conspecifics with whom they have not recently interacted. Hörner et al. (2021) examined this in African elephants in captivity, and showed that two mother–daughter pairs that were reunited after 2 and 12 years apart participated in greeting ceremonies, while unrelated elephants who were introduced to each other in the same setting showed only minor greeting behaviors. This suggests that the former behaviors are specific to familiar individuals, and that elephants can discriminate between familiar and unfamiliar conspecifics. Furthermore, this suggests that elephants may be able to remember the differences between related and unrelated individuals—or may even be able remember specific individuals—for as long as 12 years. However, other possibilities which would not require long-term memory, such as phenotype-matching with their own phenotype to determine kin (Lacy & Sherman, 1983), need to be excluded in future research.

Another behavior that may be suggestive of a long-term social memory capacity in elephants is the grief-like behaviors that elephants have been observed engaging in following the death of conspecifics. For example, in the wild, all three species of elephants have been observed investigating, touching, and sniffing carcasses, and revisiting them repeatedly over the course of a few minutes to a few months (Douglas-Hamilton et al., 2006; Goldenberg & Wittemyer, 2020; Hawley et al., 2018; McComb et al., 2006; Merte et al., 2009; Payne, 2003; Pokharel et al., 2022; Sharma et al., 2020; Stephan et al., 2020). Captive Asian elephants also show changes in social and affiliative behaviors after the loss of a herd member (Rutherford & Murray, 2021). Together, these studies may suggest that elephants store knowledge of the individual, the fact that they are deceased, and the location where they died. McComb et al. (2006) experimentally tested whether these natural grief-like behaviors are indeed driven by a particular affiliation to deceased kin, or a general interest in carcasses. They found that African savanna elephants were more interested in elephant skulls and ivory than wood, and more interested in elephant skulls than buffalo and rhinoceros skulls. However, when presented with skulls from one kin (matriarch) and one nonkin, elephants did not display different levels of interest. Therefore, the grief-like behaviors exhibited by elephants may be the result of a general interest in conspecific carcasses, instead of the recognition of kin or a particular individual. However, the skulls in this study were washed and moved to a different location, and thus may have been lacking cues (e.g., olfactory, spatial) that would be important for individual recognition. Therefore, more work would be needed to determine whether elephants could recognize kin based on skulls if certain pertinent pieces of sensory information were available. Interestingly, elephants in this study showed more interest in ivory than in skulls. The authors pointed out that, in contrast to skulls that are not observable in life, tusks may allow elephants to recognize certain deceased individuals if they had been familiar with that individual's tusks when they were alive. A study comparing how elephants respond to the tusks, other body parts, or odors—which are observable both in life and in death—of deceased kin and nonkin would be an interesting next step to further investigate whether elephants can differentiate—or remember—deceased kin.

Behavioral responses to traumatic events may also shed light on elephant memory. For example, groups of orphaned African savanna elephants have been reported killing rhinoceroses in displays of hyperaggression (Bradshaw et al., 2005; Slotow et al., 2001; Slotow & van Dyk, 2001). This behavior may be consistent with behaviors related to posttraumatic stress syndrome (PTSD; Bradshaw et al., 2005), where individuals experience a traumatic event—in this case, young elephants witnessing family members being killed by humans—and then, later in life, engage in fear-related and aggressive behaviors that are not related to the cause of the traumatic event. PTSD in humans is classically related to changes in memory, including vivid recollection of the event but also general memory loss problems (Elzinga & Bremner, 2002; Layton & Krikorian, 2002). Thus, it is possible that the behaviors of orphan elephants are due to a long-term memory of a traumatic event. However, these orphan elephants also experienced altered musth patterns (i.e., early onset and long durations). In addition, when older bulls were introduced into these young male elephant groups, young male musth (presumably along with associated elevated testosterone levels) was suppressed, and displays of hyperaggression ended (Bradshaw et al., 2005; Slotow & van Dyk, 2001). Therefore, it is possible that this behavior was simply due to a lack of social structure, and not necessarily due to the recollection of a traumatic event.

Sensory modalities to discriminate between individuals

In addition to using their senses to discriminate between visual, olfactory, and auditory stimuli in object-choice tasks (see Physical Cognition and Memory section), elephants have demonstrated proficiency in using different isolated sensory modalities to recognize individuals. For example, African savanna elephants are able to use olfaction to discriminate between different individuals. Bates et al. (2008b) placed urine samples in the wild in front of an elephant walking with or nearby her family group. These urine samples came from elephants that were either absent nonkin, absent kin, kin walking in front of, or kin walking behind the target elephant. The authors found that the elephants reacted according to what should be expected based on the identity and location of the conspecific from whom urine had been sampled. For example, the elephants showed more interest in a urine sample from an elephant who was behind them, which would be unexpected and thus might result in the target elephant spending longer investigating it, than in a sample from an elephant in front of them (which would be expected and thus possibly less interesting). In addition, the elephants showed more interest in a urine sample from absent kin compared with absent nonkin. Overall, the study provided evidence that elephants may recognize at least 17 but possibly up to 30 different individuals based on olfactory information and hold expectations about their locations. This suggests a large working memory capacity for spatial information, as well as efficient recall of the olfactory information associated with certain conspecifics. In addition, African savanna elephants may also be able to remember olfactory information of familiar individuals in the long-term. Hoerner et al. (2023) presented captive elephants with feces of kin from whom they had been separated for either 2 or 12 years. Elephants spent the most time investigating, and showed more excitement-related behaviors toward feces from these absent kin than feces from absent nonkin or present nonkin (Hoerner et al., 2023). This suggests that elephants can recognize relatives from the scent of their feces even after being separated for 12 years (Hoerner et al., 2023). However, because there was no sample from present kin in this study, more work is needed to exclude other possibilities, such as recognizing and reacting to odors from kin using phenotype-matching (Lacy & Sherman, 1983).

Elephants can also use auditory information to discriminate between individuals. For example, African savanna elephants can discriminate between familiar and unfamiliar individuals from both vocalizations (McComb et al., 2000), as well as seismic alarm calls (O'Connell-Rodwell et al., 2007). In particular, McComb et al. (2000) found that elephants can discriminate between 12 different adult female contact calls and react differently based on how frequently they encounter the associated family groups. The authors estimated that in order to make these discriminations, elephants would need to be familiar with the contact calls of approximately 100 adult females, which suggests that they have a large capacity to retain knowledge of different vocalizations from many individuals. Furthermore, this study found that elephants responded to the vocalization of a deceased family member after 23 months, and to the vocalization of a family member who had transferred to another social group after 12 years (although the two social groups still had contact during this time; McComb et al., 2000), which suggests long-term memory of these vocalizations. However, more work would be needed to determine whether the elephants remember vocalizations based on their familiarity with the sound or their association with specific individuals.

The ability of elephants to discriminate between vocalizations also appears to vary based on age. McComb et al. (2001) found that family groups of African savanna elephants with an older matriarch modified their behavioral response to playbacks of contact calls of other family groups depending on their level of familiarity. In contrast, family groups with younger matriarchs showed little variation in their behavioral responses depending on familiarity with the other group. This suggests that older matriarchs have a greater ability to discriminate and change their behavior as a function of familiarity with other groups of elephants, which suggests that they have a greater social knowledge for the appropriate response when faced with different groups. Similarly, another study showed that older matriarchs responded to a predatory threat with more sensitivity than younger matriarchs, where younger matriarchs underreacted to the playback of a male lion (McComb et al., 2011). Although these two studies did not specifically investigate memory, they suggest that older matriarchs have more social and environmental knowledge, and that individuals likely store knowledge gained from their experience over a lifetime.

Interactions with humans

There is also considerable evidence that elephants can discriminate between humans. For example, in a zoo setting, Asian elephants were able to differentiate between familiar and unfamiliar humans using visual (video playbacks) and olfactory (worn clothing) cues, but not using auditory cues (auditory playback; Polla et al., 2018). This suggests that these elephants at least retained knowledge of visual and olfactory cues associated with humans with whom they regularly interact. In addition, African savanna elephants have demonstrated that they can discriminate between different human ethnic groups, sexes, and ages. Bates et al. (2007) found that when presented with visual (colors) representing and odor cues of Massai men, who historically speared elephants, elephants showed more aggressive and fear responses than when presented with similar cues from Kamba men, who are agriculturists and pose little threat to elephants. Elephants also show more defensive bunching and investigative smelling when presented with playback of Massai voices (McComb et al., 2014). In addition, these behaviors are more frequent when the elephants are presented with playbacks from Massai men compared with Massai women and boys, who are less of a threat to elephants. These studies suggest that elephants retain knowledge of which ethnic groups are a threat—and, specifically, which ages and sexes within that ethic group are a threat—and how ethnicity, age, and sex are associated with differences in odor, visual, and auditory cues. Interestingly, because Massai men only occasionally spear elephants, elephants' responses to them could reflect a long-term memory for historic or infrequent events.

Lastly, elephants appear to be able to use certain cues from humans when making decisions. For example, African savanna elephants are able to follow human pointing cues even when subtle (Smet & Byrne, 2013, 2014). In contrast, Asian elephants do not follow human pointing cues (Ketchaisri et al., 2019; Plotnik et al., 2013); however, they can correctly choose a baited container when a human is standing next to the correct choice (i.e., local enhancement; Ketchaisri et al., 2019). Furthermore, two Asian elephants begged more often from zookeepers who could see the elephants than those who could not see the elephants (e.g., facing away or face covered; Nissani, 2004). These three studies together show that elephants are able to make decisions based on visual cues from humans and suggest that they may be using stored knowledge of an association between food and human presence, human gestures, or the visibility of human faces to make their decisions.

Spatial cognition and memory

Locating hidden food

Elephants travel long distances in search of food and water resources (de Knegt et al., 2011; Moss, 1992; Polansky et al., 2015; Tsalyuk et al., 2019), and thus it should be beneficial for them to have a strong spatial memory—or the memory of the location of an object or a place and how to navigate to it (Healy & Jozet-Alves, 2010; Olton, 1977). One simple way to test spatial cognition and memory in animals is to determine whether they can learn and remember the location of a hidden reward. One of the earliest investigations of elephant memory examined whether elephants could remember the location of food (Grzimek, 1944). Grzimek (1944) placed bread into one of five containers as an elephant observed, and then tested whether they chose the correct container after delays of different lengths. He found that one Asian elephant was able to correctly choose the container with the food after a 15-s and 45-s delay, but did not perform well in the task after delays that ranged from 2 hours to 2 days. The author concluded that elephants did not exhibit long-term memory for locations.

Another common way to study spatial memory is through a radial arm maze (Olton & Samuelson, 1976) where, instead of the animal needing to remember a specific location where food is located, they are tested on their ability to remember from which locations they have already eaten. Using an analog of a radial arm maze, Dale (2008) found that captive African elephants visited locations (there were up to eight different options) from which they had not yet eaten more often than locations from which they had already eaten. This suggests that they can hold information regarding the locations from where they had already eaten in working memory while choosing where to eat from next. Furthermore, they also maintained accuracy in performance on this spatial task after a 7-month break. Although this does not provide evidence for long-term spatial memory because elephants did not remember an association between a specific location and a food reward, it does suggest that they remember how to perform the task (i.e., long-term procedural memory).

Evidence from studies on wild elephants where food rewards are placed in different locations throughout the landscape can also provide insight into elephant spatial memory and may be more ecologically relevant for elephants who often seek resources in the wild over long distances and time periods. For example, Jacobson et al. (2023) found that, after installing two novel puzzle boxes (in a single location, ~30 m apart) baited with fruit in a protected wildlife sanctuary in Thailand, 21 of the 44 wild Asian elephants that interacted with the box returned to interact with it more than once over a 6-month period. Although the investigators were not directly studying memory, the study may suggest that elephants remembered the location of the box and returned to obtain more fruit. However, more work would be needed to exclude other possibilities, such as the elephants' use of odor cues to locate the food or that the box was on a frequent travel route.

Migration patterns

In comparison with experiments where elephants must find food rewards in specific locations, studies that investigate natural migration patterns of wild elephants can increase our understanding of how elephants may use spatial memory to navigate their environment. For example, African savanna elephants show site fidelity to particular resource locations over the long-term, and this site preference does not always correlate with resource availability (Fishlock et al., 2016). Indeed, using 6 years of telemetry data, Tsalyuk et al. (2019) found that African savanna elephants revisited areas with a history of being resource-rich within the past decade more frequently than areas where foraging opportunities were currently more plentiful. This suggests that elephants are using spatial memory to inform foraging decisions because if elephants were relying solely on local sensory input, they would likely choose the areas that were currently richer in resources, instead of maintaining their preference for previously resource-rich areas. Thus, a reliance on spatial memory could explain the mismatch between elephant migration decisions and current resource availability (Fishlock et al., 2016). Importantly, relying on long-term resource trends instead of searching for new resource areas may be more effective and increase the likelihood of finding food, especially when resources are scarce. Accordingly, Tsalyuk et al. (2019) found that elephants preferred historically rich areas in the dry season, but not in the wet season.

It is likely that elephant spatial memory when traveling to resources involves using cognitive maps. Polansky et al. (2015) used state–space models of African savanna elephant movement data and found evidence that elephant groups make rapid, directional movements to minimize travel when accessing distant water sources that are out of visual and olfactory range. Specifically, they showed that groups initiated these directional movements up to 50 km from the waterhole destination. The directional, goal-oriented movements shown in this study suggest that elephants are using cognitive maps (Bohbot, 2015; Iaria et al., 2003; O'Keefe & Nadel, 1978). Compared with simple route-following, where complex decision-making is not needed once the route is learned, using cognitive maps implies that the individual understands the relationship among landmarks in the environment in such a way that novel trajectories can be taken to reach the destination (Bohbot, 2015; O'Keefe & Nadel, 1978). Polansky et al. (2015) showed evidence for this, because elephants traveled directly to waterholes when starting from multiple starting points, suggesting that they were not simply following a single, known route. Furthermore, cognitive maps are dependent on the hippocampus (Bohbot, 2015; O'Keefe & Nadel, 1978), which is a brain region that is important for memory, and specifically spatial memory (Sherry et al., 1992). Because elephants have a large hippocampus with a high neuronal density (Shoshani et al., 2006), this provides more evidence that they are likely using hippocampus-dependent cognitive maps. However, it is important to note that Polansky et al. (2015) also acknowledge that their study cannot rule out the possibility of elephants following scent markings or odor cues of other elephants, which would not require spatial memory.

Interestingly, there is evidence that elephants use different navigation strategies depending on their familiarity with a particular location. Presotto et al. (2019) found that, when in the core area of their home range, African savanna elephants travelled to resource locations from various starting points and using many different travel paths, suggesting that they may have used cognitive maps. However, when they were on the periphery of their home range, individuals switched to using habitual routes—which are cognitively less demanding (Presotto et al., 2019). This strategy switching is similar to behavior observed in primates (Normand & Boesch, 2009; Presotto & Izar 2010), and using habitual routes in less familiar places may allow elephants to become familiar with them so that they can eventually form and use a cognitive map (Presotto et al., 2019).

Future directions of interest

The studies described above suggest that elephants can remember various types of information in the short term and likely have a large working memory capacity. However, despite the saying that an "elephant never forgets," there are only a handful of studies that investigate long-term memory. These few studies showed evidence for long-term memory of visual (Markowitz et al., 1975; Rensch, 1956, 1957), olfactory (Arvidsson et al., 2012; Rizvanovic, 2012), and auditory (Rensch, 1957) stimuli, as well as vocalizations (McComb et al., 2000) and odors (Hoerner et al., 2023) of familiar individuals. Furthermore, elephants showed long-term memory in performance of a spatial task (Dale, 2008) and for spatial memory of resources in the environment (Polansky et al., 2015; Tsalyuk et al., 2019). Although the observation of natural elephant behaviors, such as greeting ceremonies (Hörner et al., 2021) and grief-like behaviors (Douglas-Hamilton et al., 2006) may also be evidence that elephants have long-term social memories for specific individuals, more controlled experimental studies are needed to exclude other possibilities such as phenotype matching to recognize kin (Lacy & Sherman, 1983) or general interest in carcasses of conspecifics (McComb et al., 2006). We encourage future cognitive studies to consider the collection of long-term data to determine the extent of what elephants can remember and for how long. When designing experiments to investigate memory, appropriate controls should be used to exclude other possible factors (e.g., odor cues) and care should be taken to design experiments according to the sensory perspectives or *umwelt* of elephants (Jacobson & Plotnik, 2020). Below, we outline specific areas where it would be of particular interest to study memory in this taxon.

Individual variation in memory

Thus far, the few studies that have directly studied elephant memory have focused on demonstrating that elephants have the capacity to remember certain information. This is an important first step to understanding memory capabilities at the species or taxon level; however, little attention has been given to potential individual, within species differences in memory. Studies have demonstrated that individual elephants vary in a number of cognitive abilities and behaviors, such as innovation (Jacobson et al., 2022, 2023), cooperation (Plotnik et al., 2019; Li et al., 2021), and personality (Barrett & Benson-Amram, 2021), and thus it is possible that aspects of memory also differ at the individual level. For example, in other taxa, individual variation in memory is explained by factors such as sex (e.g., rodents: Jonasson, 2005; birds: Guigueno et al., 2014; Kosarussavadi et al., 2017), age (e.g., rodents: Frick, 2009; birds: Kosarussavadi et al., 2017), and developmental conditions (e.g., early-life stress in rodents: Rocha et al., 2021; birds: Bell et al., 2018; Kriengwatana et al., 2015).

In elephants, there are various biological, ecological, and social factors that may potentially lead to interindividual differences in cognition and memory. For example, life histories of males and females differ substantially. Females live in matriarchal fission–fusion societies, where they remain in their natal groups their entire lives (Archie et al., 2011; Buss & Smith, 1966; de Silva & Wittemyer, 2012; Fishlock & Lee, 2013; Schuttler et al., 2014), and the matriarch—usually the oldest, most experienced female—leads decision-making in the herd (de Silva & Wittemyer, 2012; McComb et al., 2011; Mizuno et al., 2017; Vidya & Sukumar, 2005). In contrast, males leave their natal group at sexual maturity and are either solitary or live in small "bachelor herds" (Srinivasaiah et al., 2019; Vidya & Sukumar, 2005). It is possible that these differences in life history between sexes may also be associated with differences in memory. For example, Polansky et al. (2015) found that male and female African savanna elephants displayed different movement behaviors when making decisions to travel to waterholes, where females walked longer distances to waterholes after initiating rapid and directional movement. Although there are many factors that may drive this difference in decision-making, such as variation in group structure, foraging requirements, or responsibility for dependent young, it would be interesting to determine whether it is related to a sex difference in spatial memory.

Age is also an important factor that may shape cognitive differences. For example, there is evidence that older matriarchs possess more social and environmental knowledge than younger matriarchs (McComb et al., 2001, 2011). Although this does not necessarily mean that older individuals can store more information for a longer time compared with younger individuals, it does suggest that older individuals have acquired information over their lifetimes, and are capable of remembering it. In contrast, Nissani et al. (2005) found that older elephants were less likely to meet task criteria in visual discrimination tasks. Because working memory is involved in visual discrimination tasks, it is possible that this age difference in task performance was due to a weaker working memory in older individuals; however, it could also be due to other factors that may vary by age, such as visual perception, or methodological issues that failed to account for the importance of other, nonvisual sensory information in elephant decision-making (Jacobson & Plotnik, 2020). Thus, it would be interesting to experimentally test the ability of elephants of different ages to remember newly acquired information and to control for different amounts of experience, while also controlling for confounding variables associated with potential age-related differences in certain sensory modalities.

Lastly, there is also evidence that environmental conditions during development may affect behavior and cognition. For example, African savanna elephants who were orphaned as calves display different behaviors than those who were not (Bradshaw et al., 2005; Goldenberg & Wittemyer, 2018, 2020). Because stressful early life experiences are associated with memory differences in other species (e.g., Elzinga & Bremner, 2002; Kaouane et al., 2012; Pravosudov et al., 2005), it would be interesting to determine whether similar differences in memory exist between elephants who were orphaned at a young age and those who were not. However, these studies would also have to carefully consider other environmental factors that may be different between orphans and nonorphans, such as interaction with and help from humans throughout their lives.

Overall, we suggest that future studies focus more on individual variation, and integrate factors such as sex, age, and environmental conditions into their analyses whenever possible. However, we acknowledge that this is not always possible because sample sizes are often limited, especially in zoo settings (Plotnik et al., 2010). Thus, it is likely that studies may have to focus on one particular factor (e.g., sex or age), although studies in which sample sizes are large enough to test interactive effects (e.g., sex × age) would be particularly interesting.

Trade-off between long-term memory and memory flexibility

If there are individual differences in elephant memory, it would also be interesting to determine whether memory differences covary with other cognitive abilities and expressions of behavior that vary among individuals (e.g., Barrett & Benson-Amram, 2021; Jacobson et al., 2023). For example, do the most innovative elephants also have the ability to retain knowledge for the longest period of time, or is there a trade-off? In other species, long-term memory capacity appears to be negatively related to flexibility in memory, or the ability to acquire and store new information (reviewed in Tello-Ramos et al., 2019). Once an animal stores information in long-term memory, it may be difficult to relearn new information, especially if it conflicts with the old information. Alternatively, if an animal can quickly and flexibly relearn information in a changing environment, they may not be able to retain information for long time periods. This has been examined using long-term memory tasks, coupled with reversal learning tasks, and trade-offs between long-term memory and reversal learning have been demonstrated between (Hampton et al., 1998) and within (Croston et al., 2017) species.

Interestingly, current—*albeit*, limited—evidence suggests that elephants may have both extensive long-term memories (Arvidsson et al., 2012; Dale, 2008; Hoerner et al., 2023; Markowitz et al., 1975; McComb et al., 2000; Polansky et al., 2015; Rensch, 1956, 1957; Rizvanovic, 2012; Tsalyuk et al., 2019) and cognitive flexibility (e.g., innovative problem solving; Jacobson et al., 2022, 2023). Thus, it would be interesting to investigate whether or not elephants succumb to a trade-off between long-term memory and flexibility. To investigate this, future studies that test long-term retention of certain information (e.g., longitudinal discrimination tasks) could subsequently investigate reversal learning (i.e., tasks that test for an ability to learn switching contingencies) to determine whether elephants continue to use the discrimination criteria that they learned months/years earlier, or if this learned behavior is extinguished and replaced by learning of the new criteria. Furthermore, because the intensity and directionality of this trade-off may also vary within a species (e.g., Croston et al., 2017), it would be interesting to determine whether the relationship between long-term memory and reversal learning varies across individual elephants.

Episodic memory

Once we know which information animals can store and recall and for how long, the next interesting question is—*how* do they recall that information? For example, do animals simply recall facts and knowledge, or can they recall specific events, as humans do? Episodic memory is recall through the replay of a unique event as a mental image, where the individual can remember a specific event, where it was, and when it took place (Tulving, 1972). In humans, episodic memory is characterized as a conscious recollection of a past, personal event with vivid mental imagery (Tulving, 1972, 1985). Furthermore, it is hypothesized that the "mental time travel" related to recalling past episodes is necessarily related to the ability to imagine and plan for the future (Cheke & Clayton, 2010; Clayton, 2017).

Although there is still debate as to whether episodic memory is unique to humans (Clayton, 2017; Clayton & Russell, 2009; Suddendorf & Corballis, 1997), some behaviors of elephants could suggest that they are experiencing the vivid mental imagery associated with episodic memory. For example, showing excitement during greeting ceremonies when reunited with a family member who they have not seen in years (Hörner et al., 2021), grief-like behaviors after the death of a family member (Douglas-Hamilton et al., 2006), or PTSD-like behaviors years after a traumatic event (Bradshaw et al., 2005) all could suggest that elephants are experiencing vivid memories of individuals and events rather than simply recalling facts (i.e., semantic memory). Furthermore, although anecdotal, there is some evidence for future planning in elephants (Bates et al., 2008a). For example, elephants appear to "cache" small water sources with chewed bark (Gordon, 1966), they travel to distant water sources in apparent anticipation of droughts (Moss, 1992), and there is anecdotal evidence of semicaptive elephants putting mud in the bells around their necks, possibly so that later that night they are not heard by nearby humans (Williams, 1950). Because the ability to imagine and plan for the future may be closely linked to the ability to recall mental imagery of past events (Cheke & Clayton, 2010; Clayton, 2017), these observations suggest that elephants might be experiencing mental imagery about the past and future. However, because we cannot empirically test whether animals experience mental imagery or not, it remains unknown whether elephants may experience episodic memory like humans.

Although Tulving (1972, 1985, 2005) argued that consciousness is a requirement of episodic memory, Clayton and Dickinson (1998) set out to investigate whether nonhuman animals may exhibit memory that meets the other aspects of Tulving's (1972) definition. Specifically, they aimed to determine whether animals can remember the spatiotemporal aspects of a past event (Tulving, 1972), and termed this "episodic-like memory" (Clayton & Dickinson, 1998). They experimentally tested whether scrub jays (*Aphelocoma coerulescens*) could remember the location (i.e., "*where"*) of a specific food item (peanuts or larvae; i.e., "what"), along with the time at which it was hidden (i.e., "when"). They found that birds preferred to visit locations where they had cached larvae—their preferred but perishable food—4 hours previously. However, after 124 hours—when the larvae would have decayed—birds preferred to visit locations where they had hidden another, nonpreferred but nonperishable food (peanuts). This provides evidence for episodic-like memory because the scrub jays demonstrated that they were able to remember the "what" (i.e., peanut or larvae), "where" (i.e., caching location), and "when" (i.e., when the food was cached, in relation to when larvae would decay) of a past event (Clayton & Dickinson, 1998). Since then, evidence for this "what-where-when" memory has been found in other birds (Marshall et al., 2013; Skov-Rackette et al., 2006; Zinkivskay et al., 2009) as well as nonhuman primates (Hampton & Schwartz, 2004; Martin-Ordas et al., 2010; Schwartz & Evans, 2001), rodents (Babb & Crystal, 2005; Bird et al., 2003; Dere et al., 2005; Naqshbandi et al., 2007; Panoz-Brown et al., 2016; Roberts, 2016), cetaceans (Davies et al., 2022), dogs (Lo & Roberts, 2019), and even cuttlefish (Jozet-Alves et al., 2013).

The first step to determine whether elephants may use episodic-like memory to recall past events is to adapt a version of the Clayton and Dickinson (1998) study for elephants. Specifically, future research should investigate whether elephants can simultaneously remember the "what," "where," and "when" of an event, while accounting for elephants' multimodal sensory perspective. For example, a task that relies on perceiving and remembering solely visual cues may not adequately test the cognitive abilities of elephants because the task may lack ecological validity (Jacobson & Plotnik, 2020). The experimental design employed by Martin-Ordas et al. (2010) for great apes, for instance, carefully considered the ecological validity of using caching paradigms—previously employed with corvids—with non-caching primates, and instead used the perishability of food across shorter time intervals (e.g., frozen juice that melts in less than an hour vs. less-preferred food rewards such as grapes) to see if the apes' changing preferences over time were indicative of episodic-like memory. Our own research team is considering a design for elephants that focuses on the elephants' perception of changes in food quantities over time as a method for testing for this capacity. This paradigm would be based on our previous research showing that their perception of differences in quantities based on olfaction is particularly keen and that they do consistently prefer larger quantities over smaller ones (Plotnik et al., 2019). Strong, consistent food preferences that can be manipulated over controlled time intervals has been an important factor in the design of most paradigms that have tested for episodic-like memory thus far (Clayton & Dickinson, 1998), and we would consider similar parameters in our own elephant research designs.

Studies to investigate whether elephants can plan for the future should also be considered, since all current evidence in elephants is anecdotal. Experimental studies have provided evidence that apes save tools for future use (Mulcahy & Call, 2006), and scrub jays will cache food in locations based on their future needs (Raby et al., 2007). Adapting studies like these to situations that are more relevant to elephants, such as those involving the anticipation of seasonal food sources or social interactions, would shed light on whether they may be able to imagine future situations, an ability that is closely associated with episodic memory (Cheke & Clayton, 2010; Clayton, 2017).

Comparative studies

The three extant elephant species diverged approximately 6 million years ago (Maglio, 1973; Rogaev et al., 2006) and have evolved in different environments on different continents; however, they all appear to exhibit complex social behaviors and cognitive abilities. Therefore, conducting comparative studies within the elephant taxon will further our understanding of how memory capacities may evolve under different environmental pressures in species that are cognitively flexible. However, the three species are not equally represented throughout the current body of literature. For example, there are a disproportionate number of studies on the behavior of wild African savanna elephants compared with studies on the other two species. Indeed, to our knowledge, the only three studies that directly investigate memory in wild elephants were conducted on African savanna elephants (Polansky et al., 2015; Presotto et al., 2019; Tsalyuk et al., 2019). Furthermore, no studies to date have explicitly investigated African forest elephant memory, although one study showed that they likely make long, directed movements to preferred fruiting trees, suggesting their potential use of cognitive maps in spatial navigation (Mills et al., 2018). We acknowledge that there are logistical difficulties, specifically with studying the behavior of Asian and African forest elephants in the wild, because they live in heavily forested habitats where behavioral observations are difficult. However, using camera traps appears to be a promising new technique to study elephant behavior in forests (Jacobson et al., 2023; Montero-De La Torre et al., 2023; Ngama et al., 2018; Ranjeewa et al., 2015). For example, camera traps can be programmed to record almost continuous video data (e.g., <1 s recovery time), so that precise behaviors can be observed over time (e.g., Jacobson et al., 2023). In addition to further cross-species comparisons of memory within the elephant taxon, we also strongly encourage intertaxon comparisons of memory that consider ecological validity in the design of experimental protocols. Given that elephants are evolutionarily distant from the common subjects of animal memory research (e.g., primates, rodents, corvids), more comparisons among species will improve our understanding of the evolution of memory across taxa and the use of different sensory modalities in the storage and expressions of memory (Plotnik & Clayton, 2015).

Applications

Memory in the context of crop foraging and human–elephant conflict

With increasing human development, fragmentation of elephant habitat, and expanding agriculture, elephants must increasingly look for alternative sources of food (LaDue et al., 2021a, 2021b; Leimgruber et al., 2003; Riddle et al., 2010). Because of this, some elephants have begun foraging on high-calorie crops as their main food source, which results in conflict involving elephants and farmers (Fernando et al., 2008). To access crops, elephants have learned to overcome barriers, such as electric fences, that are meant to deter them from entering crop fields (Kioko et al., 2008; Mutinda et al., 2014). This makes mitigating this human–elephant conflict even more complicated, and results in an “arms race” in which farmers implement different mitigation strategies and elephants learn how to overcome them. Interestingly, however, not every animal in a given elephant population enters into conflict with humans. Instead, there are often “problem individuals” (Barrett et al., 2019; Hoare, 2001) that regularly engage in negative interactions with humans while a large majority of elephants within a particular population may stay inside a protected area and avoid human contact (Plotnik & Jacobson, 2022). Thus, targeting mitigation toward specific individuals, instead of employing “one size fits all” mitigation strategies that do not consider individual variation in behavior, is likely one key to human–wildlife coexistence (Mumby & Plotnik, 2018; Plotnik et al., 2023; Plotnik & Jacobson, 2022). For example, if we can understand the behavioral differences between elephants who forage in crop fields and those who do not, we may be able to develop strategies, such as behavioral conditioning interventions (Plotnik & Jacobson, 2022; Snijders et al., 2019) that are specifically tailored to the behavior of the “problem” elephants.

Memory may be one important aspect of cognition in the context of human–elephant conflict mitigation (Barrett et al., 2019). For example, understanding how elephants remember certain types of information could help us understand how they may act in human-dominated landscapes. Interesting questions that would be helpful in this context include the following:

1) How long can elephants remember the location of a crop field?
2) How do elephants navigate back to the same crop field (e.g., using cognitive maps or habitual routes)?
3) After how many interactions with a positive (e.g., eating calorie-rich crops) or negative (e.g., facing an aversive mitigation strategy such as an electric fence or fire) stimulus will it take before an elephant remembers to return to or avoid a certain location?
4) If an elephant learns how to overcome a certain artificial barrier, for how long is that memory retained?

To answer these questions, future studies would need to investigate memory in wild populations and determine whether memory differs between elephants who forage on crops and those who do not. Understanding which types of memory may be associated with crop foraging can help to create targeted mitigation strategies that are tailored to the memory capacities of the particular individuals who enter crop lands (Mumby & Plotnik, 2018; Plotnik et al., 2023). For example, if crop-foraging elephants can quickly find and remember new locations, then strategies in which new, attractive habitats are created (e.g., artificial watering holes or crops provided just for elephant consumption) may be effective in luring elephants away from a village crop field. On the other hand, if crop-foraging elephants have a precise long-term memory for a specific location but have difficulty learning new locations, then strategies that make crops unpalatable (e.g., planting chili around fields: Sitati & Walpole, 2006) or deter elephants (e.g., by placing lion dung around fields; Valenta et al., 2021) may be more effective. In addition, if we can determine how elephants navigate to known crop fields (e.g., by using certain landmarks), mitigation strategies can be strategically placed at important landmarks to deter elephants before they reach the crops. However, in all of these cases, the potential consequences of each mitigation strategy must be taken into consideration. For example, crop fields dedicated to elephants could cause elephants to develop a “taste” for these crops and increase crop raiding, and growing unpalatable crops on a large scale may lead to habitat loss (Fernando et al., 2008). This could augment the root cause of the problem, which is that elephants lack resources as urbanization and habitat fragmentation increase. Therefore, although understanding elephant memory can help in the conception of new mitigation strategies, this is a complex issue that requires collaboration across disciplines.

Memory and aging

Interestingly, elephants may also serve as a useful model for understanding age-related memory decline in humans (reviewed in Chusyd et al., 2021). Elephants are long-lived, with lifespans of 60–65 years (Chusyd et al., 2021; Lee et al., 2016), and some elephants even live into their 80s (Lahdenperä et al., 2014). Furthermore, females can continue to reproduce up into their 60s (Lahdenperä et al., 2014; Moss, 2001; Turkalo et al., 2018). Despite this longevity, older individuals do not appear to suffer social inadequacies or behavioral aging (Chusyd et al., 2021; Lee et al., 2016). For example, older matriarchs appear to have the most social and ecological knowledge within a herd (McComb et al., 2001, 2011), and daughters who have their mothers and grandmothers present when they are reproducing have greater reproductive success (Lee et al., 2016). This longevity without apparent cognitive decline could be partly explained by the fact that elephants possess at least 20 copies of the gene TP5, which prevents apoptosis, or cell death, and protects elephants from cancer (Abegglen et al., 2015; Chusyd et al., 2021; Padariya et al., 2022; Sulak et al., 2016). In comparison, humans possess only one copy (Abegglen et al., 2015; Chusyd et al., 2021; Padariya et al., 2022; Sulak et al., 2016). Elephants also need fewer hours of sleep (i.e., 2–4 hours; Gravett et al., 2017) compared with humans. Because sleep is important for human cognitive functioning, including the consolidation of memories (Deak & Stickgold, 2010), it would be interesting to understand how elephants retain high cognitive functioning despite little sleep. Studying how elephant memory may change with age, which physiological mechanisms are associated with it, and how it compares to human age-related cognitive decline could help us understand the mechanisms of age-related or neurodegenerative diseases in humans, including Alzheimer’s, dementia, and cancer. To do this, more studies should examine age differences in elephant cognition studies. Multidisciplinary studies that investigate age-related differences in memory, along with physiological correlates (e.g., hormones), would be especially important in this context.

Promoting conservation

Asian and African savanna elephants are listed on the International Union for Conservation of Nature (IUCN)’s Red List as endangered (Gobush et al., 2021a; Williams et al., 2020), while the African forest elephant is listed as critically endangered (Gobush et al., 2021b). Only an estimated ~50,000 Asian elephants (Menon & Tiwari, 2019) and ~400,000 African elephants (both species combined; Thouless et al., 2016) remain in the wild. The main threats to each of these species are continent specific. The imminent threats to African elephants include both poaching and human–elephant conflict (Campbell-Staton et al., 2021; Hauenstein et al., 2022; Hoare, 2015; Maisels et al., 2013; Schlossberg et al., 2020), while the rapid decline in Asian elephant populations can be attributed to increasing human development, which has led to extensive deforestation and fragmentation of elephant habitat in addition to increased human–elephant conflict (Barnes, 1996; Compaore et al., 2020; LaDue et al., 2021a, 2021b; Leimgruber et al., 2003; Riddle et al., 2010). In addition to helping create human–elephant conflict mitigation strategies that take elephant behavior into account (Mumby & Plotnik, 2018; Plotnik et al., 2023; Plotnik & Jacobson, 2022), studying and then highlighting specific cognitive abilities in elephants that are considered comparable with humans, such as innovation and complex memory, may also foster investment in the conservation of these species (Chan, 2012; Makecha & Ghosal, 2017; Marzluff & Swift, 2017). For example, case studies of geographic areas with human–wildlife conflict show that empathy for animals and intangible benefits related to their existence is a greater predictor of community tolerance for those animals than monetary costs or benefits (e.g., Kansky & Kidd, 2024; Saif et al., 2020). Furthermore, "displays of intelligence" was regarded by the public in the UK as one of the most important traits that they wanted to see in a zoo animal (Carr, 2016). Thus, promoting empathy for and interest in endangered animals through the communication of empirical evidence of their cognitive abilities may be a way to promote conservation.

One study tested this idea of whether emphasizing elephant cognitive abilities in an educational program would increase interest in conserving them. Makecha et al. (2022) compared the attitudes of adult male villagers in Karnataka, India, toward elephants before and after either their participation in an educational program that emphasized the cognitive abilities of elephants or one that did not. They found that cognition-based and non-cognition-based programs both had similar positive effects on attitudes towards elephants, compared with a control. The authors noted that the lack of difference could be influenced by the fact that community members in areas with human–elephant conflict are likely already familiar with the cognitive abilities of elephants, especially as it pertains to their ability to overcome fences/barriers. However, their study still suggests that there are benefits of such educational programs that could lead to more favorable attitudes toward elephants.

Conclusion

Despite the popular notion that an "elephant never forgets," the jury is still out. A growing body of literature on elephant cognition, along with the few studies that directly investigated long-term memory, suggest that elephants likely have a large working memory capacity, and can remember familiar individuals, locations of resources over long periods of time, and rules in discrimination tasks. However, we are still only scratching the surface in our understanding of elephant memory. There is a clear need for new, well-controlled experiments to determine which types of information elephants can remember and for how long. Furthermore, investigating individual variation in memory among elephants would allow us to test predictions of how memory may vary based on factors such as age, sex, environmental conditions, or other cognitive factors. In addition to asking *which* types of information elephants remember, another important question to ask is *how* do they remember it? In particular, future studies should investigate whether elephants may have episodic-like memory. There is also a need for more studies on cognition in all three living elephant species to provide insight into how memory may differ among similar species that exist in different environments. Finally, a better understanding of elephant memory will not only further our understanding of how memory has evolved across evolutionarily distant and diverse taxa but may also provide insight into memory and aging in humans, aid in developing mitigation strategies for human–elephant conflict, and promote efforts to conserve the entire elephant taxon.

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