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A "thinking animal" in conflict: studying wild elephant cognition in the shadow of anthropogenic change

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While researchers interested in the evolution of human intelligence have traditionally focused on the psychology of other primates, a growing field aims to understand how similar cognitive abilities emerge in evolutionarily distant taxa. Here, we briefly review what we know, and why we do not know more, about the 'mind' of one such animal — the elephant — as well as its relevance to understanding convergent cognitive evolution across species. We also discuss the importance of studying animals such as elephants in the wild to better identify expressions of cognitive flexibility in human-impacted environments. Finally, as researchers invested in the study of an endangered species, we emphasize the need to contribute to the management of conservation-related problems from novel, cognitive perspectives.

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Introduction

A wealth of research over the past century about the evolution of intelligence in humans has provided considerable evidence about the divergent evolution of cognitive processes within the primate taxa (reviewed in Ref. [1]). Longitudinal ethological studies of nonhuman primate behavior in the wild (e.g. [2]), as well as extensive experimental work in laboratories has provided a clearer picture of whether certain cognitive capabilities are uniquely human (or ape) within the primate order [1]. Over the past several decades, however, growing interest in the proximate mechanisms underlying the behavior of nonprimates, including birds (e.g. [3,4]), cetaceans (e.g. [5]), canids (e.g. [6,7]), and elephants [8,9•], has suggested that, through convergent evolution, these animals may share similar cognitive traits with us as well. These similarities across evolutionarily distant species are almost certainly not the result of common ancestry, which is especially obvious when considering traits that apes may share with nonprimates yet not with monkeys (e.g. [10]). Instead, common environmental pressures on the need for behavioral flexibility in physical and social decision-making likely led to common cognitive traits in these distinct taxa [11]. Thus, expanding research beyond the primate lineage can provide important clues about how animals adapt to changes in the environment, and particularly whether similar needs — such as protecting young, defending against predators, or solving problems - may lead to similar physical and socio-cognitive abilities in unrelated species. Within the past 20 years, the number of research labs studying comparative cognition has grown significantly. New collaborations have emerged focused on studying common cognitive traits across species within (e.g. canids — [12]) and between (e.g., a review of corvids and other birds — [13]) families, as well as between orders (e.g., birds and primates - [14]), and have synthesized data from several labs, creating the potential for impressive datasets and allowing for important analyses of individual variation in cognitive expression [15,16].

The adage, "an elephant never forgets," implies a potential for complex cognitive abilities in elephants but, remarkably, relatively little research on elephant cognition has been done to date. Elephants live in large, fission-fusion matriarchal family groups with multimodal sensory perception and communication, and are capable of problem-solving, targeted helping, and empathy [9•,17], but we know this largely due to long-term ethological studies (e.g. [18]). The paucity of experimental data is likely due both to the difficulty of testing elephants in captivity — there are no university labs in which elephants can, or should be transported — and in the wild, where rapidly decreasing numbers and increasing conflict with humans make it difficult to establish controlled research programs [19••]. There is thus a clear need to overcome these difficulties by encouraging further research into elephant intelligence by complementing captive research with novel investigations of cognition in the wild. Existing populations of elephants in captivity in both western zoos and range country tourism or ex-logging facilities, particularly in Asia, can allow for comparisons of cognitive capacities across evolutionarily distant taxa using relatively similar experimental paradigms (e.g. [20,21]). In addition, the challenges elephants face in wild landscapes where they live between protected and disturbed habitat provide an opportunity to explore individual variation in personality, cognition, and behavior. Here, we a) explore reasons why we do not know more about elephant cognition (i.e. why it is so difficult to study it), b) briefly review what we do know about it thus far, and finally, c) explain how Asian elephants (Elephas maximus) present a unique opportunity to explore questions about the adaptive significance of cognitive and behavioral flexibility in animals in the face of rapid human-induced environmental change.

Limits on studying elephant minds

Long-term field sites have focused on the behavioral [18,22]; forest, L. cyclotis - [23]) and Asian elephants [24,25] for decades, providing considerable evidence for the complexity of elephant sociality across species. Nonetheless, relatively few studies have focused on the cognitive mechanisms underlying elephant behavior [9•,17]. While research on primate cognition has investigated a variety of physical- and socio-cognitive traits in monkeys and apes [1], with several capacities, including complex cooperation and memory, being explored in remarkable detail (e.g. [26,27]), no single capacity has been explored in-depth in elephants. In fact, the limited research in elephants has led to the drawing of rather broad assumptions about commonality in cognition across the three elephant species, even though Asian and African species diverged approximately 7.6 mya [28]. These assumptions are likely due to similarities in phenotypes and ecological niches - elephants are the largest herbivores in their environment ---even though differences in behavioral ecology have recently started to emerge [24]. Researchers should thus be cautious about generalizing cognitive abilities to all three species [29,30]. To our knowledge, there have not been any studies of African forest elephant cognition, so the cognition research discussed throughout this paper with African elephants refers to the African savanna species.

This lack of cognitive data for elephants is likely due to the significant difficulties in testing them in both captivity and the wild. Many of the reasons that it is difficult to test elephants in captivity are true for other large mammals as well, including apes [16]. First, it is extremely difficult to gain access to subjects, as facilities containing many of these species only hold several individuals and almost never in an ecologically relevant population (i.e. they are usually held in small family groups that do not consist of naturally occurring ratios of related to unrelated individuals). Researchers interested in studying elephants in locations where experimental conditions can be controlled are limited to the small populations in zoological institutions or populations in elephant range countries, particularly in Asia, where elephant captivity is prevalent in the tourism sector [31].

In both zoos in the West, where elephants are most often kept in protected contact (i.e. they can only be tested through physical barriers), and captive facilities in range countries where they are most often kept in free contact (i.e. they can be tested up-close and without artificial barriers), the animals are often tightly controlled by human handlers [31]. This control is primarily for safety reasons, but also results in high levels of variability in positive reinforcement training, or in some unfortunate situations, fear conditioning. The variation in the environments in which captive animals such as elephants are kept can greatly impact the ability to infer (and compare) natural cognitive abilities during experiments [32•], even though it does provide unique opportunities to study the interspecific relationships between elephants and humans [9•,31]. In addition, elephants are almost never kept in captivity in social groups beyond mother-infant pairs and several unrelated females; while this may allow for tests of a cognitive capacity in individuals, it makes it difficult to test for certain sociocognitive traits absent natural ecological validity. This socio-ecological validity is particularly important for any potential integration of cognitive research into our knowledge about the conservation issues facing wild populations ([19••]; Figure 1).

Such limitations suggest that a better focus of future elephant cognition research could be on wild populations, but the habitats in which wild elephants live have their own obstacles. While wild primates or birds can be followed in vehicles or tested in the wild with frequent experimental manipulations [33•], in many locations in Asia, for instance, this is difficult due to dense forest cover and the significant danger of encountering elephants. In order to avoid direct contact with wild elephants, at our own field sites in Thailand, we manipulate experiments systematically when elephants are not present, use video camera trapping to collect data remotely, and limit the number of trials and task phases we run. Even with these limitations, the sample size of test subjects and the ecological validity under which wild elephants are tested far exceed what is possible in captivity. The future of elephant cognition research will most certainly require more attention to the presentation of tasks that take the elephants' unique sensory perspectives and natural behavioral ecology into account [9•,19••], which will require novel approaches to overcoming the limitations of studying them in the wild.

Figure 1



A natural social group of elephants around a water hole in the Salakpra Wildlife Sanctuary, Kanchanaburi, Thailand. This is our primary field site for studying wild elephant cognition in Thailand. The population consists of roughly 250–300 individuals living both within the protected natural habitat of the sanctuary (a national park) and near the agricultural crop lands that border it and/or encroach within it. We are using remotesensing camera traps to collect continuous video behavioral data to aid in the identification of individuals living within this landscape. Here, you see a large family group consisting of adult and subadult females, and adolescent or juvenile males and/or females. This screenshot was captured from video recorded using a Browning Spec Ops Advantage trail camera.

Elephant cognition as we know it

Much of what we do know about elephant cognition is scattered across multiple cognitive themes, suggesting the field is new and studies often designed opportunistically. As elephants live in complex fission-fusion social environments, where they must keep track of social relationships with many partners [18,34], elephant social cognition is likely the area of research that has received the most attention. A study with wild African elephants, for instance, provided evidence that they could recognize up to 30 individuals based on odor cues and remember their relative locations [35]. All other social-cognition studies reviewed here were conducted in captivity. Asian elephants have demonstrated that they will wait for a partner when one is needed in a cooperative task [36] and can flexibly adjust their cooperative and competition-mitigation strategies in a group based on the quality of their social relationships [37•]. Individuals may also learn socially from each other, although only social facilitation has been observed experimentally, and only in African elephants [38]. Asian elephants also appear to recognize when a conspecific is in distress and will engage in affiliative behaviors with the distressed individual [39]. This is a similar reaction to what has been observed in thirdparty post-conflict affiliations or consolation in other species, such as chimpanzees (e.g. [40]), and thus may

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be suggestive of a capacity for empathic concern [41]. Asian elephants have recognized themselves in a mirror ([42]; Reiss et al., Plotnik et al., unpublished), suggesting a capacity for self-awareness on par with humans, other great apes, dolphins, magpies [10], and cleaner fish [43]. Several studies have also assessed elephant social cognition with humans as social partners in experiments. Asian elephants were not successful in a perspective-taking task requiring them to make a choice based on their understanding of a human's visual path [44], while African and Asian elephants have shown opposing capacities to follow a human's pointing cue (Asian elephants cannot: [29]; African elephants can: [30]). It is possible though that elephants' social cognition could extend to human relationships, as one captive Asian elephant organically imitated human speech, a potential method of strengthening his social bonds with his caretakers [45].

Elephants' physical cognition and problem-solving abilities have also been investigated in captive individuals, and most frequently in Asian elephants. They appear to understand means-end causal relationships, choosing to pull a tray connected to food rather than one not connected [46]. Studies have shown that Asian [47,48] and African [49] elephants can make relative quantity judgments using a combination of sensory cues, and Plotnik et al. [50] demonstrated that Asian elephants can do so when only olfactory information is available. Asian elephants were also capable of choosing a larger quantity based on a mental representation of food items and summation [51]. When provided with extractive foraging tasks, African and Asian elephants can successfully innovate to obtain food [20,52]. One Asian elephant also demonstrated insightful problem solving by using a tool to reach food without any trial-and-error learning [53].

Elephants are colloquially known for their good memories and some experiments with Asian and African elephants have supported this reputation, although the extent of their long-term memory has not been systematically investigated. Unlike the pattern of working memory decline seen in many working dogs [54], African elephants exhibited consistent working memory when tested in a match-to-sample task [55]. Asian elephants trained in other operant conditioning tasks have also showed long-term memory for rewarded stimuli in choice paradigms presented 16 weeks [56], 1 year [57], and 8 years [58] after initial learning. There is also some evidence of recognition by offspring of chemical cues from their mothers after almost 30 years of separation [59]. Given elephants' strong bonds with a large number of other individuals within and between their family groups [34], long-term memory for social partners should be the focus of, or considered carefully in future research.

While experimental playback studies have been used to ask questions about the behavioral ecology and acoustic communication capacities of wild elephants [60], very little research has focused on cognition in wild populations. In addition to the aforementioned study by Bates et al. [35], two other studies have employed sensory cues in the field to assess elephants' abilities to discriminate and categorize groups of humans. Bates et al. [61] showed that, when exposed to garments from different tribal groups, wild African elephants reacted differentially to the garment color and odor of the tribal group which most frequently threatened them. African elephants also behaved differently toward acoustic playbacks of the voices of different ethnic groups, responding defensively to the voices of the male warriors from a single tribal group that was a known threat [62]. Contrastingly, they did not respond as defensively to playbacks from other members of the same tribal group (females and children), or to vocalizations from members of a different tribal group with whom they did not have conflict, demonstrating the elephants' ability to discriminate and categorize the level of threat within and between these different human populations [62].

Cognition, anthropogenic change, and human-elephant conflict

While elephants face a number of anthropogenic threats (e.g. ivory poaching), all three species are faced with a growing number of negative interactions with humans with whom they share habitat [63•]. Human-wildlife conflict — which describes conflict between different human stakeholders over wildlife issues (IUCN SSC Human-Wildlife Conflict & Coexistence Specialist Group, URL: http://hwctf.org) — is growing worldwide due to increasing human development, population growth, and encroachment on protected/natural habitat. While natural wildlife behavior (such as foraging and social interactions) may exacerbate conflicts simply because it interferes with human activity in shared landscapes, some behaviorally flexible animals such as elephants are of particular concern because they seem to be adapting to anthropogenic change by learning to circumvent conflict mitigation strategies [19••,64••]. This suggests that attempts to simply keep wildlife and humans apart without addressing the ecological and cognitive needs of the former may be problematic.

In Asia, roughly 50 000 elephants remain $[63\circ]$. These elephants live almost exclusively in fragmented habitats, typically inside protected areas or between these areas and the agriculture that surround them. The loss of natural forest cover and the close proximity of existing habitat to human development has led to increased human–elephant conflict across the elephant range, with most of the negative interactions caused by competition for food grown for human consumption (i.e. agricultural

 $crops - [63 \bullet]$). Elephants forage on high-quality crops, and farmers react by using a number of mitigation strategies aimed at deterring elephants from entering crop fields. While in extreme cases these methods can be lethal, most of the strategies use varying degrees of fearbased conditioning to simply discourage elephants from entering crop fields, or to delay them from doing so, with the overall intention of decreasing rather than eliminating the crop yield lost to elephants. These strategies include stone, wire, electric and chili fencing (Figure 2), buffer cropping, noise making, predator playbacks, and honevbee fencing (for a review, see Ref. [63•]). The effectiveness of these different methods varies widely [63•,65], and likely depends on the location and the quality of the landscape shared by the humans and elephants in conflict, as well as individual variation in elephant behavior and cognition [19••]. The aforementioned mitigation strategies are often selected by local farmers based on their affordability and their traditional effectiveness [63•], but they are rarely used flexibly based on the identity of individual elephants who may respond differently to various mitigation strategies, nor are they often changed as elephants habituate to existing methods.

Our own research program aims to take a novel approach to human-elephant conflict by taking the elephant's

Figure 2



An adult male elephant approaching an electric fence near the Udawalawe National Park, Sri Lanka. This photo illustrates clearly how a mitigation strategy, an electric fence, is often employed to deter elephants from entering agricultural landscapes. While these fences can work temporarily, if not maintained properly or if challenged by a particularly innovative individual, elephants can manipulate and circumvent them to get on the other side. Individual variation in personality and other behavioral traits and cognition may explain why some elephants actively engage with these mitigation methods, while others do not. Identifying these differences could aid in the development of new strategies that take the behavior of the elephants into account. Published with permission from the photographer, Sreedhar Vijayakrishnan.



A wild elephant interacts with an innovative problem-solving apparatus in the Salakpra Wildlife Sanctuary, Kanchanaburi, Thailand. The multiaccess device or puzzle box seen in this video screenshot has three solutions (from top to bottom: slide a door open, pull a chain to open a door, or push a door open). Behind each door is a piece of jackfruit. Wild elephants can investigate and manipulate the boxes at will. Investigating variation in elephant innovative behavior may inform our understanding of variation in cognitive expression in elephants more generally. In addition, installing these boxes both within the protected area of the sanctuary and within or near agricultural areas can help determine whether innovation is a factor in crop-raiding or conflict-related behavior. This screenshot was captured from video recorded using a Browning Spec Ops Advantage trail camera.

'perspective' into account when designing mitigation efforts. This is particularly relevant when considering that the foraging behavior of elephants in and around crop fields is likely influenced by nonvisual sensory information [9•], social cues [66], and variation in personality and cognitive abilities between individual elephants [19••]. For example, recognizing the elephants' use of olfaction in foraging and social decisionmaking could be exploited to establish buffer zones of unattractive crops to deter entry from a safe distance [63•]. Identifying personality differences in elephants with a greater propensity to crop raid — including, potentially, innovation, neophobia, and boldness - could lead to the design of new mitigation strategies, or the implementation of existing ones using varied schedules. In our own work, we hope the study of individual variation in elephant personality and cognition could allow farmers to target specific mitigation toward elephants most likely to be affected by it. This provides a novel opportunity to not only move the study of elephant cognition from the 'lab' into the wild, but also to attempt to apply experimental and theoretical principles from the field of comparative cognition to endangered species' conservation in practice [19••].

Conclusions and future directions

The study of individual variation in behavior and cognition in anthropogenic landscapes is particularly interesting because it suggests that certain cognitive traits may be adaptive if flexibility allows an animal to keep up with rapid and often unpredictable environmental change [64••]. However, recent research with several species has not provided a clear picture of this issue. Studies of innovation (manipulation of one's environment in novel ways) in birds, for instance, have found a connection between innovation and success in urban environments [67], but urban hvenas were observed to be less innovative than hyenas living in a rural environment [68]. Perhaps the large-scale changes species often face in urban landscapes might, directly or indirectly, affect them differently as anthropogenic environmental changes are not often targeted toward these animals in particular. Studying elephants living in both stable and changing landscapes, however, may provide a unique perspective: many of the rapid changes they face are aimed specifically, by humans, at affecting the elephants' behavior. In other words, the elephants' behavior, unfortunately, is the direct cause of anthropogenic environmental intervention in the form of conflict-mitigation strategies. Thus, in real time, researchers can observe or test the behavioral and cognitive flexibility of elephants in relation to their interactions with human interventions. In addition, in many places elephants inhabit, they exist between adjacent a) protected habitat and b) agricultural land, allowing for studies of individual variation in behavior between these landscapes, as well as between individuals that reside in one, the other, or both of them.

We have already begun to investigate innovative problem solving in wild elephants using steel multi-access boxes (after [20], and similar to those discussed in Ref. [69] in the current issue) installed in a number of protected and human-disturbed areas, and have found that more than 50 individuals have interacted with or solved the boxes (Figure 3), with possible variation in success, in solving strategy, and between locations (Jacobson et al., unpublished data). In order to collect behavioral and cognitive data remotely, we have expanded existing methodologies for identifying elephants from photographs to include the use of remote camera traps set to record videos [70]. The elephants' engagement with our puzzle boxes and our ability to record them using remote monitoring in their natural habitat is promising for future cognitive studies with wild elephants as it demonstrates that elephants will interact with novel apparatuses absent human intervention and can be recorded doing so. We also have plans for investigating variation in a number of personality traits, as well as tool use and cooperation, with particular interest in how this variation is related to population dynamics (including between solitary adult males, smaller male-centric bachelor groups, and larger, female-centric matriarchal family groups) and how it is expressed within and between protected and human-disturbed landscapes.

From a basic psychological perspective, the goal of studying elephant cognition in a natural, wild context is to provide insight into expressions of cognitive traits in ecologically valid environments and populations. We can ask questions about flexibility in cooperation, tool use, and problem solving, for example, using paradigms designed and refined in captivity for use in the wild. While there are trade-offs between access to large naturally occurring populations and limited experimental control. adapting traditional cognitive paradigms and developing novel ones for wild populations, particularly in elephants, provides opportunities not possible in any captive population anywhere in the world. From an applied perspective, we propose that cognitive scientists studying species living in and affected by anthropogenic landscapes also consider how their work can promote coexistence between humans and wildlife by encouraging people to consider the behavior and cognition of the latter.

Author contributions

Joshua M Plotnik: Conceptualization, Writing – original draft, Writing – review & editing. Sarah L Jacobson: Writing – original draft, Writing – review & editing.

Conflict of interest statement

J.M.P. is president of Think Elephants International, Inc., a charity dedicated to elephant conservation.

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While observational research has shown that elephants are highly cooperative, this study investigated the potential mechanisms that help maintain cooperation. Specifically, the researchers studied how, in a task requiring the simultaneous pulling of two rope ends to obtain food, elephants a) choose to cooperate, b) engage in competition and c) mitigate such competition depending on the quality of the relationship between them. Elephants worked to maintain cooperation until the costs of competition became too high, at which point it broke down completely. This behavior has also been observed in humans, suggesting the mechanisms that underlie the capacity for flexible cooperation may not be unique to us.

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This is a comprehensive review of the strategies in use to mitigate human-elephant conflict in elephant range countries, and would be of significant interest to anyone that wants to understand why this conflict is so difficult to solve. The limited success of many of these strategies is due to a combination of cultural, social, political and economic pressures, as well as the behavior and complex needs of the humans and elephants involved in the conflict. The paper also provides a model for promoting long-term coexistence by considering elephant, human and landscape variables that contribute to the conflict.

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