Declaration of Michael A. Pardo

I, Michael A. Pardo, declare as follows:

Introduction and Qualifications

- 1. My name is Michael A. Pardo. I graduated with a Bachelor of Science (Summa Cum Laude) in Environmental Biology from the State University of New York College of Environmental Science and Forestry in 2012. I earned a Ph.D. in Behavioral Biology from the Department of Neurobiology and Behavior at Cornell University in 2019, where I studied vocal communication and social cognition in both Asian elephants and acorn woodpeckers. From November 2019 to October 2023, I was a National Science Foundation Postdoctoral Research Fellow in the Department of Fish, Wildlife and Conservation Biology at Colorado State University, where I studied vocal communication in African savannah elephants. Since November 2023 I have been a postdoctoral associate in the K. Lisa Yang Center for Conservation Bioacoustics at the Cornell Lab of Ornithology.
- I submit this declaration in support of the Nonhuman Rights Project, Inc.'s petition for a
 writ of habeas corpus regarding the captive elephants at the Pittsburgh Zoo & Aquarium. I
 am a nonparty to this proceeding.
- 3. I study vocal communication, social cognition, and population ecology in animals, and most of my work has been with elephants or birds. My research focuses on animal vocalizations from a variety of perspectives, including investigating how wild animals communicate with one another, playing back pre-recorded vocalizations to wild animals to explore their cognitive ability to understand complex social scenarios, and using recordings of vocalizations to monitor wild animal populations for the purposes of conservation.

- 4. I have been studying elephant vocal communication and behavior for approximately 13 years, since August 2012. For six of those years, I was exclusively focused on elephants, and for the remaining years I was also studying birds, while continuing to spend part of my time analyzing data and publishing scientific papers about elephants. I have spent over 21 months observing elephant behavior in the wild, including 7 months observing wild Asian elephants in Sri Lanka in 2012-2014, and 14+ months observing wild African savannah elephants in Kenya in 2019-2023. I have worked and co-authored studies with many of the world's preeminent elephant biologists, several of whom are also submitting declarations in this matter.
- 5. I have authored 10 peer-reviewed scientific journal articles about communication and cognition in elephants and other animals, as well as a book chapter about vocal communication in elephants. I have also co-authored a peer-reviewed book on statistical analysis geared toward other scientists who study animal behavior. My articles have been published in top scientific journals, including *Nature Ecology and Evolution*, *Current Biology*, *Proceedings of the Royal Society B*, *Royal Society Open Science*, *Behavioral Ecology*, and *Biological Reviews*. I have also written popular science articles about my work with elephants for *The Conversation* and *The UNESCO Courier*.
- 6. Additionally, my work on elephant vocal communication has been featured in more than 3,000 news articles, TV and radio broadcasts, and podcasts in at least 92 countries, including by major outlets such as the New York Times, the Associated Press, BBC World News, National Geographic Magazine, Scientific American, the Washington Post, CNN, Reuters, MSNBC, NPR: Morning Edition, The Atlantic, Fox News, Al Jazeera, and Vox.

- My work was also featured in a documentary by Scripps News titled "How scientists are using AI technology to communicate with animals".
- 7. I have given several invited talks throughout the world, including: (1) Universidad CES, Medellin, Colombia, 2018; (2) University of Vienna, 2019; (3) Decoding Communication in Nonhuman Species Workshop, 2023; (4) Protolang Conference Symposium: Elephants as a promising model for studying language evolution, 2023; (5) Our Honor (continuing education for veterinarians), 2024; (6) Princeton University, 2024; (7) Interspecies Internet (consortium of scientists studying animal communication), 2024; (8) Leadership for Conservation in Africa: Unlocking Nature panel, 2024; (9) International Association of Lawyers: Elephants, Science and the Law panel, 2024; (10) Performing Animal Welfare Society, 2024; (11) University of California San Diego, 2024; (12) Frontiers in Social Evolution Seminar, 2025; and (13) Bridging Brains and Bioacoustics Seminar, 2025.
- 8. I was recently named to the EC50 Class of 2025 by The Explorers Club, an award given each year to "50 extraordinary people who are doing remarkable work to promote science and exploration."
- 9. My Curriculum Vitae fully sets forth my educational background and experience and is annexed hereto as "Exhibit A".

Basis for Opinions

10. The opinions I state in this Declaration are based on my professional knowledge, education, training, and years of experience observing and studying elephants, as well as my knowledge of peer-reviewed literature about elephant behavior and intelligence published in the world's most respected scientific journals and books that are generally accepted as

authoritative in the field. Much of this literature was written by myself or colleagues whom I have known for years and with whose research and field work I am personally familiar.

Opinions

Premise

- 11. Elephants are autonomous beings. Autonomy in humans and nonhuman animals is defined as self-determined behavior that is based on freedom of choice. As a psychological concept it implies that the individual is directing their behavior based on some non-observable, higher-order cognitive processes, rather than simply responding reflexively. Although we cannot observe these internal processes directly, we can infer their presence if animals exhibit behavior that would require higher-order cognitive processing in humans.
- 12. I shall indicate which elephant species specific observations refer to: African savannah elephants (*Loxodonta africana*), African forest elephants (*Loxodonta cyclotis*), both African species ("African elephants"), or Asian elephants (*Elephas maximus*). If the general term "elephants" is used with no specific delineation, it can be assumed that the comment in question applies to all three species. Note that in many cases the presence of a particular behavior has only been assessed in one or two of the three elephant species and data on the other species are lacking. Data are especially likely to be absent for African forest elephants, which are the most difficult of the three species to study. Thus, if a behavior is only mentioned as occurring in one or two elephant species, it should not be assumed that the behavior is absent in the other species unless I state otherwise.

Awareness of self and others

13. Self-awareness, or a conscious sense of self, is a strong indication that an individual is an autonomous being. The most widely used test for self-awareness in animals is the mirror

self-recognition test, in which the subject is marked on a part of their body they cannot see without the aid of a mirror, and if they touch the mark significantly more in the presence of the mirror than its absence, they are considered to have passed the test (Gallup 1970). One Asian elephant has been shown to recognize herself in a mirror in this way (Plotnik et al. 2006). Although two other Asian elephants tested in the same study failed, the mirror self-recognition test is widely recognized to be highly conservative, meaning that many animals may fail the strict requirements of the test even if they are self-aware (Brandl 2018). Even human children as old as six years often fail the mirror test depending on their cultural background (Broesch et al. 2011). Given that elephants naturally cover their bodies with mud and other debris as a form of sunscreen/insect repellent, they may not be motivated to remove a mark on their head (Plotnik et al. 2006). Thus, the fact that even one Asian elephant has passed this test suggests that Asian elephants are very likely self-aware.

14. Self-awareness is thought to be linked to theory of mind, or the ability to attribute mental states to others and understand that they do not necessarily have the same thoughts, beliefs, and feelings as oneself (van Veluw and Chance 2014). Elephants demonstrate an awareness of what others can see, a key component of theory of mind. Both Asian elephants and African savannah elephants were more likely to use begging gestures to obtain food from a human experimenter when the experimenter was facing them than when the experimenter was facing away (Nissani 2004; Smet and Byrne 2014a). In another study, African savannah elephants were more likely to use silent gestures when greeting another elephant who was looking at them, but were more likely to touch the intended receiver or vocalize when greeting an individual who was looking away (Eleuteri et al. 2024).

- 15. There are several anecdotal reports by experienced elephant researchers of adult African savannah elephants leading calves away from terrain that the adult could traverse but the calf could not toward an area that was easier for the calf to pass through. For example, adults have been observed to lead calves toward a less steep part of a riverbank, even though the adult herself had no issue climbing over the steeper part. This suggests that adult African savannah elephants understand that calves do not have the same physical abilities that they do (Bates, Lee, et al. 2008).
- 16. African savannah elephants understand human pointing and can use it to find hidden food (Smet and Byrne 2014b). They can also infer the direction of an olfactory stimulus based on the direction in which other elephants are sniffing, even if they have not yet smelled the stimulus themselves (Smet and Byrne 2020). This provides further evidence for African savannah elephants' ability to understand the mental states of others. Asian elephants do not respond to human pointing on average, although some individual Asian elephants may respond to the gesture (Ketchaisri et al. 2019). However, this should not be taken to mean that Asian elephants lack an ability to understand the mental states of others. Asian elephants' ability to take into account what humans can see (Nissani 2004) and to comfort other elephants in distress (Plotnik and de Waal 2014; see below) strongly suggests that, like African elephants, they do in fact understand others' mental states. They may simply not respond to pointing because it is a human gesture that is not part of their natural behavioral repertoire or because they don't rely very heavily on vision (Ketchaisri et al. 2019).

Behavior towards the dead

- 17. Both African savannah elephants and Asian elephants display unusual interest in the remains of deceased elephants, suggesting that they may have an awareness of death. They frequently react to dead elephants by standing near the body and repeatedly touching it (Douglas-Hamilton et al. 2006; Goldenberg and Wittemyer 2020; Sharma et al. 2020). In two separate experiments, researchers presented African savannah elephants with the bones of elephants and other large mammals (giraffes, rhinos, and buffalos) and the elephants extensively touched and smelled the elephant bones but ignored the bones of the other species, indicating that they recognize the remains of their own species, even when all the soft tissue has rotted away (McComb et al. 2006; Goldenberg and Wittemyer 2020). Both African savannah and Asian elephants been observed attempting to lift or support dying and very recently deceased elephants, but they have not been observed to do so with older remains, suggesting that they may understand the finality of death (Goldenberg and Wittemyer 2020; Sharma et al. 2020).
- 18. Elephants sometimes transport elephant remains. African savannah elephants frequently carry the bones and tusks of deceased elephants away from the carcass, and female African savannah and Asian elephants have been observed carrying or dragging dead calves (Goldenberg and Wittemyer 2020; Pokharel et al. 2022).
- 19. On several occasions, African savannah elephants have been observed partially covering elephant carcasses or the severed body parts of other elephants with soil or branches (Goldenberg and Wittemyer 2020). They also frequently visit the carcasses of deceased elephants. In a long-term study of African savannah elephants in Northern Kenya, all carcasses recorded in protected areas exhibited signs of repeated visitation by other

- elephants, and elephants visited the carcasses of both relatives and non-relatives (Goldenberg and Wittemyer 2020).
- 20. A recent study documented five Asian elephant calves who were found partially buried in irrigation ditches in West Bengal, India, with only their legs protruding above the ground (Kaswan and Roy 2024). The authors argued that the calves were intentionally buried by other elephants based on several indirect pieces of evidence. 1) The calves all died of natural causes (cardiac arrest or bacterial infection), and there were no signs of humancaused injury, suggesting that the calves were not killed and buried by humans. 2) At least 3 of the 5 calves were surrounded by elephant footprints and/or elephant dung, indicating that a family group of elephants was present after the calf was buried. 3) At least 4 of the 5 calves had bruising or bleeding on their backs, consistent with the carcass being dragged some distance after death. 4) One of the calves was discovered 500 m from a human settlement and a post-mortem exam concluded that he had been dead for 60-72 hours. Kaswan and Roy argued that it is unlikely that the half-buried calf carcass would have gone unnoticed for 60-72 hours, suggesting that he was dragged there after death. 5) The irrigation ditches were 0.6-0.7 m deep, which Kaswan and Roy argued was likely too shallow for a calf to become trapped in. If these calves were indeed buried by other elephants, it would be an unprecedented example of sophisticated funerary behavior outside of humans.
- 21. Interestingly, Asian elephant family groups avoided the places where the calves were buried immediately after the burial, even though some of the calves were located along routes that were previously heavily trafficked by elephants (Kaswan and Roy 2024). This contrasts starkly with African savannah elephants going out of their way to visit elephant

carcasses (Goldenberg and Wittemyer 2020) and might reflect a difference in how the two species relate to death.

Social structure and relationships

- 22. Elephants live in complex societies with many differentiated social relationships. In all three species, males leave their mother's group as adolescents, and adult males live mostly separately from females and their dependent offspring (Moss and Poole 1983; de Silva and Wittemyer 2012; Fishlock and Lee 2013).
- 23. Female African savannah elephants live in a society with nested tiers of social affiliation. The most fundamental social unit is an adult female and her dependent calves. Multiple related females form a tightly knit "family group", led by the oldest female, or "matriarch". Multiple related family groups form a more loosely knit "bond group", and multiple unrelated bond groups form a "clan" (Moss and Poole 1983; Wittemyer et al. 2005). Female African savannah elephants regularly separate from and rejoin with their social affiliates in a "fission-fusion" dynamic, with larger groups tending to form in the wet season when more food is available (Wittemyer et al. 2005).
- 24. Female Asian elephants also live in social groups comprised of multiple related females and their dependent offspring, and like African savannah elephants exhibit a high degree of fission-fusion dynamics (Vidya and Sukumar 2005; de Silva, Ranjeewa, and Kryazhimskiy 2011; Nandini et al. 2018). However, their social groups tend to be smaller and less tightly knit than those of female African savannah elephants (de Silva, Ranjeewa, and Kryazhimskiy 2011; de Silva and Wittemyer 2012).
- 25. Female African forest elephants typically travel in very small social groups consisting of just a mother and her dependent offspring due to the constraints of finding food in a dense

rainforest environment (Fishlock and Lee 2013). However, they frequently congregate in forest clearings for the purpose of social interaction (Fishlock and Lee 2013). Moreover, genetic analysis of dung samples has revealed that African forest elephants preferentially associate with related individuals at a dispersed spatial scale, which suggests that they maintain social relationships with kin even if they are not always close together (Schuttler et al. 2014).

- 26. Female African savannah elephants rely on the knowledge of the matriarch to navigate social interactions and avoid threats. Groups with more experienced matriarchs are better able to distinguish between the calls of familiar and unfamiliar elephant families and better at distinguishing between the roars of male and female lions, which pose different degrees of threat to elephants (McComb et al. 2001; McComb et al. 2011).
- 27. Matriarchs are also important sources of spatial knowledge in African savannah elephants. One study examined the movement patterns of three elephant clans in Tarangire National Park, Tanzania during a drought. Two of the clans had several family groups with matriarchs over the age of 30, and these clans left the park in search of food and water elsewhere. The third clan had only one family matriarch over the age of 30 due to heavy poaching. This clan stayed in the park during the drought, and as a result, suffered much higher infant mortality than the two clans that left. This suggests that female African savannah elephants rely on the knowledge accumulated by matriarchs to find water and food during times of drought (Foley 2002).
- 28. In semi-captive Asian elephants in Myanmar, the mortality rate of calves was eight times lower if their grandmother lived with them, suggesting that older females play a critical role in Asian elephant society as well (Lahdenperä et al. 2016).

- 29. In the 1980's, South Africa culled African savannah elephants in Kruger National Park by shooting the adult members of family groups and capturing the young calves. Some of the juvenile elephants orphaned by these culls were translocated to Pilanesberg National Park, where they matured in the absence of older adults. Decades after the culling operations, female elephants in Pilanesberg showed impoverished social skills compared to a relatively undisturbed population in Amboseli National Park, Kenya. The Pilanesberg elephants failed to distinguish between the voices of familiar and unfamiliar individuals and failed to recognize vocal cues to the age of the caller, in sharp contrast to the Amboseli elephants. This indicates the importance of social learning for normal elephant behavior and the lasting negative impact of early social trauma in elephants (Shannon et al. 2013).
- 30. While male elephants were once thought to be solitary, it is now known that this is not the case (Morris-Drake and Mumby 2018; LaDue et al. 2022). Males frequently associate with other males in small loosely-knit groups with fission-fusion dynamics, and at least in African savannah elephants, studies have shown that they have preferred social partners and are more likely to associate with males to whom they are related (Evans and Harris 2008; Chiyo et al. 2011; Goldenberg et al. 2014; LaDue et al. 2022). Male Asian elephants in India form long-term, stable groups in human-modified landscapes, likely as a response to the danger associated with living near humans (Srinivasaiah et al. 2019).
- 31. Mature male elephants go through a period called musth every year, which is characterized by elevated testosterone levels, aggression, and sexual activity, and different individuals enter musth at different times of the year (Poole 1987). While male African savannah elephants tend to associate with each other most when they are not in musth, some males, especially older individuals, maintain their social ties even when in musth (Goldenberg et

- al. 2014). Musth also affects social behavior in male Asian elephants, with older males primarily associating with other males when not in musth and with female groups when in musth, and younger males exhibiting the opposite pattern (LaDue et al. 2022).
- 32. At least in African savannah elephants, older males play a critical role in male sociality, just as matriarchs do for female African savannah elephants. Adolescent male African savannah elephants prefer to be near older males (Evans and Harris 2008), and older males are more socially connected and have stronger social relationships, suggesting that they are important for the cohesion of male social groups (Chiyo et al. 2011). Mature and highly socially integrated males are also more likely to initiate coordinated group movement, suggesting that they play a leadership role (O'Connell-Rodwell et al. 2024).
- 33. Young males in Pilanesberg National Park, South Africa, who matured in the absence of adult role models after their families were killed in government culls entered musth at a much younger age than is typical in undisturbed populations. They also exhibited the aberrant behavior of attacking and killing rhinos, possibly as a result of the psychological trauma they experienced as juveniles. When older males were introduced into the Pilanesberg population, this suppressed musth and rhino killing in the younger males, (Slowtow et al. 2000). Another study found that wild male African savannah elephants were less aggressive toward vehicles and non-elephant animals when older males were present (Allen et al. 2021). These studies further highlight the key leadership role of older males in African savannah elephant society.
- 34. Elephant social bonds appear to have a strong emotional component, evidenced by the behaviors that elephants exhibit when separated from and re-united with bonded social partners. When reuniting after a period of separation, bonded elephants produce greeting

displays that involve loud overlapping vocalizations, touching one another with their trunk, spinning around to stand in parallel with each other, and producing olfactory signals (urinating, defecating, and streaming fluid from their temporal glands) (Poole 2011; Eleuteri et al. 2024). Many of the vocalizations produced during these displays have acoustic properties that are associated with emotional arousal in many mammals (including humans), such as nonlinear phenomena and higher and more variable fundamental frequencies (Wood et al. 2005; Poole 2011; Soltis et al. 2011). Similar displays also occur in other social contexts likely to involve high emotional arousal, such as the birth of a calf, after the family group has been threatened, or when a member of the group mates (Poole 2011).

- 35. The strongest bond in elephants is between a mother and her offspring. Because female African savannah and Asian elephants usually stay in the group they were born into, the bonds between mothers and female offspring are normally retained for life (Moss and Poole 1983; Wittemyer et al. 2005; Archie et al. 2006).
- 36. Female African savannah elephants rely on their mother to help them form other social relationships, especially with older individuals (Goldenberg et al. 2016; Goldenberg and Wittemyer 2017). Orphaned females tend to have fewer social relationships with older (and therefore more dominant) females, which may restrict their access to resources (Goldenberg and Wittemyer 2017).

Cooperation and empathy

37. Elephants are highly cooperative, reflecting their prosocial tendencies. In one study, captive Asian elephants were presented with food on a sliding platform with a rope threaded around it. The elephants could access the food by pulling on the rope, but only if

another elephant pulled on the opposite end of the rope simultaneously. If the subject tried to pull the rope by herself, it would simply become unthreaded, and the platform would not move. The elephants quickly learned to only pull the rope when their partner was present, and waited up to 45 seconds for their partner to arrive, indicating that they can act intentionally rather than impulsively (wait times longer than 45 sec were not tested) (Plotnik et al. 2011).

- 38. In another study, semi-captive Asian elephants were presented with a similar apparatus and cooperated with each other 80.8% of the time, even if they were not closely bonded. When competition was introduced to the task by modifying the apparatus such that the food could be monopolized by one individual, the elephants used various competition mitigation strategies to allow cooperation to continue. The way that elephants responded to competition also depended on their relationship; for example, elephants were more likely to tolerate freeloading from individuals with whom they had closer relationships (Li-Li et al. 2021).
- 39. In the wild, female elephants often help take care of each other's calves, a behavior known as allomothering (Lee 1987; Vidya 2014). At least in African savannah elephants, allomothers are typically related to the calf but are not necessarily first order relatives (Lee 1987). Allomothers comfort the calf when the calf exhibits distress, accompany the calf to prevent it from getting lost when separated from its mother, help retrieve the calf if it does become lost, help protect it from danger, and sometimes allow the calf to suckle from them, regardless of whether or not they are lactating (Lee 1987).
- 40. The renowned anthropologist Margaret Mead famously said that the earliest sign of civilization is a healed femur (thigh bone), because this indicates that people had empathy

and cared for injured members of their group (Gautam and Singh 2022). Elephants also help other elephants who are sick, injured, or in distress, which suggests that they likewise have a capacity for empathy. When an elephant is unable to stand due to illness or injury, other elephants often stand by them, nudge them in an attempt to make them stand, and sometimes attempt to lift them or support them to keep them from collapsing (Douglas-Hamilton et al. 2006; Bates, Lee, et al. 2008; Sharma et al. 2020, Pokharel et al. 2022).

- 41. Asian elephants sometimes produce vocalizations such as trumpets, roars, and squeaks in the presence of dead individuals (Pokharel et al. 2022). These call types are typically associated with heightened emotion, suggesting that the elephants experience a strong emotional response to the death of a family member or acquaintance (Nair et al. 2009; de Silva 2010). In one such case, a wild adult female Asian elephant was observed near an injured calf who was unable to move. After the calf collapsed, the female produced three trumpets. She then stayed with the calf until he died, touching him, attempting to help him stand, and charging at a veterinary team who came to examine the calf. Although the calf was too young to have been weaned, the female showed no signs of lactating, suggesting that she might not have been the calf's mother (Sharma et al. 2020).
- 42. During my own fieldwork with African savannah elephants in Kenya, I often observed a family group known as the M8s. The matriarch of the group, Silvia, was shot and injured by poachers more than a decade prior and often lagged behind the rest of the family when they walked from the hills down to the river, possibly as a result of her old injury. Silvia's younger sister Adelaide would frequently wait by the river for Silvia to catch up, sometimes calling to Silvia repeatedly, before they crossed the river together.

- 43. Adult African savannah elephants frequently help calves who are stuck in the mud or in a ditch by pulling or pushing the calf out or by digging a path for the calf to climb out on its own. Pushing the stuck calf or digging a path for it imply an understanding of the calf's intentions, as these behaviors cannot be explained by the adult simply trying to come closer to a calf in distress. While it is most often the mother who helps the calf, other adult females often do so as well, and in one case a calf who had fallen over was helped back up by an unrelated adult male (Bates, Lee, et al. 2008).
- 44. Elephants also comfort individuals who are in emotional distress, even if they are no longer in physical danger. African savannah elephants frequently comfort calves who have emitted distress calls by gently touching them and producing specific vocalizations known as "coo rumbles" (Bates, Lee, et al. 2008; Poole 2011). In one study of captive Asian elephants, the elephants directed more affiliative physical contact toward both adults and juveniles who had just exhibited distress, suggesting that Asian elephants also comfort each other (Plotnik and de Waal 2014). The Asian elephants also produced more squeak vocalizations and trunk bounces after another individual in the group exhibited distress (Plotnik and de Waal 2014), which are signals generally associated with agitation (de Silva 2010). This suggests that they exhibit emotional contagion, a key component of empathy in which individuals adopt one another's emotional state (Plotnik and de Waal 2014).

Memory

45. As might be expected given their complex social networks and strong social bonds, elephants have an impressive ability to recognize and remember other individuals. Female African savannah elephants can distinguish between the calls of close social affiliates (family or bond group members), distant social affiliates (clan members), and non-

- affiliates. This implies that, on average, a female African savannah elephant can recognize the voices of at least 100 individuals, including individuals with whom she interacts very infrequently (McComb et al. 2000).
- 47. Even though male adult African savannah elephants primarily socialize with other males, they also recognize many if not most of the females in their population by voice. They can discriminate between the calls of females from their population and females from a different population, and show greater interest in the calls of unfamiliar females (Stoeger and Baotic 2017).
- 48. Evidence suggests that elephants can remember bonded social companions for many years. When male Asian elephants were presented with the urine of their mother after 2-27 years of separation, they still recognized her scent and discriminated between their mother's urine and the urine of other elephants (Rasmussen and Krishnamurthy 2000).
- 49. In another study, researchers played the call of a family member who had died 23 months prior to one family of African savannah elephants and played the call of a family member who had transferred to a different group 12 years prior to another family of African savannah elephants. Elephants in both families called back and/or approached the speaker in response to the call of a family member who had died or changed groups. Calling back and/or approaching the speaker is a typical response that elephants give to the calls of current family members, but very different from the response they give to unfamiliar individuals (bunching together and/or retreating), suggesting that the elephants remembered their family members' calls for years (McComb et al. 2000).
- 50. In a third study of long-term social memory, two mother-daughter pairs of captive African savannah elephants who had been separated for 2 and 12 years, respectively, were

reintroduced to each other in a zoo setting. Both mother-daughter pairs performed exuberant greeting displays upon reintroduction, including running toward each other, vocalizing, entwining their trunks together, touching heads, spinning around, urinating, and defecating. By contrast, unrelated elephants being introduced to each other for the first time primarily exhibited aggressive behavior. Only one out of the six unrelated elephants vocalized during the initial introduction and none of them ran toward each other, entwined their trunks, touched heads, spun around, urinated, or defecated (Hörner et al. 2021).

- 51. Studies of the movement patterns of African savannah elephants in the arid region of northern Namibia have revealed that they have highly developed spatial memories. These elephants often move long distances (sometimes >60 km or 37 miles) in a mostly straight line to waterholes that they have not visited in months (Viljoen 1989). Their movements are highly directional and they head to the closest waterhole 90% of the time, which is best explained by detailed spatial memory for the locations of waterholes (Polansky et al. 2015). They also very rarely leave their home ranges, which is consistent with their survival being dependent on detailed knowledge of the location of resources within a familiar area (Viljoen 1989).
- 52. Three captive Asian elephants who had previously been trained to discriminate between light and dark disks to obtain a food reward were tested on the same task eight years later. One of the elephants chose the correct disk 41 out of 43 times, a much better performance than elephants who had no prior exposure to this task, indicating that she remembered the task for eight years. While the other two elephants struggled to complete the task after eight years, this turned out to be because they had a visual impairment and could no longer easily see the difference between the disks (Markowitz et al. 1975).

- 53. In addition to their impressive long-term memory, elephants also have exceptional working memory, defined as the ability to retain information in the short term while actively using it. One study presented wild female African savannah elephants with the urine of adult family members who were either walking in front of them or behind them. The elephants spent significantly more time sniffing the urine of individuals who were walking behind them, indicating that they keep track of the spatial positions of family members during group movement, and understand that an individual walking behind them cannot urinate in front of them. Elephants do not always walk in the same order and often overtake each other and switch positions during group movement, which means that they must continually update their knowledge about the locations of their family members. The average number of individuals per family group in this study was 14 (8 adults), with a maximum of 30 (17 adults), which suggests that African savannah elephants may be able to keep track of the locations of at least 17 if not 30 individuals at once (Bates, Sayialel, et al. 2008). For comparison, some studies suggest that humans can only hold 3-5 items in our working memory at once (Cowan 2010).
- 54. Further evidence that elephants have unusually well-developed working memory comes from an experiment in which captive African savannah elephants were trained to match human body scent to a corresponding sample. The elephants were presented with a target scent and then tasked with identifying which scent in a line-up of nine scents from different individual humans (some of whom were closely related to each other) matched the target sample. They identified the correct scent in 82% of trials on average and showed no decrease in performance when the target scent was at the end of the line-up compared to when it was at the beginning. This contrasts with forensic dogs, who were 15% less likely

to make the correct choice when the target scent was near the end of the line-up, even though the dogs were only presented with a six-scent line-up compared to the elephants' nine. This study suggests that African savannah elephants have a better working memory for scents than trained forensic dogs. This study also demonstrates that elephants can recognize individual humans by smell, including distinguishing between the scents of humans who are closely related (von Dürckheim et al. 2018).

Mental categorization of threats

- 55. Elephants can make fine-scale distinctions between different threats, which helps them survive in the wild. African savannah elephants can distinguish between human ethnic groups who differ in their propensity to attack elephants by both the smell of their clothing and the sound of their language (Bates et al. 2007; McComb et al. 2014). Furthermore, within the same ethnic group they can distinguish between the voices of men, who pose the greatest threat, and the voices of women and children (McComb et al. 2014).
- 56. Larger prides of lions and prides with more males pose a greater threat to elephants. Family groups of African savannah elephants responded more strongly to playbacks of three lions roaring vs. one lion roaring, indicating that they recognize the different levels of danger posed by different numbers of lions. Families with older matriarchs (but not families with young matriarchs) also responded more strongly to playbacks of male lions vs. females, highlighting the importance of learned experience for fine-scale categorization of threats (McComb et al. 2011).
- 57. Asian elephants can discriminate between the growls of tigers, who pose a threat to elephant calves, and leopards, who do not. They called aggressively in response to

playbacks of leopard growls but retreated silently in response to playbacks of tiger growls (Thuppil and Coss 2013).

Communication

- 58. Elephants communicate with a rich array of vocal, gestural, and chemical signals (Rasmussen and Krishnamurthy 2000; de Silva 2010; Poole 2011; Poole and Granli 2011). The total number of signals that elephants use to communicate is unknown, as it is difficult and time consuming to determine whether human classifications of signals align with the elephants' perception. However, dozens of potential call types (Poole 2011; Soltis et al. 2014) and hundreds of potential gestures (Poole and Granli 2011) have been described in African savannah elephants, and some of these signals have been experimentally shown to carry distinct meanings to the elephants (Poole 1999; Soltis et al. 2014).
- 59. Elephant vocalizations can be divided into several broad categories based on the acoustic properties of the call. Rumbles, roars, trumpets, snorts, barks/cries, and combination calls are produced by all elephant species (Poole 2011; Stoeger and de Silva 2014; Hedwig et al. 2021), and two additional call categories (squeaks and squeals) are produced only by Asian elephants (de Silva 2010). However, within these broad categories there are many call subtypes that differ substantially in their acoustic structure and meaning (Poole 1999; Poole 2011). There are also some rare calls that do not fall into any of these major categories (de Silva 2010; Poole 2011).
- 60. Anywhere from 66-91% of the vocalizations made by wild elephants fall into the broad category of "rumbles" (Thompson 2009; de Silva 2010; Poole 2011). There are several apparent parallels between rumbles and human speech, possibly because both humans and elephants have a need for unusually complex and flexible communication. First, rumbles

are extremely variable and used in almost every behavioral context, whereas other call categories are primarily produced in contexts associated with emotional arousal (de Silva 2010; Poole 2011; Hedwig et al. 2019). This may be analogous to the way in which humans use speech (a highly variable broad category of vocalization) in nearly every context, while producing other vocalizations such as laughter, screaming, and crying in specific emotional contexts.

- 61. Second, acoustic features known as formants are important for carrying information in both human speech and elephant rumbles. In humans, formants are the primary distinguishing feature between different vowel sounds and we can voluntarily change the frequencies of the formants in the sounds we make by moving our tongue and lips (Kent and Vorperian 2018). Elephants can also manipulate the formant frequencies in their rumbles, and doing so affects the meaning of the rumble (Stoeger, Heilmann, et al. 2012; Soltis et al. 2014; Beeck et al. 2022).
- 62. Finally, it seems to be easier for elephants to learn to produce rumbles on command than trumpets (Stoeger and Baotic 2021). This parallels the way in which it is easier for humans to intentionally produce speech compared to emotional vocalizations such as spontaneous laughter (Bryant and Aktipis 2014).
- 63. Language is a voluntary behavior in humans, whereby a person can choose whether to communicate with another. Therefore, human language reflects autonomous thinking and intentional behavior. Elephants also communicate intentionally and voluntarily, which likewise reflects their status as autonomous individuals. The fact that African savannah elephants adjust their gestural communication based on whether the individual with whom they are trying to communicate can see them is evidence that they communicate

- intentionally, in addition to showing that they have at least one component of theory of mind (see above) (Smet and Byrne 2014a; Eleuteri et al. 2024).
- 64. Asian elephants produce significantly fewer audible vocalizations when in areas with greater human presence, presumably to avoid detection by humans (Srinivasaiah et al. 2019). Similarly, African forest elephants reduce their overall vocal activity and shift to calling more at night after hearing gunshots (Verahrami 2023). This further suggests that elephants choose when to communicate based on a complex assessment of the circumstances.
- 65. Another key feature of human language is compositionality, in which two or more words are combined to create a compound word or sentence that conveys a new meaning, while still retaining some aspects of the meanings of its constituent components (Hedwig and Kohlberg 2024). Elephants also combine calls (specifically, rumbles and roars) together in ways that may be compositional (Pardo et al. 2019; Hedwig and Kohlberg 2024). In African forest elephants, the contexts of these combination calls differed from the contexts of standalone rumbles and roars while still having some contextual overlap, which suggests that combination calls may convey a new meaning partially derived from the meanings of their component calls (i.e., compositionality) (Hedwig and Kohlberg 2024).
- 66. In another possible parallel to human grammar, the order in which roars and rumbles are combined appears to follow certain rules. Nearly all combination calls follow the ordering "roar-rumble", "rumble-roar", or "rumble-roar-rumble", despite the fact that elephants are physically capable of producing other orderings, as evidenced by the fact that other combinations do occur extremely rarely (Pardo et al. 2019). The relative prevalence of the three most common orders differs significantly among the three species of elephants and

- even between different populations of the same species (Pardo et al. 2019). Finally, in African savannah elephants, "rumble-roar-rumble" combinations are disproportionately likely to occur in the context of separation, suggesting that the order in which calls are combined may affect the meaning of the utterance (Pardo et al. 2019).
- 67. Elephants are among the few mammals capable of learning to produce completely novel sounds outside of their species' typical vocal repertoire. Mlaika, a semi-captive African savannah elephant, learned to imitate the sounds of trucks (Poole et al. 2005). Calimero, a captive African savannah elephant housed with Asian elephants, learned to imitate the squeak calls that are frequently produced by Asian elephants but never observed in African elephants in the wild (Poole et al. 2005). Finally, Koshik, an Asian elephant in a South Korean zoo, learned to imitate at least five Korean words (Stoeger, Mietchen, et al. 2012). His imitations were close enough to the original that Korean speakers who had no previous familiarity with Koshik could reliably identify the vowels, though not the consonants, of the words he imitated. This type of open-ended vocal learning is critical for language in humans, and its existence in elephants highlights the flexibility and sophistication of their vocal behavior.
- 68. Elephant vocalizations differ between populations of the same species, which may be analogous to dialect or accent differences between human populations. For example, the rumbles of African savannah elephants in Samburu National Reserve, Kenya have higher and more variable fundamental frequencies than the rumbles of African savannah elephants in Amboseli National Park, Kenya (Pardo, Lolchuragi, et al. 2024). In one study, African savannah elephants in Namibia responded more strongly to playback of alarm vocalizations from their own population than from a population in Kenya, raising the possibility that the

- vocal differences among elephant populations could present a barrier to communication (O'Connell-Rodwell et al. 2007).
- 69. Historically, nonhuman animal vocalizations were thought to be mere expressions of the caller's internal emotional state rather than references to specific entities external to the caller (Seyfarth et al. 1980). However, studies on African savannah elephants have found evidence for calls that refer to external entities. For example, African savannah elephants produce different alarm rumbles in response to different types of threats, such as humans and bees (King et al. 2010; Soltis et al. 2014). Playback of bee alarm rumbles caused elephants to retreat and shake their head more than usual, while playback of human alarm rumbles caused elephants to retreat without any increase in headshaking. As headshaking is a behavior that is used to dislodge stinging bees, this suggests that elephant alarm rumbles are references to specific threats, rather than generic expressions of fear (Soltis et al. 2014).
- 70. I led a study showing that African savannah elephants address each other with individual names, another example of elephant calls that refer to entities external to the caller. My colleagues and I found that African savannah elephants use distinct rumbles when addressing different members of their family group, and different callers appear to use at least partially similar rumbles to address the same individual. Moreover, when we played these rumbles back to the elephants, they responded more strongly to a rumble that was originally addressed to them compared to a rumble from the same caller that was originally addressed to someone else. This indicates that African savannah elephants can determine just by hearing a call if it was intended for them or for another individual (Pardo, Fristrup, et al. 2024). The existence of names in elephants is a testament to the importance of their

- social bonds and suggests that they have complex mental representations of other individuals.
- 71. Evidence suggests that African savannah elephants may be more likely to include names in long-distance rumbles or in rumbles addressed to young calves in a caregiving context, and less likely to use names when greeting adults at close distance (Pardo, Fristrup, et al. 2024). The potentially high prevalence of name-use in calls addressed to young calves raises the possibility that mother elephants actively name their calves. This remains an untested hypothesis at present; however, both African savannah elephants and Asian elephants who have just given birth have been observed repeatedly rumbling to the newborn calf (personal observation; J. Poole and S. Lokhandwala, personal communication).
- 72. Both female and male African savannah elephants produce specific vocalizations known as "let's go" rumbles that indicate when they want the group to begin moving in a particular direction. These rumbles are typically followed by a back-and-forth exchange of rumbles between multiple members of the group, suggesting that African savannah elephants negotiate group decisions about movement (Poole 2011; O'Connell-Rodwell et al. 2012; O'Connell-Rodwell et al. 2024).
- 73. Elephants communicate over long distances, reflecting the fact that they have evolved to live in extremely large home ranges and repeatedly separate from and reunite with their social companions. Under ideal sound propagation conditions in a savannah environment, African savannah elephants can detect rumbles from up to 4 km (2.5 miles) away (Langbauer et al. 1991), and can recognize the caller from 1.5 km (0.9 miles) away (McComb et al. 2003). In a rainforest environment, African forest elephant rumbles can be

detected up to 3.2 km (2.0 miles) away under ideal propagation conditions, and 0.8 km (0.5 miles) away under average propagation conditions (Hedwig et al. 2018). Rumbles also couple with the ground to create a seismic wave that can travel even further than the sound wave travels through the air, and studies with African savannah elephants have found that they can detect and react to these seismic vibrations (O'Connell-Rodwell et al. 2006; O'Connell-Rodwell et al. 2007).

Personality

- 74. Elephants have unique personalities. Personality is defined as a set of behavioral and emotional traits that an individual exhibits consistently over time, which are different from the traits exhibited by other individuals of the same species. Individual elephants differ in a variety of traits, including activeness, affectionateness, aggressiveness, anxiety, curiosity, defiantness, excitability, mischievousness, protectiveness, sociability, and shyness (Barrett and Benson-Amram 2021).
- 75. Elephants' personality affects their performance on problem-solving tasks. For example, more aggressive elephants were faster at solving certain types of puzzles to get food (Barrett and Benson-Amram 2021).

Problem solving and tool use

76. Both Asian and African savannah elephants have been observed using a variety of simple tools. Asian elephants use branches as switches to repel flies and will intentionally modify branches to make them more effective for fly switching (Hart et al. 2001). Other types of tool use observed in both species include, but are not limited to, elephants using twigs to scratch themselves, dabbing cuts with clumps of grass, and throwing objects at other animals to repel them (Chevalier-Skolnikoff and Liska 1993).

- 77. Elephants can learn to solve a variety of complex problems by trial-and-error. One study presented 12 captive Asian elephants with a marshmallow inside a tube, where the only way to extract the marshmallow was to add water to the tube so that the marshmallow would float to the top. One of the elephants, Shanthi, figured out how to solve this problem on her own after just two trials (Barrett and Benson-Amram 2020). Two captive Asian elephants in another zoo learned to push food items out of inaccessible locations by blowing air at them (Mizuno et al. 2016). Both captive and wild Asian elephants learned via trial-and-error to solve a puzzle in which food is placed inside a box with doors that the elephant must either push, pull, or slide to open (Jacobson et al. 2022; Jacobson et al. 2023).
- 78. In comparative psychology, insight refers to the ability to "think through" a problem and spontaneously come up with a novel solution without trial-and-error learning. It is considered a highly advanced form of cognition as it requires individuals to understand the nature of the problem and imagine a solution to it. One study assessed whether Asian elephants are capable of insight by presenting three captive Asian elephants (two adults and a juvenile) with food hanging from a tree just out of reach. They also placed a moveable cube or tub in the enclosure that the elephants could use as a stepstool to reach the food. While the two adults never did this, the juvenile, Kandula, spontaneously pushed the cube underneath the tree and stood on it to reach the food. He did so without any trial-and-error learning, suggesting that he relied on insight to solve this challenge. In further trials, the researchers hid the cube and Kandula searched for it, retrieved it, and used it to access the food, indicating that his behavior was intentional and goal oriented. When the cube was replaced with a large tire, Kandula also immediately understood that the tire could be used in the same way (Foerder et al. 2011).

- 79. To further test Kandula's problem-solving ability, the researchers removed the cube and tire but provided several smaller objects, including a ball and several cutting boards. Kandula tried unsuccessfully to reach the food by standing on one of the cutting boards and then the ball. He then stacked two of the cutting boards together, but this was still not tall enough. The session ended before he tried stacking three boards together, which would have allowed him to reach the food. Nonetheless, this experiment suggests that he understood, without any training, the concept of stacking two objects together to increase their height (Foerder et al. 2011).
- 80. A possible case of insightful problem solving in the wild involved the response of a wild adolescent female Asian elephant named Genette to a calf who was repeatedly attempting to suck on her (nonlactating) nipple. This was apparently uncomfortable for Genette, as she kept trying to push the calf away, and eventually she offered the calf the tip of her trunk to suck on instead (Vidya 2014). Using the trunk as a pacifier in this way was an apparently novel behavior that had not previously been observed. While it is impossible to make strong inferences about cognition from a single observation such as this, it is possible that Genette understood the calf's intentions and spontaneously came up with a novel solution to stop the calf from harassing her.
- 81. According to another report, after government officials created a new road and began to use it to cull African savannah elephants, the elephants broke branches and piled them in the road, effectively blocking it off. When park officials cleared the branches, the elephants replaced them four times (Chevalier-Skolnikoff and Liska 1993). This raises the possibility that the elephants intentionally blocked the road to prevent it from being used to shoot

them, which would be an exceptionally sophisticated example of cause-and-effect reasoning and insightful problem solving.

Numerical reasoning

- 82. Both Asian and African savannah elephants can discriminate between different quantities of food and select the larger quantity (Irie-Sugimoto et al. 2009; Perdue et al. 2012; Snyder et al. 2021). An experiment with Asian elephants showed that they can discriminate between two quantities of sunflower seeds based on smell alone (Plotnik et al. 2019).
- 83. Most animals discriminate between quantities using visual estimations of the total quantity rather than by counting individual objects. In these species, the ability to discriminate between quantities decreases as the quantities become more similar in relative magnitude. Two studies found that this was also the case for African savannah and Asian elephants, suggesting that elephants likewise discriminate between quantities using visual estimation rather than by counting the individual items (Perdue et al. 2012; Snyder et al. 2021). However, two other studies found that Asian elephants' performance in a quantity discrimination task did *not* decline when the quantities were closer in relative size, suggesting that Asian elephants might be capable of counting individual objects rather than simply estimating relative quantities (Irie-Sugimoto et al. 2009; Irie et al. 2019). More research is necessary to resolve this question, but these results suggest that Asian elephants might be capable of more sophisticated numerical reasoning than most animals.
- 84. Asian elephants can also mentally add two quantities together. In one study, Asian elephants watched as an experimenter placed some food items one by one into one bucket, then placed some food items into a second bucket, then placed some additional food items into the first bucket and finally placed some additional food items into the second bucket.

Thus, in order to determine which bucket had more food, the elephants would have to remember the original quantity placed in each bucket and add it to the second quantity placed in the same bucket. The elephants chose the bucket with the larger quantity significantly more often than expected by chance, indicating that they were capable of mentally adding two quantities (Irie and Hasegawa 2012).

Autonomy in mate choice

- 85. Wild elephants are selective about who they mate with, reflecting their status as autonomous individuals. Male African savannah elephants avoid mating with both maternal and paternal relatives (Archie et al. 2007). Unlike some animals, who evolved to avoid inbreeding by simply moving far away from where they were born, male elephants do not always disperse far away from their natal group and occasionally visit their female relatives even after they have become independent (personal observation). This indicates that elephants recognize their kin and actively choose not to mate with them.
- 86. At least in African savannah elephants and Asian elephants, females usually prefer to mate with males who are older/larger and in musth (Poole 1989; Chelliah and Sukumar 2015). When a female elephant is in estrus (heat), she is often pursued by multiple males, and she runs away from them while roaring loudly (Poole 2011). If a female wants to mate with a male, she will eventually let him catch up to her and then stand still as he mounts her. In the wild, females can prevent a male from mating with her simply by refusing to stand still, as it is very difficult for the male to balance on his hind legs without the female's cooperation (Moss 1983; Poole 1989).
- 87. In wild African elephants, mating is an emotionally charged occasion. When a female mates, other females in the vicinity rush over to her, produce loud, overlapping

vocalizations and exhibit other signs of emotional arousal such as urinating, defecating, and streaming fluid from their temporal glands (Poole et al. 1988; Thompson 2009). This behavior, known as a "mating pandemonium", is similar to what is observed in other highly emotional social scenarios, such as the birth of a calf or when bonded individuals greet each other after a period of separation (Poole 2011).

Elephant welfare issues in zoos

- 88. In the wild, elephant home ranges are typically hundreds to thousands of square kilometers (Leggett 2006; Fernando et al. 2008; Alfred et al. 2012; Wall et al. 2021). By contrast, the Association of Zoos and Aquariums (AZA) recommends a minimum of just 0.0005 km² of outdoor space per elephant, 0.000056 km² of indoor space per male elephant, and 0.000037 km² of indoor space per female elephant (AZA 2024). Even the largest elephant exhibits in zoos are orders of magnitude smaller than the smallest elephant home range in the wild (e.g., 0.028 km² for Disney's Animal Kingdom, 0.013 km² for the San Diego Zoo Safari Park) (Doyle et al. 2024).
- 89. Studies that have attempted to measure how space affects elephant welfare in zoos have been hampered by the fact that even the largest zoo enclosures are so much smaller than elephants' natural home ranges that the existing variation in enclosure size among zoos likely makes no difference to the elephants (Greco et al. 2016; Doyle et al. 2024). However, lack of space in zoos is directly linked to many of the welfare issues experienced by captive elephants, including lack of exercise, improper diet, and lack of mental stimulation (Doyle et al. 2024).
- 90. Wild African savannah elephants walk an average of about 9-12 km/day and occasionally walk considerably more than 20 km in a single day (Leggett 2009; Polansky et al. 2013).

Although elephants in captivity do not need to walk long distances to find food and water, they still require the exercise provided by walking to stay healthy (Morfeld and Brown 2017). A study of Asian and African savannah elephants across 30 North American zoos found that they walked 5.3 km/day on average (no significant difference between the two species), about half of what is typical for wild African savannah elephants (Holdgate et al. 2016).

- 91. The lack of space in zoos makes it impossible for elephants to graze and browse as they would in the wild, because elephants will quickly destroy the limited amount of vegetation that can grow in a zoo enclosure. Thus, elephants in zoos are fed a diet that is lacking in fiber and certain essential vitamins and minerals compared to the food that elephants evolved to eat while simultaneously being higher in calories (Tsuchiya et al. 2023; Doyle et al. 2024). This, combined with the lack of sufficient exercise in zoos, frequently leads to dental problems, gastrointestinal issues, and obesity in zoo elephants (Doyle et al. 2024). One study of 132 African savannah elephants and 108 Asian elephants across 65 North American zoos found that 74% of the elephants were overweight and 34% were obese (Morfeld et al. 2016).
- 92. In the wild, where elephants typically range over hundreds to thousands of square kilometers, they encounter a wide variety of sensory experiences, social interactions, and mental challenges that cannot be reproduced in a zoo environment. Multiple studies have found that increased exhibit complexity is positively correlated with metrics of elephant welfare, indicating that environmental complexity matters to elephants (Scott and LaDue 2019; Brown et al. 2020). However, even the most enriched zoo enclosure is severely impoverished compared to the natural environment and cannot provide elephants with the

- level of mental stimulation that they require to avoid chronic boredom and frustration (Atkinson and Lindsay 2022).
- 93. Elephants are naturally active both day and night, averaging only a few hours of sleep in a 24-hour period spread across multiple short naps (Gravett et al. 2017). However, most zoos lock elephants indoors all night long, which means they only have access to a small fraction of their exhibit for a significant portion of their waking hours (Miller et al. 2016).
- 94. A strong indication that elephants are chronically bored and stressed in zoos is the high prevalence of stereotypic behavior in zoo elephants. Stereotypic behavior refers to repetitive movements such as rocking, swaying, head-bobbing, and pacing that serve no adaptive function. When animals are chronically bored, frustrated, and stressed, they exhibit elevated levels of glucocorticoids, or stress hormones, in their blood. This causes dysregulation of the motor circuits in the brain, a form of brain damage, which results in repetitive movements (Jacobs et al. 2022). Stereotypic behavior has never been observed in wild elephants, but studies have found that up to 85% of zoo elephants exhibit stereotypic behavior (Clubb and Mason 2002; Mason and Veasey 2010; Greco et al. 2016). One study of 47 African savannah elephants and 42 Asian elephants across 39 North American zoos found that stereotypic behavior was the second most common behavior exhibited by the elephants, accounting for 15.5% of their time during the day and 24.8% of their time at night (Greco et al. 2016).
- 95. It is unheard of for a mother elephant to intentionally kill her calf in the wild, but this behavior is relatively common in zoo elephants (Kurt and Mar 1996; Clubb et al. 2008).

 One study of 121 Asian elephants born in European zoos found that 10% were killed by

- their mother (Kurt and Mar 1996). The prevalence of this highly aberrant behavior in zoos is another indication of the damaging effects of captivity on elephant psychology.
- 96. All extant species of elephants are native to tropical and subtropical regions. Thus, zoo elephants in cold climates must spend much of their time indoors, further limiting their opportunities for exercise and mental stimulation. Low temperatures have been found to exacerbate stereotypic behaviors among Asian elephants who were already predisposed to stereotypic behavior (Rees 2004).
- 97. Zoo environments are often extremely noisy, which may be especially stressful for animals like elephants with sensitive hearing (Jakob-Hoff et al. 2019). Sources of noise include crowds of human visitors, loud fans in indoor spaces, and construction. The limited space of zoo enclosures exacerbates the negative impacts of noise by preventing elephants from moving away from it.
- 98. Zoos are unable to provide elephants with a normal social environment. While wild female elephants live in large social networks of mostly related individuals (Moss and Poole 1983; Wittemyer et al. 2005; Archie et al. 2006; de Silva, Ranjeewa, and Kryazhimskiy 2011), female elephants in zoos are typically housed in much smaller groups of mostly unrelated individuals who did not grow up together, and some are even housed alone (Doyle et al. 2024). Despite the abundant evidence that male elephants also have complex social lives in the wild (Evans and Harris 2008; Chiyo et al. 2011; Goldenberg et al. 2014; LaDue et al. 2022), most male elephants in zoos are housed alone due to their greater aggressiveness and the challenges of safely integrating them with other elephants in a small space (Doyle et al. 2024).

- 99. These unnatural social groupings negatively impact elephant welfare. Elephants housed alone or in smaller groups exhibit more stereotypic behavior and have higher levels of stress hormone metabolites in their dung than elephants housed in larger groups, indicating that social deprivation causes chronic stress in elephants (Greco et al. 2016; Brown et al. 2020). Moreover, elephants housed with unrelated individuals exhibit more aggression towards one another (Williams et al. 2019).
- Elephants are often transferred between zoos due to space limitations or to facilitate captive breeding programs, and over 80% of elephants in North American zoos have experienced at least one such transfer (Prado-Oviedo et al. 2016). Inter-zoo transfers break up social relationships that would normally be maintained for a lifetime in wild elephants. Elephants who have been transferred between zoos exhibit more stereotypic behavior than elephants who have not (Greco et al. 2016). Asian elephants who have experienced a transfer also have a lower life expectancy than their counterparts who were never transferred (Clubb et al. 2008). This suggests that the disruption to elephants' social lives caused by inter-zoo transfers has a major negative impact on elephant welfare.
- 101. Elephants exhibit more stereotypic behavior and higher levels of stress hormone metabolites in their dung when they have less opportunity to choose where to spend their time, which emphasizes the importance of autonomy for elephant welfare (Greco et al. 2016; Brown et al. 2020). Zoos restrict the autonomy of elephants in many ways, including restricting their movement, restricting their social interactions, and restricting their ability to choose when and what to eat.
- 102. Captive breeding programs in zoos also remove elephants' autonomy over their reproduction, in contrast to the wild where choice is an important component of elephant

sexual behavior (Moss 1983; Poole 1989; Archie et al. 2007; Chelliah and Sukumar 2015). Captive breeding in North American zoos most often occurs via artificial insemination. This involves first collecting semen from the male by inserting an arm into his rectum to stimulate his prostate. A similarly invasive procedure is then performed on the female to insert the semen into her reproductive tract, often multiple times. Elephants are usually restrained during these procedures (Hildebrandt and Goeritz 2023).

- 103. Many zoo enclosures have hard substrates such as concrete, which exert more pressure on elephants' feet than the natural substrates they evolved to walk on and cause chronic foot and musculoskeletal issues (Miller et al. 2016). Studies have documented foot disease in 50-80% of the zoo elephants examined (Doyle et al. 2024), and post-mortem exams on 21 deceased zoo elephants discovered foot pathologies in every single individual, suggesting that most zoo elephants will develop foot issues by the time they die (Regnault et al. 2017). Osteoarthritis, a painful condition caused by breakdown of the cartilage and bone in joints, is also common in zoo elephants, with one study documenting confirmed cases of osteoarthritis in 21.9% of the elephants examined and suspected cases in an additional 16.4% (Chusyd et al. 2023).
- 104. Elephants naturally push their tusks against hard surfaces such as trees, but in zoos, most of the available surfaces are made of materials such as concrete or metal that do not yield as easily. This leads to tusk fractures occurring much more frequently in zoos than in most wild populations (Doyle et al. 2024). One study of 350 Asian and African savannah elephants across 60 North American zoos found that 31% had tusk fractures, compared to a median of just 1.3% across 15 populations of wild African savannah elephants (Steenkamp et al. 2007). These fractures can be very painful if they expose the pulp of the

tusk where nerves are located and can even be fatal if the pulp becomes infected (Rose et al. 2022).

- 105. Elephants often exhibit reproductive health issues in zoos, likely caused by a combination of obesity and the stress of living in captivity. Many captive female elephants develop ovarian cysts, stop cycling, or cycle irregularly (Doyle et al. 2024). Approximately 20% of Asian elephants born in Western zoos are stillborn or die within 24 hours of birth, compared to only 3% for captive working elephants in Asia (Taylor and Poole 1998; Perrin et al. 2021).
- 106. Zoo elephants are also more susceptible to certain infectious diseases than wild elephants, especially tuberculosis and elephant endotheliotropic herpesvirus (Perrin et al. 2021; Doyle et al. 2024). The high susceptibility of zoo elephants to tuberculosis is likely due at least in part to the stress of captivity (Mikota 2009).
- 107. At least for African savannah elephants, life expectancy in zoos is significantly lower than their natural lifespan (i.e., the lifespan of wild elephants who die of natural causes). A 2008 study of zoo elephants born between 1960-2005 found that the median lifespan for female African savannah elephants in zoos was only 19.6 years, compared to 56.0 years for wild females in Amboseli National Park, Kenya who were not killed by humans (Clubb et al. 2008). More recently, a 2023 study found that even among the youngest adult cohort of African savannah elephants born in zoos (i.e., elephants born between 1990-2009), survival was significantly lower than in wild populations with low rates of human-caused mortality (Scherer et al. 2023). This suggests that even with modern husbandry practices, the life expectancy of African elephants in zoos still fails to approach the natural life expectancy of this species. Unfortunately, it is difficult to make similar

comparisons for Asian elephants due to a lack of data on the survival rates of wild populations with low rates of human-caused mortality.

Best alternatives to zoos

- them into the wild. Reintroduction to the wild has almost exclusively been attempted for captive elephants in elephant range states. For example, 10 captive African savannah elephants who were used for elephant-back safaris in the Shambala Game Reserve in South Africa were gradually introduced to the wild in the same reserve over a period of seven months in 2016. Despite having spent most or all of their lives in captivity, the elephants successfully integrated into the wild. The concentration of stress hormone metabolites in their dung increased in the first year after release, but by the second year it decreased to pre-release levels. This indicates that while the elephants at first experienced some physiological stress associated with needing to fend for themselves, they adjusted relatively quickly. Most notably, all stereotypic behavior stopped immediately as soon as the elephants were released into the wild, suggesting a substantial and immediate improvement in their psychological welfare (Pretorius et al. 2023).
- 109. In cases where release into the wild is impossible, the best option for elephants is to be released to an accredited sanctuary. Three accredited sanctuaries for elephants currently exist in the Western Hemisphere: The Elephant Sanctuary in Tennessee, the PAWS Sanctuary in California, and the Global Sanctuary for Elephants in Brazil (Atkinson and Lindsay 2022). While sanctuaries are also a form of captivity, they have orders of magnitude more space than zoos, making them a much better option for elephants' welfare. For example, the Elephant Sanctuary in Tennessee is 12.4 km² in total, with the largest

enclosure being 6.9 km² (Atkinson and Lindsay 2022; Doyle et al. 2024). This is several hundred times larger than the largest elephant exhibit in any zoo.

- 110. Due to their vastly larger size compared to zoos, sanctuaries give elephants more opportunity for exercise, which mitigates many of the detrimental physical effects of captivity. Additionally, sanctuaries encompass much more varied and naturalistic habitat than zoos, including grasslands, woodlands, and bodies of water, which gives elephants far more opportunity for exploration, mental stimulation, and natural foraging behavior (Atkinson and Lindsay 2022). Sanctuaries also afford elephants more autonomy over their movements and activities, which is linked to improved welfare in elephants (Greco et al. 2016; Brown et al. 2020).
- 111. Finally, sanctuaries provide better social environments for elephants than zoos. Although sanctuaries cannot provide truly natural social groups for elephants (i.e., multigenerational herds of many related individuals), they allow elephants to live in much larger social groups than zoos typically do, which is positively associated with welfare (Greco et al. 2016). Moreover, the increased space allows elephants to choose who to interact with, giving them greater autonomy over their lives and reducing aggression (Atkinson and Lindsay 2022).

Tasha, Savanna, Angeline, Victoria, and Zuri

112. Tasha, Savanna, Angeline, Victoria, and Zuri are female African savannah elephants currently held captive by the Pittsburgh Zoo. Tasha and Savanna are approximately 49 and 42 years of age, respectively, and are both wild-born elephants who were captured from the wild when they were about two years old. Angeline is Savanna's

- daughter and was born in 2008 at the Pittsburgh Zoo. Victoria and Zuri are sisters, born at the Pittsburgh Zoo in 1999 and 2008, respectively.
- 113. Victoria and Zuri's mother, Moja, was separated from her daughters in 2015 and transferred to the Winston Wildlife Safari. At the time, Zuri was 6 years old, which is still a juvenile (Lee 1987). In the wild, female African savannah elephants typically stay with their mother for life and maintain a strong lifelong bond with her, and they are especially dependent on their mothers throughout their juvenile years (Wittemyer et al. 2005; Archie et al. 2006). Thus, it is very likely that being separated from each other caused Moja, Victoria, and Zuri substantial emotional distress.
- 114. From 2014-2015, the Pittsburgh Zoo used dogs to help control the elephants. The United States Department of Agriculture (USDA) cited the zoo for using dogs to manage elephants in this manner and ordered them to stop, stating that this "may cause undue stress to the elephants". The USDA inspection report noted that the dogs had "bitten the elephants during the course of their work" and that "the elephants exhibited signs of distress when charged by one of the dogs" (Campitelli 2015).
- The Pittsburgh Zoo also used bullhooks to control the elephants until 2017, when the Pittsburgh City Council voted to ban the use of bullhooks on exotic animals (https://www.wesa.fm/politics-government/2017-12-19/pittsburgh-city-council-votes-to-ban-use-of-bullhooks-baseball-bats-on-wild-animals). Bullhooks are poles with a sharp metal hook on the end used to force elephants to comply with human commands via the infliction of pain. The zoo voluntarily relinquished its accreditation with the Association of Zoos and Aquariums (AZA) from 2015-2024 because it did not wish to comply with new AZA regulations limiting free contact between keepers and elephants, the situation in

which bullhooks are primarily utilized (https://www.aza.org/aza-news-releases/posts/azas-statement-on-pittsburgh-zoo--ppg-aquariums-decision-to-forfeit-aza-accreditation-).

- 116. Tasha, Savanna, Angeline, Victoria, and Zuri have access to approximately 0.75 acres (0.003 km²) of outdoor space, which is five orders of magnitude smaller than the median home range for wild African savannah elephants (Wall et al. 2021). Moreover, part of the enclosure is taken up by a water feature, which further limits the space available for the elephants to walk.
- 117. Based on videos and photographs I reviewed of the elephant exhibit at the Pittsburgh Zoo, the outdoor enclosure appears to be mostly devoid of live foliage, preventing the elephants from engaging in natural foraging behavior. Moreover, the indoor elephant barn is largely barren. There is an extensive body of research linking barren housing environments to neuropathologies such as underdeveloped brains and stereotypic behavior, chronic boredom, and adverse physical health in many species of animals, including elephants (Scott and LaDue 2019, Brown et al. 2020, Han et al. 2022; Jacobs et al. 2022; Mieske et al. 2022).
- I reviewed six videos of the elephants at the Pittsburgh Zoo that showed them engaging in stereotypic behavior, including pacing repeatedly back and forth in both the indoor and outdoor enclosures and swaying from side to side. As detailed above, these behaviors are a direct manifestation of brain damage caused by chronic stress, and are a very strong indicator that the elephants are suffering in a zoo environment (Jacobs et al. 2022).
- 119. The floor of the elephant barn at the Pittsburgh Zoo is made of poured concrete, which has been linked to foot and musculoskeletal pathologies in elephants (Miller et al.

- 2016). Due to the cold climate of Pittsburgh, Tasha, Savanna, Angeline, Victoria, and Zuri spend a significant amount of time indoors on this concrete floor.
- 120. Transferring Tasha, Savanna, Angeline, Victoria, and Zuri to an accredited sanctuary would be substantially better for their welfare than leaving them in the Pittsburgh Zoo. Due to its vastly larger size compared to the Pittsburgh Zoo, a sanctuary environment would provide these elephants with much more varied habitat and opportunity for natural foraging, which will be notably better for their mental and physical welfare (Atkinson and Lindsay 2022).
- Additionally, a sanctuary would provide the elephants with much more opportunity for naturalistic social interaction than the Pittsburgh Zoo. An important component of elephant social interaction in the wild is fission-fusion dynamics, in which elephants repeatedly separate from and rejoin their social companions (Wittemyer et al. 2005; de Silva, Ranjeewa, and Weerakoon 2011). The small size of the elephant exhibit at the Pittsburgh Zoo deprives Tasha, Savanna, Angeline, Victoria, and Zuri of the opportunity to choose with whom to spend time, when to spend time with them, and for how long. By contrast, a sanctuary environment, with its greater space and focus on providing elephants with maximum autonomy, will allow the elephants to exercise much greater control over their social lives. This will very likely have a positive effect on their welfare, as lack of autonomy over social interaction and space use often leads to stress in elephants (Greco et al. 2016; Atkinson and Lindsay 2022).

I declare under penalty of perjury under the law of the Commonwealth of Pennsylvania that the foregoing is true and correct.

Signed on the 25 day of July 2025,

at Fort Collins, Colorado, USA

Michael A. Pardo

Michael A Pardo

REFERENCES

Alfred R, Ahmad AH, Payne J, Williams C, Ambu LN, How PM, Goossens B. 2012. Home range and ranging behaviour of Bornean elephant (*Elephas maximus borneensis*) females. PLoS One. 7(2):e31400. doi:10.1371/journal.pone.0031400.

Allen CRB, Croft DP, Brent LJN. 2021. Reduced older male presence linked to increased rates of aggression to non-conspecific targets in male elephants. Proc R Soc B. 288:20211374. doi:10.1098/rspb.2021.1374.

Archie EA, Hollister-Smith JA, Poole JH, Lee PC, Moss CJ, Maldonado JE, Fleischer RC, Alberts SC. 2007. Behavioural inbreeding avoidance in wild African elephants. Mol Ecol. 16(19):4138–4148. doi:10.1111/j.1365-294X.2007.03483.x.

Archie EA, Moss CJ, Alberts SC. 2006. The ties that bind: genetic relatedness predicts the fission and fusion of social groups in wild African elephants. Proc R Soc B. 273:513–522. doi:10.1098/rspb.2005.3361.

Atkinson R, Lindsay K. 2022. Expansive, diverse habitats are vital for the welfare of elephants in captivity. https://www.conservativeanimalwelfarefoundation.org/wp-content/uploads/2022/07/Digital-CAWF-Elephants-in-Captivity-Report-final-v3.pdf.

AZA. 2024. Standards for elephant management & care. In: The Accreditation Standards & Related Policies. p. 43–70. https://assets.speakcdn.com/assets/2332/aza-accreditation-standards.pdf.

Barrett LP, Benson-Amram S. 2020. Can Asian elephants use water as a tool in the floating object task? Anim Behav Cogn. 7(3):310–326. doi:10.26451/abc.07.03.04.2020.

Barrett LP, Benson-Amram S. 2021. Multiple assessments of personality and problem-solving performance in captive Asian elephants (*Elephas maximus*) and African savanna elephants (*Loxodonta africana*). J Comp Psychol. 135(3):406–419. doi:10.1037/com0000281.

Bates LA, Lee PC, Njiraini N, Poole JH, Sayialel K, Sayialel S, Moss CJ, Byrne RW. 2008. Do elephants show empathy? J Conscious Stud. 15(10–11):204–225.

Bates LA, Sayialel KN, Njiraini NW, Moss CJ, Poole JH, Byrne RW. 2007. Elephants classify human ethnic groups by odor and garment color. Curr Biol. 17(22):1938–1942. doi:10.1016/j.cub.2007.09.060.

Bates LA, Sayialel KN, Njiraini NW, Poole JH, Moss CJ, Byrne RW. 2008. African elephants have expectations about the locations of out-of-sight family members. Biol Lett. 4(1):34–36. doi:10.1098/rsbl.2007.0529.

Beeck VC, Heilmann G, Kerscher M, Stoeger AS. 2022. Sound visualization demonstrates velopharyngeal coupling and complex spectral variability in Asian elephants. Animals. 12(16):2119. doi:10.3390/ani12162119.

Brandl JL. 2018. The puzzle of mirror self-recognition. Phenomenol Cogn Sci. 17(2):279–304. doi:10.1007/s11097-016-9486-7.

Broesch T, Callaghan T, Henrich J, Murphy C, Rochat P. 2011. Cultural variations in children's

mirror self-recognition. J Cross Cult Psychol. 42(6):1018–1029. doi:10.1177/0022022110381114.

Brown JL, Bansiddhi P, Khonmee J, Thitaram C. 2020. Commonalities in management and husbandry factors important for health and welfare of captive elephants in North America and Thailand. Animals. 10:737. doi:10.3390/ani10040737.

Bryant GA, Aktipis CA. 2014. The animal nature of spontaneous human laughter. Evol Hum Behav. 35(4):327–335. doi:10.1016/j.evolhumbehav.2014.03.003.

Campitelli K. 2015. Inspection report: Zoological Society of Pittsburgh. United States Department of Agriculture, Animal and Plant Health Inspection Service.

Chelliah K, Sukumar R. 2015. Interplay of male traits, male mating strategies and female mate choice in the Asian elephant, *Elephas maximus*. Behaviour. 152(7–8):1113–1144. doi:10.1163/1568539X-00003271.

Chevalier-Skolnikoff S, Liska J. 1993. Tool use by wild and captive elephants. Anim Behav. 46(2):209–219. doi:10.1006/anbe.1993.1183.

Chiyo PI, Archie EA, Hollister-Smith JA, Lee PC, Poole JH, Moss CJ, Alberts SC. 2011. Association patterns of African elephants in all-male groups: The role of age and genetic relatedness. Anim Behav. 81(6):1093–1099. doi:10.1016/j.anbehav.2011.02.013.

Chusyd DE, Brown JL, Golzarri-Arroyo L, Dickinson SL, Kraus VB, Siegal-Willott J, Griffin TM, Huebner JL, Edwards KL, Allison DB, et al. 2023. Relationship between reproductive and bone biomarkers and osteoarthritis in zoo Asian and African elephants. J Zoo Wildl Med. 53(4):801–810. doi:10.1638/2021-0080.RELATIONSHIP.

Clubb R, Mason G. 2002. A review of the welfare of zoo elephants in Europe. A report commissioned by the RSPCA. Horsham, West Sussex, UK: University of Oxford. https://endcap.eu/wp-content/uploads/2012/06/A-review-of-the-welfare-of-zoo-elephants-in-Europe-2008-Commissioned-by-RSPCA.pdf.

Clubb R, Rowcliffe M, Lee P, Mar KU, Moss C, Mason GJ. 2008. Compromised survivorship in zoo elephants. Science. 322:1649. doi:10.1126/science.1164298.

Cowan N. 2010. The magical mystery four: How is working memory capacity limited, and why? Curr Dir Psychol Sci. 19(1):51–57. doi:10.1177/0963721409359277.

Douglas-Hamilton I, Bhalla S, Wittemyer G, Vollrath F. 2006. Behavioural reactions of elephants towards a dying and deceased matriarch. Appl Anim Behav Sci. 100(1–2):87–102. doi:10.1016/j.applanim.2006.04.014.

Doyle C, Rally H, O'Brien L, Tennison M, Marino L, Jacobs B. 2024. Continuing challenges of elephant captivity: The captive environment, health issues, and welfare implications. PeerJ. 12(9):1–41. doi:10.7717/peerj.18161.

von Dürckheim KEM, Hoffman LC, Leslie A, Hensman MC, Hensman S, Schultz K, Lee S. 2018. African elephants (*Loxodonta africana*) display remarkable olfactory acuity in human scent matching to sample performance. Appl Anim Behav Sci. 200:123–129. doi:10.1016/j.applanim.2017.12.004.

Eleuteri V, Bates L, Rendle-worthington J, Hobaiter C, Stoeger A. 2024. Multimodal communication and audience directedness in the greeting behaviour of semi-captive African savannah elephants. Commun Biol. 7:472. doi:10.1038/s42003-024-06133-5.

Evans KE, Harris S. 2008. Adolescence in male African elephants, *Loxodonta africana*, and the importance of sociality. Anim Behav. 76(3):779–787. doi:10.1016/j.anbehav.2008.03.019.

Fernando P, Wikramanayake ED, Janaka HK, Jayasinghe LKA, Gunawardena M, Kotagama SW, Weerakoon D, Pastorini J. 2008. Ranging behavior of the Asian elephant in Sri Lanka. Mamm Biol. 73(1):2–13. doi:10.1016/j.mambio.2007.07.007.

Fishlock V, Lee PC. 2013. Forest elephants: Fission-fusion and social arenas. Anim Behav. 85(2):357–363. doi:10.1016/j.anbehav.2012.11.004.

Foerder P, Galloway M, Barthel T, Moore DE, Reiss D. 2011. Insightful problem solving in an Asian elephant. PLoS One. 6(8):e23251. doi:10.1371/journal.pone.0023251.

Foley CAH. 2002. The effect of poaching on elephant social systems. PhD thesis, Princeton University.

Gallup GG. 1970. Chimpanzees: Self-recognition. Science. 167(3914):86–87. doi:10.1126/science.167.3914.86.

Gautam M, Singh UP. 2022. Techniques for detecting trauma in ancient human remains. Indian J Phys Anthropol Hum Genet. 41(2):135–143.

Goldenberg SZ, Douglas-Hamilton I, Wittemyer G. 2016. Vertical transmission of social roles drives resilience to poaching in elephant networks. Curr Biol. 26:75–79. doi:10.1016/j.cub.2015.11.005.

Goldenberg SZ, De Silva S, Rasmussen HB, Douglas-Hamilton I, Wittemyer G. 2014. Controlling for behavioural state reveals social dynamics among male African elephants, *Loxodonta africana*. Anim Behav. 95:111–119. doi:10.1016/j.anbehav.2014.07.002.

Goldenberg SZ, Wittemyer G. 2017. Orphaned female elephant social bonds reflect lack of access to mature adults. Sci Rep. 7(1):1–7. doi:10.1038/s41598-017-14712-2.

Goldenberg SZ, Wittemyer G. 2020. Elephant behavior toward the dead: A review and insights from field observations. Primates. 61(1):119–128. doi:10.1007/s10329-019-00766-5.

Gravett N, Bhagwandin A, Sutcliffe R, Landen K, Chase MJ, Lyamin OI, Siegel JM, Manger PR. 2017. Inactivity/sleep in two wild free-roaming African elephant matriarchs - Does large body size make elephants the shortest mammalian sleepers? PLoS One. 12(3):e0171903. doi:10.1371/journal.pone.0171903.

Greco BJ, Meehan CL, Hogan JN, Leighty KA, Mellen J, Mason GJ, Mench JA. 2016. The days and nights of zoo elephants: Using epidemiology to better understand stereotypic behavior of African elephants (*Loxodonta africana*) and Asian elephants (*Elephas maximus*) in North American zoos. PLoS One. 11(7):e0144276. doi:10.1371/journal.pone.0144276.

Han Y, Yuan M, Guo YS, Shen XY, Gao ZK, Bi X. 2022. The role of enriched environment in neural development and repair. Front Cell Neurosci. 16:1–18. doi:10.3389/fncel.2022.890666.

Hart BL, Hart LA, McCoy M, Sarath CR. 2001. Cognitive behavior in Asian elephants: Use and modification of branches for fly switching. Anim Behav. 62(5):839–847. doi:10.1006/anbe.2001.1815.

Hedwig D, Debellis M, Wrege PH. 2018. Not so far: attenuation of low-frequency vocalizations in a rainforest environment suggests limited acoustic mediation of social interaction in African forest elephants. Behav Ecol Sociobiol. 72:33. doi:10.1007/s00265-018-2451-4.

Hedwig D, Kohlberg A. 2024. Call combination in African forest elephants *Loxodonta cyclotis*. PLoS One. 19(3):e0299656. doi:10.1371/journal.pone.0299656.

Hedwig D, Poole J, Granli P. 2021. Does social complexity drive vocal complexity? Insights from the two African elephant species. Animals. 11(11):1–21. doi:10.3390/ani11113071.

Hedwig D, Verahrami AK, Wrege PH. 2019. Acoustic structure of forest elephant rumbles: A test of the ambiguity reduction hypothesis. Anim Cogn. 22:1115–1128. doi:10.1007/s10071-019-01304-y.

Hildebrandt TB, Goeritz F. 2023. Artificial insemination in elephants. In: Miller E, Lamberski N, Calle P, editors. Fowler's Zoo and Wild Animal Medicine Current Therapy: Volume 10. Elsevier Ltd. p. 655–660.

Holdgate MR, Meehan CL, Hogan JN, Miller LJ, Soltis J, Andrews J, Shepherdson DJ. 2016. Walking behavior of zoo elephants: Associations between GPS-measured daily walking distances and environmental factors, social factors, and welfare indicators. PLoS One. 11(7):e0150331. doi:10.1371/journal.pone.0150331.

Hörner F, Oerke AK, Müller DWH, Westerhüs U, Azogu-Sepe I, Hruby J, Preisfeld G. 2021. Monitoring behaviour in African elephants during introduction into a new group: Differences between related and unrelated animals. Animals. 11:2990. doi:10.3390/ani11102990.

Irie-Sugimoto N, Kobayashi T, Sato T, Hasegawa T. 2009. Relative quantity judgment by Asian elephants (*Elephas maximus*). Anim Cogn. 12:193–199. doi:10.1007/s10071-008-0185-9.

Irie N, Hasegawa T. 2012. Summation by Asian elephants (*Elephas maximus*). Behav Sci (Basel). 2(2):50–56. doi:10.3390/bs2020050.

Irie N, Hiraiwa-Hasegawa M, Kutsukake N. 2019. Unique numerical competence of Asian elephants on the relative numerosity judgment task. J Ethol. 37:111–115. doi:10.1007/s10164-018-0563-y. https://doi.org/10.1007/s10164-018-0563-y.

Jacobs B, Rally H, Doyle C, O'Brien L, Tennison M, Marino L. 2022. Putative neural consequences of captivity for elephants and cetaceans. Rev Neurosci. 33(4):439–465. doi:10.1515/revneuro-2021-0100.

Jacobson SL, Dechanupong J, Horpiencharoen W, Yindee M, Plotnik JM. 2023. Innovating to solve a novel puzzle: Wild Asian elephants vary in their ability to problem solve. Anim Behav. 205:227–239. doi:10.1016/j.anbehav.2023.08.019.

Jacobson SL, Puitiza A, Snyder RJ, Sheppard A, Plotnik JM. 2022. Persistence is key: investigating Innovative problem solving by Asian elephants using a novel multi-access box. Anim Cogn. 25(3):657–669. doi:10.1007/s10071-021-01576-3.

Jakob-Hoff R, Kingan M, Fenemore C, Schmid G, Cockrem JF, Crackle A, Van Bemmel E, Connor R, Descovich K. 2019. Potential impact of construction noise on selected zoo animals. Animals. 9:504. doi:10.1093/oso/9780198753629.003.0005.

Kaswan P, Roy A. 2024. Unearthing calf burials among Asian elephants *Elephas maximus* Linnaeus, 1758 (Mammalia: Proboscidea: Elephantidae) in northern Bengal, India. J Threat Taxa. 16(2):24615–24629.

Kent RD, Vorperian HK. 2018. Static measurements of vowel formant frequencies and bandwidths: A review. J Commun Disord. 74:74–97. doi:10.1016/j.jcomdis.2018.05.004.

Ketchaisri O, Siripunkaw C, Plotnik JM. 2019. The use of a human's location and social cues by Asian elephants in an object-choice task. Anim Cogn. 22:907–915. doi:10.1007/s10071-019-01283-0.

King LE, Soltis J, Douglas-Hamilton I, Savage A, Vollrath F. 2010. Bee threat elicits alarm call in African elephants. PLoS One. 5(4):e10346. doi:10.1371/journal.pone.0010346.

Kurt F, Mar KU. 1996. Neonate mortality in captive Asian elephants (*Elephas maximus*). Zeitschrift für Säugetierkd. 61:155–164.

LaDue CA, Vandercone RPG, Kiso WK, Freeman EW. 2022. Social behavior and group formation in male Asian elephants (*Elephas maximus*): The effects of age and musth in wild and zoo-housed animals. Animals. 12:1215.

Lahdenperä M, Mar KU, Lummaa V. 2016. Nearby grandmother enhances calf survival and reproduction in Asian elephants. Sci Rep. 6:27213. doi:10.1038/srep27213.

Langbauer WR, Payne KB, Charif R a, Rapaport L, Osborn F. 1991. African elephants respond to distant playbacks of low-frequency conspecific calls. J Exp Biol. 157:35–46.

Lee PC. 1987. Allomothering among African elephants. Anim Behav. 35(1):278–291. doi:10.1016/S0003-3472(87)80234-8.

Leggett K. 2009. Daily and hourly movement of male desert-dwelling elephants. Afr J Ecol. 48:197–205. doi:10.1111/j.1365-2028.2009.01101.x.

Leggett KEA. 2006. Home range and seasonal movement of elephants in the Kunene Region, northwestern Namibia. African Zool. 41(1):17–36. doi:10.3377/1562-7020(2006)41[17:HRASMO]2.0.CO;2.

Li-Li L, Plotnik JM, Xia S-W, Meaux E, Quan R-C. 2021. Cooperating elephants mitigate competition until the stakes get too high. PLoS Biol. 19(9):1–23. doi:10.1371/journal.pbio.3001391.

Markowitz H, Schmidt M, Nadal L, Squier L. 1975. Do elephants ever forget? J Appl Behav Anal. 8(3):333–335. doi:10.1901/jaba.1975.8-333.

Mason GJ, Veasey JS. 2010. What do population-level welfare indices suggest about the well-being of zoo elephants? Zoo Biol. 29(2):256–273. doi:10.1002/zoo.20303.

McComb K, Baker L, Moss C. 2006. African elephants show high levels of interest in the skulls and ivory of their own species. Biol Lett. 2(1):26–28. doi:10.1098/rsbl.2005.0400.

McComb K, Moss C, Durant SM, Baker L, Sayialel S. 2001. Matriarchs as repositories of social knowledge in African elephants. Science. 292:491–494. doi:10.1126/science.1057895.

McComb K, Moss C, Sayialel S, Baker L. 2000. Unusually extensive networks of vocal recognition in African elephants. Anim Behav. 59:1103–1109. doi:10.1006/anbe.2000.1406.

McComb K, Reby D, Baker L, Moss C, Sayialel S. 2003. Long-distance communication of acoustic cues to social identity in African elephants. Anim Behav. 65:317–329.

McComb K, Shannon G, Durant SM, Sayialel K, Slotow R, Poole J, Moss C. 2011. Leadership in elephants: the adaptive value of age. Proc R Soc B. 278(1722):3270–3276.

McComb K, Shannon G, Sayialel KN, Moss C. 2014. Elephants can determine ethnicity, gender, and age from acoustic cues in human voices. Proc Natl Acad Sci. 111(14):5433–8. doi:10.1073/pnas.1321543111.

Mieske P, Hobbiesiefken U, Fischer-Tenhagen C, Heinl C, Hohlbaum K, Kahnau P, Meier J, Wilzopolski J, Butzke D, Rudeck J, et al. 2022. Bored at home?—A systematic review on the effect of environmental enrichment on the welfare of laboratory rats and mice. Front Vet Sci. 9. doi:10.3389/fvets.2022.899219.

Mikota SK. 2009. Stress, disease and tuberculosis in elephants. In: Forthman D, Kane L, Hancocks D, Waldau P, editors. An Elephant in the Room: The Science and Well-Being of Elephants. North Grafton, MA: Tufts University, Center for Animals and Public Policy. p. 74–85.

Miller MA, Hogan JN, Meehan CL. 2016. Housing and demographic risk factors impacting foot and musculoskeletal health in African elephants [*Loxodonta africana*] and Asian elephants [*Elephas maximus*] in North American zoos. PLoS One. 11(7):e0155223. doi:10.1371/journal.pone.0155223.

Mizuno K, Irie N, Hiraiwa-Hasegawa M, Kutsukake N. 2016. Asian elephants acquire inaccessible food by blowing. Anim Cogn. 19:215–222. doi:10.1007/s10071-015-0929-2.

Morfeld KA, Brown JL. 2017. Metabolic health assessment of zoo elephants: Management factors predicting leptin levels and the glucose-to-insulin ratio and their associations with health parameters. PLoS One. 12(11):e0188701. doi:10.1371/journal.pone.0188701.

Morfeld KA, Meehan CL, Hogan JN, Brown JL. 2016. Assessment of body condition in African (*Loxodonta africana*) and Asian (*Elephas maximus*) elephants in North American zoos and management practices associated with high body condition scores. PLoS One. 11(7):e0155146. doi:10.1371/journal.pone.0155146.

Morris-Drake A, Mumby HS. 2018. Social associations and vocal communication in wild and captive male savannah elephants *Loxodonta africana*. Mamm Rev. 48:24–36. doi:10.1111/mam.12106.

Moss CJ. 1983. Oestrous behaviour and female choice in the African elephant. Behaviour. 86(3/4):167–196.

Moss CJ, Poole JH. 1983. Relationships and social structure in African elephants. In: Hinde RA, editor. Primate Social Relationships: An Integrated Approach. Oxford, UK: Blackwell Science,

Inc. p. 315-325.

Nair S, Balakrishnan R, Seelamantula CS, Sukumar R. 2009. Vocalizations of wild Asian elephants (*Elephas maximus*): Structural classification and social context. J Acoust Soc Am. 126(5):2768–2778. doi:10.1121/1.3224717.

Nandini S, Keerthipriya P, Vidya TNC. 2018. Group size differences may mask underlying similarities in social structure: A comparison of female elephant societies. Behav Ecol. 29(1):145–159. doi:10.1093/beheco/arx135.

Nissani M. 2004. Theory of mind and insight in chimpanzees, elephants, and other animals? In: Rogers LJ, Kaplan G, editors. Comparative Vertebrate Cognition: Are Primates Superior to Non-Primates? New York, NY. p. 227–261.

O'Connell-Rodwell CE, Berezin JL, Pignatelli A, Rodwell TC. 2024. The use of vocal coordination in male African elephant group departures: Evidence of active leadership and consensus. PeerJ. 12:e17767. doi:https://doi.org/10.7717/peerj.17767.

O'Connell-Rodwell CE, Wood JD, Kinzley C, Rodwell TC, Poole JH, Puria S. 2007. Wild African elephants (*Loxodonta africana*) discriminate between familiar and unfamiliar conspecific seismic alarm calls. J Acoust Soc Am. 122(2):823–830. doi:10.1121/1.2747161.

O'Connell-Rodwell CE, Wood JD, Rodwell TC, Puria S, Partan SR, Keefe R, Shriver D, Arnason BT, Hart L a. 2006. Wild elephant (*Loxodonta africana*) breeding herds respond to artificially transmitted seismic stimuli. Behav Ecol Sociobiol. 59(6):842–850. doi:10.1007/s00265-005-0136-2.

O'Connell-Rodwell CE, Wood JD, Wyman M, Redfield S, Puria S, Hart LA. 2012. Antiphonal vocal bouts associated with departures in free-ranging African elephant family groups (*Loxodonta africana*). Bioacoustics. 21(3):215-224. doi:10.1080/09524622.2012.686166.

Pardo MA, Fristrup K, Lolchuragi DS, Poole J, Granli P, Moss C, Douglas-Hamilton I, Wittemyer G. 2024. African elephants address one another with individually specific name-like calls. Nat Ecol Evol. 8:1353–1364. doi:10.1038/s41559-024-02420-w.

Pardo MA, Lolchuragi DS, Poole J, Granli P, Moss C, Douglas-Hamilton I, Wittemyer G. 2024. Female African elephant rumbles differ between populations and sympatric social groups. R Soc Open Sci. 11:241264. doi:10.5061/dryad.rv15dv4dt.

Pardo MA, Poole JH, Stoeger AS, Wrege PH, O'Connell-Rodwell CE, Padmalal UK, De Silva S. 2019. Differences in combinatorial calls among the 3 elephant species cannot be explained by phylogeny. Behav Ecol. 30(3):809–820. doi:10.1093/beheco/arz018.

Perdue BM, Talbot CF, Stone AM, Beran MJ. 2012. Putting the elephant back in the herd: Elephant relative quantity judgments match those of other species. Anim Cogn. 15(5):955–961. doi:10.1007/s10071-012-0521-y.

Perrin KL, Nielsen SS, Martinussen T, Bertelsen MF. 2021. Quantification and risk factor analysis of elephant endotheliotropic herpesvirus-haemorrhagic disease fatalities in Asian elephants (*Elephas maximus*) in Europe (1985-2017). J Zoo Aquarium Res. 9(1):8–13.

Plotnik JM, Brubaker DL, Dale R, Tiller LN, Mumby HS, Clayton NS. 2019. Elephants have a

nose for quantity. Proc Natl Acad Sci. 116(25):12566–12571. doi:10.1073/pnas.1818284116.

Plotnik JM, Lair R, Suphachoksahakun W, de Waal FBM. 2011. Elephants know when they need a helping trunk in a cooperative task. Proc Natl Acad Sci. 108(12):5116–5121. doi:10.1073/pnas.1101765108.

Plotnik JM, de Waal FB. 2014. Asian elephants (*Elephas maximus*) reassure others in distress. PeerJ. 2:e278. doi:10.7717/peerj.278.

Plotnik JM, De Waal FBM, Reiss D. 2006. Self-recognition in an Asian elephant. Proc Natl Acad Sci. 103(45):17053–17057. doi:10.1073/pnas.608062103.

Pokharel SS, Sharma N, Sukumar R. 2022. Viewing the rare through public lenses: Insights into dead calf carrying and other thanatological responses in Asian elephants using YouTube videos. R Soc Open Sci. 9(5). doi:10.1098/rsos.211740.

Polansky L, Douglas-Hamilton I, Wittemyer G. 2013. Using diel movement behavior to infer foraging strategies related to ecological and social factors in elephants. Mov Ecol. 1:13. doi:10.1186/2051-3933-1-13.

Polansky L, Kilian W, Wittemyer G. 2015. Elucidating the significance of spatial memory on movement decisions by African savannah elephants using state-space models. Proc R Soc B. 282:20143042. doi:10.1098/rspb.2014.3042.

Poole JH. 1987. Rutting behavior in African elephants: The phenomenon of musth. Behaviour. 102(3/4):283–316.

Poole JH. 1989. Mate guarding, reproductive success and female choice in African elephants. Anim Behav. 37:842–849. doi:10.1016/0003-3472(89)90068-7.

Poole JH. 1999. Signals and assessment in African elephants: Evidence from playback experiments. Anim Behav. 58:185–193.

Poole JH. 2011. Behavioral contexts of elephant acoustic communication. In: Moss CJ, Croze H, Lee PC, editors. The Amboseli Elephants: A Long-Term Perspective on a Long-Lived Mammal. Chicago, USA: University of Chicago Press. p. 125–159.

Poole JH, Granli P. 2011. Signals, gestures, and behavior of African elephants. In: Moss CJ, Croze H, Lee PC, editors. The Amboseli Elephants: A Long-Term Perspective on a Long-Lived Mammal. Chicago, USA: University of Chicago Press. p. 109–124.

Poole JH, Payne K, Langbauer WRJ, Moss CJ. 1988. The social contexts of some very low-frequency calls of African elephants. Behav Ecol Sociobiol. 22(6):385–392. doi:10.1007/BF00294975.

Poole JH, Tyack PL, Stoeger-Horwath AS, Watwood S. 2005. Elephants are capable of vocal learning. Nature. 434:455–456. doi:10.1029/2001GL014051.

Prado-Oviedo NA, Bonaparte-Saller MK, Malloy EJ, Meehan CL, Mench JA, Carlstead K, Brown JL. 2016. Evaluation of demographics and social life events of Asian (*Elephas maximus*) and African elephants (*Loxodonta africana*) in North American zoos. PLoS One. 11(7):e0154750. doi:10.1371/journal.pone.0154750.

Pretorius Y, Eggeling T, Ganswindt A. 2023. Identifying potential measures of stress and disturbance during a captive to wild African elephant reintegration. PLoS One. 18(10):e0291293. doi:10.1371/journal.pone.0291293.

Rasmussen LEL, Krishnamurthy V. 2000. How chemical signals integrate Asian elephant society: The known and the unknown. Zoo Biol. 19(5):405–423. doi:10.1002/1098-2361(2000)19:5<405::AID-ZOO10>3.0.CO;2-J.

Rees PA. 2004. Low environmental temperature causes an increase in stereotypic behaviour in captive Asian elephants (*Elephas maximus*). J Therm Biol. 29(1):37–43. doi:10.1016/j.jtherbio.2003.10.004.

Regnault S, Dixon JJI, Warren-Smith C, Hutchinson JR, Weller R. 2017. Skeletal pathology and variable anatomy in elephant feet assessed using computed tomography. PeerJ. 5:e2877. doi:10.7717/peerj.2877.

Rose JB, Leeds A, Yang LM, Lemont R, Fayette MA, Proudfoot JS, Bowman MR, Woody A, Oosterhuis J, Fagan DA. 2022. Treatment and outcomes of tusk fractures in managed African savanna and Asian elephants (*Loxodonta africana* and *Elephas maximus*) across five continents. Animals. 12(9). doi:10.3390/ani12091125.

Scherer L, Bingaman Lackey L, Clauss M, Gries K, Hagan D, Lawrenz A, Müller DWH, Roller M, Schiffmann C, Oerke AK. 2023. The historical development of zoo elephant survivorship. Zoo Biol. 42(2):328–338. doi:10.1002/zoo.21733.

Schuttler SG, Philbrick JA, Jeffery KJ, Eggert LS. 2014. Fine-scale genetic structure and cryptic associations reveal evidence of kin-based sociality in the African forest elephant. PLoS One. 9(2):e88074. doi:10.1371/journal.pone.0088074.

Scott NL, LaDue CA. 2019. The behavioral effects of exhibit size versus complexity in African elephants: A potential solution for smaller spaces. Zoo Biol. 38(5):448–457. doi:10.1002/zoo.21506.

Seyfarth RM, Cheney DL, Marler P. 1980. Vervet monkey alarm calls: Semantic communication in a free-ranging primate. Anim Behav. 28:1070–1094.

Shannon G, Slotow R, Durant SM, Sayialel KN, Poole J, Moss C, McComb K. 2013. Effects of social disruption in elephants persist decades after culling. Front Zool. 10:62. doi:10.1186/1742-9994-10-62.

Sharma N, Pokharel SS, Kohshima S, Sukumar R. 2020. Behavioural responses of free-ranging Asian elephants (*Elephas maximus*) towards dying and dead conspecifics. Primates. 61:129–138. doi:10.1007/s10329-019-00739-8.

de Silva S. 2010. Acoustic communication in the Asian elephant, *Elephas maximus maximus*. Behaviour. 147(7):825–852. doi:10.1163/000579510X495762.

de Silva S, Ranjeewa ADG, Kryazhimskiy S. 2011. The dynamics of social networks among female Asian elephants. BMC Ecol. 11:17. doi:10.1186/1472-6785-11-17.

de Silva S, Ranjeewa ADG, Weerakoon D. 2011. Demography of Asian elephants (*Elephas maximus*) at Uda Walawe National Park, Sri Lanka based on identified individuals. Biol

Conserv. 144(5):1742–1752. doi:10.1016/j.biocon.2011.03.011. http://dx.doi.org/10.1016/j.biocon.2011.03.011.

de Silva S, Wittemyer G. 2012. A comparison of social organization in Asian elephants and African savannah elephants. Int J Primatol. 33(5):1125–1141. doi:10.1007/s10764-011-9564-1.

Slowtow R, van Dyk G, Poole J, Page B, Klocke A. 2000. Older bull elephants control young males. Nature. 408:425–426.

Smet AF, Byrne RW. 2014a. African elephants (*Loxodonta africana*) recognize visual attention from face and body orientation. Biol Lett. 10(7):20140428. doi:10.1098/rsbl.2014.0428.

Smet AF, Byrne RW. 2014b. Interpretation of human pointing by African elephants: Generalisation and rationality. Anim Cogn. 17:1365–1374.

Smet AF, Byrne RW. 2020. African elephants interpret a trunk gesture as a clue to direction of interest. Curr Biol. 30:R926–R927. doi:10.1016/j.cub.2020.06.070.

Snyder RJ, Barrett LP, Emory RA, Perdue BM. 2021. Performance of Asian elephants (*Elephas maximus*) on a quantity discrimination task is similar to that of African savanna elephants (*Loxodonta africana*). Anim Cogn. 24(5):1121–1131. doi:10.1007/s10071-021-01504-5.

Soltis J, Blowers TE, Savage A. 2011. Measuring positive and negative affect in the voiced sounds of African elephants (*Loxodonta africana*). J Acoust Soc Am. 129:1059–1066. doi:10.1121/1.3531798.

Soltis J, King LE, Douglas-Hamilton I, Vollrath F, Savage A. 2014. African elephant alarm calls distinguish between threats from humans and bees. PLoS One. 9(2):e89403. doi:10.1371/journal.pone.0089403.

Srinivasaiah N, Kumar V, Vaidyanathan S, Sukumar R, Sinha A. 2019. All-male groups in Asian elephants: A novel, adaptive social strategy in increasingly anthropogenic landscapes of Southern India. Sci Rep. 9:8678. doi:10.1038/s41598-019-45130-1.

Steenkamp G, Ferreira SM, Bester MN. 2007. Tusklessness and tusk fractures in free-ranging African savanna elephants (*Loxodonta africana*). J S Afr Vet Assoc. 78(2):75–80. doi:10.4102/jsava.v78i2.294.

Stoeger AS, Baotic A. 2017. Male African elephants discriminate and prefer vocalizations of unfamiliar females. Sci Rep. 7:46414. doi:10.1038/srep46414.

Stoeger AS, Baotic A. 2021. Operant control and call usage learning in African elephants. Philos Trans R Soc B. 376(1836):10–15. doi:10.1098/rstb.2020.0254.

Stoeger AS, Heilmann G, Zeppelzauer M, Ganswindt A, Hensman S, Charlton BD. 2012. Visualizing sound emission of elephant vocalizations: Evidence for two rumble production types. PLoS One. 7(11):e48907. doi:10.1371/journal.pone.0048907.

Stoeger AS, Mietchen D, Oh S, de Silva S, Herbst CT, Kwon S, Fitch WT. 2012. An Asian elephant imitates human speech. Curr Biol. 22(22):2144–2148. doi:10.1016/j.cub.2012.09.022.

Stoeger AS, de Silva S. 2014. African and Asian elephant vocal communication: A cross-species comparison. In: Witzany G, editor. Biocommunication of Animals. 1st ed. Dordrecht,

Netherlands: Springer Netherlands. p. 233–247.

Taylor VJ, Poole TB. 1998. Captive breeding and infant mortality in Asian elephants: A comparison between twenty Western zoos and three Eastern elephant centers. Zoo Biol. 17:311–332. doi:10.1002/(SICI)1098-2361(1998)17:4<311::AID-ZOO5>3.0.CO;2-C.

Thompson ME. 2009. African forest elephant (*Loxodonta africana cyclotis*) vocal behavior and its use in conservation. PhD thesis, Cornell University.

Thuppil V, Coss RG. 2013. Wild Asian elephants distinguish aggressive tiger and leopard growls according to perceived danger. Biol Lett. 9(5):20130518. doi:10.1098/rsbl.2013.0518.

Tsuchiya Y, Yayota M, Kashima Y, Shiota Y. 2023. Nutritional effect of feeding enrichment using bamboo Pleioblastus spp. in zoo-kept Asian elephants Elephas maximus. J Zoo Aquarium Res. 11(2):267–273. doi:doi.org.10.19227/jzar.v11i2.686.

van Veluw SJ, Chance SA. 2014. Differentiating between self and others: An ALE meta-analysis of fMRI studies of self-recognition and theory of mind. Brain Imaging Behav. 8(1):24–38. doi:10.1007/s11682-013-9266-8.

Verahrami AK. 2023. Forest elephants modulate their behavior to adapt to sounds of danger. Colorado State University.

Vidya TNC. 2014. Novel behaviour shown by an Asian elephant in the context of allomothering. Acta Ethol. 17(2):123–127. doi:10.1007/s10211-013-0168-y.

Vidya TNC, Sukumar R. 2005. Social organization of the Asian elephant (*Elephas maximus*) in southern India inferred from microsatellite DNA. J Ethol. 23(2):205–210. doi:10.1007/s10164-005-0144-8.

Viljoen PJ. 1989. Spatial distribution and movements of elephants (*Loxodonta africana*) in the northern Namib Desert region of the Kaokoveld, South West Africa/Namibia. J Zool. 219(1):1–19. doi:10.1111/j.1469-7998.1989.tb02561.x.

Wall J, Wittemyer G, Klinkenberg B, LeMay V, Blake S, Strindberg S, Henley M, Vollrath F, Maisels F, Ferwerda J, et al. 2021. Human footprint and protected areas shape elephant range across Africa. Curr Biol. 31:2437–2445. doi:10.1016/j.cub.2021.03.042.

Williams E, Carter A, Hall C, Bremner-Harrison S. 2019. Social interactions in zoo-housed elephants: Factors affecting social relationships. Animals. 9(10). doi:10.3390/ani9100747.

Wittemyer G, Douglas-Hamilton I, Getz WM. 2005. The socioecology of elephants: Analysis of the processes creating multitiered social structures. Anim Behav. 69:1357–1371. doi:10.1016/j.anbehav.2004.08.018.

Wood JD, Mccowan B, Langbauer WR, Viljoen JJ, Hart LA. 2005. Classification of African elephant *Loxodonta africana* rumbles using acoustic parameters and cluster analysis. Bioacoustics. 15(2):143–161. doi:10.1080/09524622.2005.9753544.

EXHIBIT A: CURRICULUM VITAE

Michael A. Pardo K. Lisa Yang Center for Conservation Bioacoustics Cornell Lab of Ornithology map385@cornell.edu

CURRENT POSITION

Postdoctoral associate

1 Nov 2023-Present

K. Lisa Yang Center for Conservation Bioacoustics, Cornell Lab of Ornithology

Supervisor: Dr. Connor Wood

PROJECT TITLE: Acoustic monitoring of riparian biodiversity in Southern California

PREVIOUS POSITION

NSF postdoctoral research fellow in biology

1 Nov 2019 - 31 Oct 2023

Host institution: Colorado State University Sponsoring scientist: Dr. George Wittemyer

PROJECT TITLE: The function of vocal learning ability in African elephants

EDUCATION

Ph.D., Neurobiology and Behavior

15 August 2019

Cornell University

Advisors: Dr. Walter Koenig and Dr. Michael Webster

DISSERTATION: Vocal recognition and social cognition in the Acorn Woodpecker

Bachelor of Science, Summa Cum Laude, Environmental Biology

May 2012

State University of New York College of Environmental Science and Forestry

HONORS THESIS: Tail communication in the Eastern gray squirrel, Sciurus carolinensis

MANUSCRIPTS IN REVIEW AND PREP

- **M. A. Pardo**, L. Gallagher, R. Byers*, J. Winiarski, J. Keane, M. Z. Peery, C. Wood. (In review). Passive acoustic monitoring reveals surprising patterns of avian community antipredator behavior at a landscape scale. *Ecology*.
- **M. A. Pardo**, P. Dumont*, D. Lolchuragi, and G. Wittemyer. (In prep). Elephant greeting rumbles vary with both absolute caller age and caller age relative to receiver age.

PUBLICATIONS

- **M. A. Pardo**. (2024) Elephant vocal communication. In: *International Encyclopedia of Linguistics* (ed. R. Boobalan).
- M. A. Pardo, D. S. Lolchuragi*, J. Poole, P. Granli, C. Moss, I. Douglas-Hamilton, and G. Wittemyer. (2024) Female African elephant rumbles differ between populations and sympatric social groups. *Royal Society Open Science* 11:241264.

- **M. A. Pardo**, K. Fristrup, D. S. Lolchuragi*, J. Poole, P. Granli, C. Moss, I. Douglas-Hamilton, and G. Wittemyer. (2024) African elephants address one another with individually specific name-like calls. *Nature Ecology and Evolution* 8:1353-1364.
- K. Odom, M. Araya-Salas, J. Morano, R. Ligon, G. Leighton, C. Taff, A. Dalziell, A. Billings, R. Germain, M. Pardo, L. Guimarães de Andrade, D. Hedwig, S. Keen, Y. Shiu, R. Charif, M. Webster, A. Rice. (2021) Comparative bioacoustics: a roadmap for quantifying and comparing animal sounds across diverse taxa. *Biological Reviews* 96:1135-1159.
- **M. A. Pardo**, E. L. Walters, W. D. Koenig. (2020) Experimental evidence that acorn woodpeckers recognize relationships among third parties no longer living together. *Behavioral Ecology* 31:1257-1265.
- M. A. Pardo, C. E. Hayes*, E. L. Walters, W. D. Koenig. (2020) Acorn woodpeckers vocally discriminate current and former group members from non-group members. *Behavioral Ecology* 31:1120-1128.
- M. A. Pardo, J. H. Poole, A. S. Stoeger, P. H. Wrege, C. E. O'Connell-Rodwell, U. K. Padmalal, S. de Silva. (2019) Differences in combinatorial calls among the 3 elephant species cannot be explained by phylogeny. *Behavioral Ecology* 30:809-820.
- **M. A. Pardo**, E. A. Sparks, T. S. Kuray, N. D. Hagemeyer, E. L. Walters, W. D. Koenig. (2018) Wild acorn woodpeckers recognize associations between individuals in other groups. *Proceedings of the Royal Society B* 285: 20181017 (cover article)
- L. King, **M. Pardo**, S. Weerathunga, T. V. Kumara, N. Jayasena, J. Soltis, and S. de Silva. (2018) Wild Sri Lankan elephants (*Elephas maximus*) retreat from the sound of disturbed Asian honey bees (*Apis cerana indica*). *Current Biology* 28:R64-R65.
- S. A. Pardo and M. A. Pardo. (2018) Statistical methods for field and laboratory studies in behavioral ecology. CRC Press, Boca Raton, FL 308p.
- **M. A. Pardo**, S. A. Pardo, and W. M. Shields. (2014) Eastern gray squirrels (*Sciurus carolinensis*) communicate with the positions of their tails in an agonistic context. *American Midland Naturalist* 172:360-366.

SELECT INVITED TALKS

M. A. Pardo, D. Omer. What's in a name? Discovering individual vocal labels in African elephants. Invited talk for Bridging Brains and Bioacoustics Seminar, April 17, 2025.

^{*}Undergraduate authors

- **M. A. Pardo.** Elephant vocal communication: A promising model for language evolution. Invited talk for Frontiers in Social Evolution Seminar, March 25, 2025.
- **M. A. Pardo.** Elephant cognition and its implications for welfare. Invited talk for Performing Animal Welfare Society Conference, 2024, Los Angeles, CA.
- **M. A. Pardo.** Invited panelist for "Elephants, Science, and the Law" webinar, 2024, International Association of Lawyers.
- **M. A. Pardo.** Vocal communication in African savannah elephants. Invited talk for Unlocking Nature panel, 2024, Leadership for Conservation in Africa.
- M. A. Pardo, K. Fristrup, D. Lolchuragi, J. Poole, P. Granli, C. Moss, I. Douglas-Hamilton, and G. Wittemyer. What's in a name? Elephants address one another with individually specific calls. Invited talk for Interspecies Conversation Lecture Series, 2024, Interspecies Internet.
- **M. A. Pardo**. Chicken cognition and its implications for welfare. Invited talk for Our Honor Continuing Education Lecture Series, 2024.
- **M. A. Pardo,** K. Fristrup, D. Lolchuragi, J. Poole, P. Granli, C. Moss, I. Douglas-Hamilton, and G. Wittemyer. Do elephants have names? Individual vocal labeling in African elephants. Invited oral presentation at Protolang Conference Symposium: Elephants as a promising model for studying language evolution, 2023, Rome, Italy.
- M. A. Pardo, K. Fristrup, D. Lolchuragi, J. Poole, P. Granli, C. Moss, I. Douglas-Hamilton, and G. Wittemyer. Do elephants have names? Individual vocal labeling in African elephants. Invited talk at Decoding Communication in Non-human Species Workshop, 2023, Berkeley, CA.
- M. A. Pardo, E. L. Walters, and W. D. Koenig. Social cognition in the acorn woodpecker. Invited talk at University of Vienna, 2019, KLF Grünau, Austria.
- M. A. Pardo, E. L. Walters, and W. D. Koenig. Social cognition in the acorn woodpecker (presented in Spanish). Invited talk at Universidad CES, 2018, Medellín, Colombia

TEACHING EXPERIENCE

Mapping culture and conservation

Fall 2020, 2022

Designed and taught units on human-wildlife conflict and tribal conservation, Colorado State University

Batch detection of species-specific vocalizations in R

Spring 2021

Virtual workshop on acoustic analysis in R for students at Northern Colorado University

Introduction to acoustic analysis in R

Spring 2021

Virtual workshop on acoustic analysis in R for Colorado chapter of The Wildlife Society

Lying birds and dancing bees: How animals communicate

Spring 2019

Instructor of record for First-year Writing Seminar on animal communication, Cornell University

Hormones and Behavior

Fall 2016, 2018

Teaching assistant, Cornell University

Introduction to Animal Behavior

Fall 2014

Teaching assistant, Cornell University

COMPETITIVE AWARDS, GRANTS AND FELLOWSHIPS (total funds received: \$415,132)

•	Explorers Club EC50 Class of 2025	2025
•	NSF Postdoctoral Research Fellowship in Biology	2019
•	NSF Doctoral Dissertation Improvement Grant	2017
•	National Geographic Young Explorers Grant	2017
•	Athena Fund, Cornell Lab of Ornithology	2016
•	Animal Behavior Society Student Research Grant	2014
•	American Society of Mammalogists Student Research Grant	
	2014	
•	Sigma Xi Grant-in-Aid-of-Research	2014
•	Athena Fund, Cornell Lab of Ornithology	2013
•	NSF Graduate Research Fellowship (GRFP)	2013
•	Athena Fund, Cornell Lab of Ornithology	2012

MENTORING EXPERIENCE

- Iroshmal Peiris (PhD student) Current
 - o Studying the function of greeting calls in Acorn Woopeckers
- Riley Byers (undergrad) Summer 2024
 - Using passive acoustics to identify Mountain Chickadee responses to Northern Goshawks in the Sierra Nevada
- Piper Dumont (undergrad) 2020-2024
 - o The social contexts of greeting rumbles in wild African elephants
- Moeumu Uili (Master's student) Fall 2022
 - o Acoustic detection of the critically endangered and endemic Tooth-billed Pigeon
- Casey Hayes (undergrad) Spring & Summer 2018
 - Vocal recognition in Acorn Woodpeckers
- Robert Anderson and Sarah Heimbach (undergrad and recent grad) 2017
 - Vocal communication and social behavior in Acorn Woodpeckers
- Emilee Sparks and Tejal Kuray (recent grads) Spring 2016
 - Vocal communication and social cognition in Acorn Woodpeckers

SERVICE AND OUTREACH

- Peer reviewer for Nature Ecology & Evolution, Behavioral Ecology, Ethology, Ibis, Animals, New Zealand Journal of Zoology
- Wrote article for "The UNESCO Courier" about animal language (February 2025)
- Member of Onboarding and Professional Development Working Group for DEIJ committee of Cornell Lab of Ornithology (July 2024-present)
- Wrote article for "The Conversation" about my research on elephant vocal communication (June 2024) https://theconversation.com/african-elephants-address-one-another-with-name-like-calls-similar-to-humans-232096
- Presentation to staff of Save The Elephants in Kenya (April 2022)
- Designed and taught workshop on Microsoft Excel for Kenyan staff members of Save The Elephants, Ewaso Lions, and Grevy's Zebra Trust (November 2021)
- Designed and taught mini course on animal communication to teach to 4th grade students in Spring 2019 as part of Cornell GRASSHOPR program
- Helped teach workshop on ornithology to teach to 7th-9th grade girls in Spring 2019 as part of Expanding Your Horizons program at Cornell
- Mist-netting demonstration and presentation to undergraduates of underprivileged backgrounds from UC Berkeley (May 2018)
- Mist-netting demonstration and presentation for high school students from underprivileged backgrounds through California Academy of Sciences (Spring 2017)
- Presentation to undergraduate class from University of Chicago visiting Hastings Reserve (Spring 2017)
- Presentation about STEM career paths to underprivileged high school students through California Academy of Sciences (Spring 2016)
- Mist-netting demonstration and presentation for underprivileged high school students through California Academy of Sciences (Spring 2015)
- Presentation to undergraduate class from University of Chicago visiting Hastings Reserve (Spring 2015)
- Presentation to group of local schoolchildren and national park staff in Udawalawa, Sri Lanka (Spring 2014)
- Wrote blog posts about fieldwork with Asian elephants for maximus.trunksnleaves.org blog (December 2012 through May 2019)

SELECT MEDIA COVERAGE (>3,000 articles and broadcasts in at least 92 countries)

- T. Danovich. "Elephants are doing something deeply human." The Atlantic, June 18, 2024.
- K. Golembiewski. "Every elephant has its own name, study suggests." New York Times, June 13, 2024.
- N. Greenfieldboyce. "Wild elephants may have names that other elephants use to call them." NPR: Morning Edition, June 11, 2024.
- "Elephants have names for each other, new study finds." BBC Newshour, June 11, 2024.
- K. Ables. "Elephants call each other by name, study suggests." Washington Post, June 11, 2024.
- C. Larson. "African elephants call each other by unique names, new study shows." Associated Press, June 10, 2024.

- W. Dunham. "Study shows elephants might call each other by name." Reuters, June 10, 2024.
- Orie. "African elephants use names to call each other, study suggests." CNN, June 10, 2024.
- "Elephants call each other by name, study finds." The Guardian, June 10, 2024.
- M. Zaraska. "Elephants call individuals' names across the savanna." Scientific American, June 10, 2024.
- L. Neme. "Elephants may call each other by name, a rare trait in nature." National Geographic, June 10, 2024.
- Scripps News (documentary film). "How scientists are using AI to communicate with animals". May, 2023.