Declaration of Bob Jacobs

I, Bob Jacobs, declare as follows:

Introduction and Qualifications

1. My name is Bob Jacobs. I graduated with a Bachelor of Arts, *Magna Cum Laude*, in German from Whitman College in 1980. I received an M.A. in Germanics, with a minor in Teaching English as a Second Language, from the University of Washington in 1982. I received my Ph.D. from the University of California, Los Angeles (UCLA) in Applied Linguistics in 1991, completing a neuroanatomy dissertation under the supervision of Drs. Arnold B. Scheibel and John Schumann. The dissertation was entitled: "A Quantitative Dendritic Analysis of Wernicke's Area." During this time, I also worked with Dr. Marian Diamond of the University of California, Berkeley. Post-doctoral research in neuroimaging was also completed from 1991-1993 under the supervision of Dr. Harry Chugani at UCLA. I began my tenure track professorship in the Department of Psychology at Colorado College in 1993, started the school's Neuroscience major in 1996, and was there for 30 years, retiring in 2023. I now reside in Lakebay, Washington.
2. 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 and Aquarium. I have professional knowledge of the facts to which I attest and am not a party to this proceeding.
3. I have conducted research on the mammalian brain since 1984, when I began my dissertation research in the Laboratory of Dr. Arnold B. Scheibel at the UCLA Brain Research Institute. I have 48 peer-reviewed publications to my name, all in well-respected scientific journals. I also have two chapters in edited volumes, and 63 professional talks/posters presented at academic conferences, and over 60 invited lectures about the brain. From 1984 to 2010, my main research focus on the human cerebral cortex, specifically on the quantitative neuromorphology in the cerebral cortex, that is, the shape and size of nerve cells (neurons) in the outmost layers

of the brain involved in higher cognitive functions—18 publications have focused on human tissue.

4. From 2010 onward, I focused on comparative neuroanatomy, examining the brains of a variety of species—for many of these species, our studies constitute the first time anyone had explored the neurons in the brains of these animals. Species examined included: African elephant, giraffe, minke whale, humpback whale, bottlenose dolphin, Siberian tiger, clouded leopard, Florida manatee, cheetah, African leopard, chimpanzee, African wild dog, domestic dog, banded mongoose, caracal, zebra, wildebeest, pygmy hippopotamus, greater kudu, ring-tailed lemur, golden lion tamarin, chacma baboon, macaque monkey, Flemish giant rabbit, Bennett's wallaby, and Long-Even's rat. A total of 18 publications have focused on these non-human animals.
5. With regards to the African elephant, we documented the types of neurons in both the cerebral cortex and in the cerebellum, a part of the brain involved in balance, body control, and coordination. This research was conducted on adult and newborn elephants—resulting in a total of 4 publications focused exclusively on the elephant brain, which had not been explored previously. In addition to academic publications, I have presented these results at several scientific conferences (e.g., Society for Neuroscience, Performing Animal Welfare Society), and have written summaries of this research for the online publication known as "The Conversation" (see here and here).
6. My Curriculum Vitae fully sets forth my educational background and experience and is attached as "Exhibit A."

Basis for opinions

7. My early interest in brain research involved using the research techniques of Dr. Scheibel to extend both his and Dr. Diamond's interest into the effects of the environment on the brain. Dr. Diamond was a pioneer in documenting the effects of an impoverished and enriched environment on neuroanatomy in non-human animals; my dissertation extended that to the human brain, where we found education related differences in the neurons of the cerebral

cortex. Specifically, individuals with a university education had more complex neurons than individuals with a high school or less than high school education.

8. I have followed this area of research my entire career, including when we examined the brains of both free and captive animals. As such, several decades of neuroscientific research has led me to several conclusions about the state of the brain in captive non-human animals, particularly with regard to long-lived, large-brained mammals such as elephants.

9. One of the main findings of our elephant cortex paper (Jacobs et al., 2011) was that pyramidal neurons in the elephant are just as complex as similar neurons in the human cortex. As is the case in humans, these neurons are also more complex in the frontal lobe, involved with higher cognitive function, than in the occipital lobe, involved in the early processing of incoming visual information. There are remarkable parallels in terms of overall complexity of neurons and the functional involvement of these neurons. One difference was noted between the cortical neurons in the African elephant and in humans—those in the African elephant appear to extend their branches more broadly than neurons in the human, which tend to be more compact. As such, elephant neurons sample a very wide array of information because of the length of their dendrites. This broad synthesis of information in the African elephant may contribute to their contemplative nature—elephants often appear to be examining their surroundings and thinking very deeply about what is going on around them. They have the leisure of their great size and few natural predators, which allows them to consider their decisions very carefully. Primate cortical neurons, by contrast, seem more designed for quick responses to the environment. This contemplative aspect of the elephant further supports the findings expressed below with regards to how their brain responds to captivity.

10. Although my own research has focused on the African elephant, all of conclusions here apply equally to Asian elephants as well—in fact, the conclusion applies across all mammals studied to date. In terms of general neuroanatomy, the Asian elephant brain is very similar to the African elephant brain (Shoshani et al, 2006). There is no reason to suspect that the brain of an Asian elephant be different in terms of physiology, neurochemistry, and basic cellular

makeup (Barasa & Schochatovitz, 1961) than any other mammal. All evidence suggests it is remarkably similar to the brain of an African elephant, both in terms of structure (Maseko et al., 2012) and function (Plotnick et al., 2006; Hart et al., 2008).

11. I recently published a co-authored comprehensive review article on the neural consequences of impoverished environments for elephants and cetaceans (Jacobs et al., 2021; see here). In addition, I also a co-authored the most comprehensive and up to date scientific review of the severe challenges faced by elephants in captivity (Doyle et al., 2024; see here). In that review, we discuss quantitative and qualitative aspects of the enclosed space for elephants as well as sociocognitive factors, dietary differences, and health/welfare concerns (e.g., stereotypies, physical health, nutrition, reproduction, life expectancy). These review articles form the basis of the opinions expressed in this declaration.

Opinions

12. In addition to a rather large list of well-documented physical ailments (Riddle & Stremme, 2011) and behavioral abnormalities (Greco et al., 2017) that afflict elephants in captivity (Doyle et al., 2024), ~~e~~xtensive neural consequences to an impoverished environment have been demonstrated in many species to date: mice, rats, rabbits, cats, and primates, including humans (Jacobs et al., 1993, 2021). No research of this nature has been completed on elephants as these are post-mortem studies and would therefore require killing of the animal; as such, we extrapolated from controlled scientific studies with all evidence suggesting that the brains of animals such as elephants would not "behave" any differently than the brain of any other mammal, including humans. There is a great deal of evolutionary continuity across the brains of the species that have been examined, which makes this a very logical extension of the existing research. Indeed, much of what we know about the neuropsychiatric consequences of chronic stress in humans derives from nonhuman animal models (Lecorps et al., 2021).

13. Over 60 years of neuroscience research indicates that an impoverished environment negatively affects the cerebral cortex (Diamond et al., 1964; Diamond, 2001). These effects include a thinner cerebral cortex, decreased blood supply, smaller neuronal cells bodies with few glial

("helper") cells for metabolic support, decreased dendritic branching for synthesizing information, fewer dendritic spines (indicating fewer connections with other neurons), and smaller, less efficient synapses. Additional studies reveal similar epigenetic-related deficiencies at the molecular (van Praag et al., 2000) and neurochemical (Kozorovitskiy et al., 2005) level throughout the brain. These changes at the cortical level are associated with deficits in an animal's emotional and cognitive functioning (Neidl et al., 2016).

14. A crucial component to an enriched environment is exercise (Basso & Suzuki, 2017), which not only increases the supply of oxygenated blood to a metabolically expensive brain, but also contributes to potential neurogenesis and enhanced cognitive abilities through a series of complex biochemical cascades (Horowitz et al., 2020). Large, captive mammals are severely deprived of the exercise component of enrichment, particularly when one realizes that elephants naturally travel tens of kilometers a day (sometimes more than 100 kilometers) across diverse terrain with numerous plants and various substrates, something they cannot do in the small, monotonous enclosures that typify zoo exhibits (Holdgate et al., 2016; Doyle et al., 2024). Not only do elephants in larger enclosures exhibit lower glucocorticoid metabolite concentrations than their cohorts in smaller enclosures, but they also exhibit lower cortisol (stress hormones) levels when they can access diverse enrichment options and are allowed to be in compatible social groups (Brown et al., 2019). In Asian elephants, cortisol levels negatively correlate with locomotion and positively correlate with stereotypies (Schmid et al., 2001). Overall, these findings imply that cortical neurons in impoverished/captive animals are less complex, receive less metabolic support, and process information less efficiently than cortical neurons from animals in an enriched, more natural environment (Rosenzweig & Bennett, 1969).

15. Two other brain areas are affected negatively by a captive/impoverished environment because such an environment severely constrains or even prevents the natural behavior of animals, resulting in chronic frustration, boredom, and stress. Two subcortical (beneath the cortex) brain structures negatively affected by such stress are the hippocampus, involved primarily in

declarative (i.e., facts and events) and spatial memory formation, and the amygdala, involved in emotional processing. Decades of neuroscientific research in the laboratory and in the field (Sapolsky, 2005) have demonstrated that prolonged stress results in chronically elevated levels of glucocorticoids (stress hormones) (Sapolsky, 1996). Chronic exposure to these stress hormones contributes to wide-ranging neurodegeneration (Vyas et al., 2016), including neuronal damage/death in the hippocampus (Sapolsky et al., 1990), resulting in memory deficits, and in the amygdala (McEwen et al., 2015), resulting in emotional processing deficits. In natural environments, the body's stress-response system is designed for quick activation to escape from danger; in captivity, there is no escape. In captivity, animals have an almost complete lack of control (Sapolsky, 2012) over their environment. The resulting chronic stress tends to inhibit the immune system (Schedlowski & Schmidt, 1996), with negative health and neural consequences (McEwen et al., 2015). Under chronic psychological or physical stress, pro-inflammatory cytokines are released by activated immune cells and can interact with multiple corticolimbic brain structures, dysregulating different growth factors and neurogenesis, several neurotransmitter systems, and neuroendocrine communication (Capuron & Miller, 2011). Moreover, animals kept in social isolation exhibit increased aggression and depression like symptoms (Miura et al., 2002).

16. Stress from captivity often fosters learned helplessness and conditioned defeat (Maier & Seligman, 2016), which involves the amygdala (Hammack et al., 2012) and broad dysregulation of the neurotransmitter serotonin (Maier & Watkins, 2005). Under similar conditions (Chugani et al., 2001), stress is associated with a variety of neuropsychiatric diseases in humans, such as anxiety/mood disorders (Zhang et al., 2018), including major depression, and post-traumatic stress disorder (PTSD) (Koenigs & Grafman, 2009). Current human research, in fact, suggests that childhood trauma may subsequently make the adult brain more vulnerable to maladaptive stress responses (Banihashemi et al., 2020), an issue particularly relevant for long-lived, highly social animals such as elephants and cetaceans born into captivity. One neural consequence under such conditions is microglia activation and a

sustained release of inflammatory mediators (Leszek et al., 2016). Subsequent neuroinflammation contributes to physiological, behavioral, affective, and cognitive disorders (de Pablos et al., 2014; McLeod et al., 2001). To the extent that captivity induces stress-related immuno-suppression, captive animals are thus more susceptible not only to neuroinflammation but also to opportunistic infections and possible disruptions of fertility (Edwards et al., 2019). Given the highly conserved (Nikolova et al., 2018) nature of neural structures (i.e., brains have a lot in common across species), there is no logical reason to believe that the large, complex brains of animals such as elephants (Jacobs et al., 2011) would react any differently to a severely stressful environment than does the human brain.

17. Captivity and the psychosocial stress it engenders has negative effects on complex circuitry between a subcortical collection of nuclei (groups of neurons) known as the basal ganglia and the cerebral cortex. Through a series of reciprocal connections, the basal ganglia select and orchestrate appropriate cortical activity for a given situation, including the two pathways involved in movement: the direct pathway and the indirect pathway. The direct pathway tends to be involved in generating movement/behavior whereas the indirect pathway is more crucial for inhibition of movement/behavior. Normal movement depends on a delicate balance between these two pathways. Stereotypic behavior resulting from stress has been documented in a large number of species (e.g., poultry, rodents, pigs, voles, cows, sheep, dogs, horses, and primates, including humans), and is invariably associated with an imbalance in the direct/indirect pathways (McBride & Parker, 2015). More specifically, the indirect pathway is suppressed as a result of dysregulation of two neurotransmitter systems, dopamine and serotonin (Langen et al., 2011). Such behavioral stereotypies may represent a coping strategy as the animal attempts to mitigate the overwhelming effects of psychosocial stress (Poirier & Bateson, 2017). It is worth noting that elephants, in their natural habitat, have never been noted to have exhibit such stereotypies, which reflect underlying (abnormal) disruption of neural mechanisms.

18. Stereotypies are common human and non-human responses to chronic stress. Children with a history of early institutional care are more likely to exhibit stereotypies, underscoring the influential role of the environment during early development (Bos et al., 2010). In nonhuman animals, such behavioral stereotypies are seldom if ever observed in nature (Boorer, 1972), but have been consistently documented in many captive animals beyond murid rodents. Chronic stress also creates heightened dopamine sensitivity in the nucleus accumbens, which is part of the mesolimbic pathway associated with motivation (Cabib, 2006). Environmental deprivation and social isolation have repeatedly been shown to dysregulate these motor control pathways in several species, resulting in stereotypies (Martin et al., 1991; McBride & Hemmings, 2005). By extension, comprehensive environmental enrichment appears to rebalance activity in these pathways, thus at least partially ameliorating or even preventing the emergence of stereotypies. Comprehensive environmental enrichment appears to prevent stereotyped behaviors by increasing metabolic activity in the motor cortex, the striatum, and the nucleus accumbens (Turner et al., 2002).

Summary

19. Long-lived individuals with large, complex brains integral to their intricate sociobehavioral existence cannot function normally in captivity (Doyle et al., 2024). The neural perspective outlined in Jacobs et al. (2021) underscores the sociobehavioral assessment of elephant needs. Physical and behavioral abnormalities are easy to observe, but one must look deeper to see the neural consequences. Evolution has constructed the brain—of all organisms—to be extremely and exquisitely responsive to the environment (for better and worse). This responsivity extends to the level of gene expression, meaning that the environment can turn on or turn off different genes (Sapolsky, 2017). As such, the captive environment we place animals in significantly and sometimes permanently alters their brains in a negative manner. From a neural perspective, imprisoning large mammals and putting them on display is undeniably cruel.

20. Elephants exhibit behavioral patterns and physical abnormalities similar to other mammals in impoverished environments. Moreover, they possess very similar, highly conserved, neurobiological systems as do other mammals for responding to impoverishment and chronic stress. Therefore, elephants sustain neurobiological insults from living in confined, artificial environments. Insofar as most captive elephants cannot be "rewilded" for scientific and ethical reasons, the case can be made for transferring them to authentic sanctuaries, where they may live in a more natural environment. Authentic sanctuaries report improved physical and psychological health in elephants after their arrival, including decreased frequency or extinction of stereotypies, reduced aggression toward keepers, muscle tone gain, and formation of social bonds between elephants with different social histories, including elephants who were abused, traumatized, or solitary for decades (Buckley, 2009; Derby, 2009). Thus, elephants should either remain free (and protected) or, if already in captivity, they should be released into well-designed sanctuaries—several already exist for elephants; for example in Tennessee (see here), in Georgia (see here), and in Northern California (see here).

Observations related to the elephants at the Pittsburgh Zoo and Aquarium

21. I have examined several videos of the elephant exhibit at the Pittsburgh Zoo and Aquarium, including multiple videos of the five elephants on display. Having seen the conditions that the elephants endure, it is not surprising to me that the Zoo lost its Association of Zoos and Aquariums (AZA) accreditation in 2015. In 2019, the zoo was ranked as the worst zoo for elephants in North America by In Defense of Animals (https://www.idausa.org/campaign/elephants/10-worst-zoos-for-elephants-2019), it has appeared on this 10-worst zoos for elephants list multiple times (e.g., in 2016, 2017, 2020). Although this accreditation was restored in 2024, the AZA standards touted by zoos remain woefully inadequate for the well-being of elephants. My observation of the zoo facilities and the elephants' behavior in these videos leads me to the following observations/conclusions:

a) **Quantity of space.** Although the overall size of the Pittsburgh Zoo elephant exhibit (~0.75 acres, or ~4,046 m^2, outside area; 1,254 m^2 barn, divided into smaller stalls) meets the minimum AZA requirement for six elephants (500 m^2 each, with a minimum shared space of 3,000 m^2), it is immediately obvious that the allotted space at the zoo is woefully inadequate. The barn space is particularly insufficient. Insofar as elephants in their natural habitat have expansive home ranges, extending from 10s to 10,000 km^2 (Fernando et al., 2008; Bahar et al., 2018), the enclosure space provided by any zoo is simply insufficient—especially year after year, decade after decade (Doyle et al., 2024). The barn is barely large enough to hold the elephants, but not for any length of time, which is clearly necessary during winter months.

b) **Quality of space:** Within the barns, there is nothing of interest to the elephants (see videos here, here, and here). It is a featureless, extremely impoverished environment with a concrete floor, which is about the worst substrate one can have for elephants as it contributes significantly to musculoskeletal foot disease (e.g., osteoarthritis), which is very common among captive elephants (Miller et al., 2916; Doyle et al., 2024). Such ailments are associated with pain and joint stiffness, inability to stand, and sometimes leads to euthanasia (Issa and Griffin, 2012; Buckwalter et al., 2013). Although the outside environment has a water feature (video here) and some rock features, it is not much better than the inside environment. It is mostly compacted soil. which is similar to concrete in terms of hardness (video here). Within 10 minutes of entering their yard, the elephants could easily explore every aspect of the environment. There is also minimal shade, which is very important for the health of elephant skin. Shade is extremely important given the altitude of the zoo, as is access to mud baths, which is how the elephants protect their skin from the sun.

c) **Vegetation:** There is no live vegetation available to the elephants—although it is visible from their enclosure, it is off limits to them (something that must be extremely frustrating for a large herbivore) because of barriers or electric wires (video here).

d) **Food:** The food available to the elephants appears to be mostly hay, scattered fruits and vegetables (video here), and some browse—a monotonous diet that requires little manipulation and is quickly consumed. In their natural habitat, elephants are highly diverse feeders, consuming more than 100 seasonally and geographically varying food species (e.g., grasses, trees, bark, roots, fruits, and aquatic plants; Dierenfeld, 2006), and spending 60-80% of their waking hours foraging over long distances (Poole & Granli, 2009). In zoos, feeding schedules tend to be predictable. A more varied feeding regime would certainly enhance the well-being the elephants (Holdgate et al., 2016).

e) **Exercise:** The elephants receive very little exercise in such a small enclosure. Such exercise is not only important for their overall cardiovascular, immune, cognitive, and neural health (Jacobs et al., 2021), but also for the health of their feet. Approximately 60 million years of evolution has led to a range of anatomical and physiological specializations for long distance living (Shoshani, 1998; Poole & Granli, 2009). In particular, long-distance walking helps them maintain foot health (Panagiotopoulou et al., 2016), something not possible in a zoo environment.

f) **Social interaction:** There appears to be little social interaction among the elephants in the existing videos (here and here), and they often appear to be isolated from each other (video here). Many elephant management problems are linked to inappropriate social groupings (Veasey, 2006; Doyle et al., 2024). Free elephants tend to live in matriarcal, multi-generational family groups of two to 10 adult females and juveniles (Vance et al., 2009). Elephant family groups share a fission-fusion structure, separating and merging with larger groups of up to several hundred elephants (Poole & Moss, 2008; de Silva et al., 2011). At the Pittsburgh Zoo, Angeline is the daughter of Savanna; Victoria and Zuri appear to have the same biological parents, neither of whom being at the Pittsburgh Zoo. Their mother, Moja, was transferred to the Winston Wildlife Safari in 2015. This is not a normal social grouping.

g) **Stereotypies:** The elephants at the zoo exhibit clear stereotypies; in this indoor video (here) repetitive (and agitated) pacing behavior is obvious. Outdoors, the incessant pacing continues along the edge of the pond (here), presumably because there is really nothing else to do. Between ~47% and ~ 85% of elephants in zoos exhibit stereotypies, which can consume up to ~20% of the animal's daily activity (Mason & Latham, 2004; Mason & Veasey, 2010; Doyle et al., 2024). It is clear that large portions of time involve such stereotypies, which can further aggravate foot issues. Moreover, as noted above, the existence of stereotypies is a direct reflection of dysregulation of motor control circuitry in the brain, that is, a form of brain damage. Such stereotypies are not exhibited in the wild.

h) **Enrichment:** Although there is no evidence in videos of any type of meaningful or effective enrichment for the elephants at the Pittsburgh Zoo, it is likely that they attempt to enrich the environment in the form of feeding devices or objects (e.g., tires, puzzle feeders). The following video is an example of such so-called "enrichment" (here)—providing an animal with a box, a St. Patrick's Day sign, and some cabbage scraps is hardly enriching. However, these represent only a very limited type of directed enrichment (Markowitz, 1982) and are employed in an attempt to alleviate the specific psychological/behavioral/neural problems arising from the captive, inarguably impoverished environment. They are band-aids, not cures. Current evidence suggests that targeted, ad hoc zoo/aquarium enrichment remains insufficient for the overall neural health of mammals such as elephants as long as they remain constrained by traditional captive conditions (Doyle et al., 2024). Here it is worth noting a couple of additional points: natural environments appear to be better for the emotional health of rats than artificially enriched environments (Lambert et al., 2016), with similar findings in humans (Lambert et al., 2015). A sanctuary would provide these elephants with a much more natural, and thus enriching, environment. In conclusion, the transient, inconsistent enrichment (as is the case with zoo "enrichment") can create more stress and frustration for the elephants than no enrichment at all (Latham & Mason, 2010). The very fact that accrediting organizations like the AZA require zoos to provide enrichment to elephants is a de facto admission that the elephants are housed in impoverished environments that harmful to the brains of the animals on display (Jacobs et al., 2021).

i) **Autonomy:** Even cursory examination of the day-to-day life of captive elephants, with the Pittsburgh Zoo elephants being no exception, clearly reveals that these elephants exist in a very controlled environment that removes almost all autonomy. It is estimated that elephants spend ~ 50% of their daytime hours under behavioral control in caregiver- managed activities (*e.g.*, exercise sessions, foot and skin care, training; Greco et al., 2016). Not surprisingly, there is an inverse relationship between time spent with keepers and an elephant's rate of stereotypy. In this regard, it was the zoo's reluctance to give up using bullhooks that, in part, led to their losing their AZA accreditation. Moreover, the very fact that the Pittsburgh Zoo thought it appropriate to use dogs in 2014 to herd elephants is a blatant example of the controlled environment these elephants are forced to endure. Lack of control over one's environment, and the chronic stress that accompanies such situations (Lecorps et al., 2021; Radley et al, 2015), is a significant predictor of learned helplessness and depression in a variety of species (Maier & Seligman, 2016), including elephants (Jacobs et al., 2021).

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

Signed on the....16...day of.........April.........,

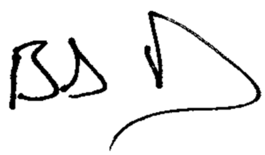
At …….Lakebay, WA…….

(date)......16....(month)....April.......(year)..........2025..........

(county or other location, and state)............Pierce County, WA............

(country)............USA....................

(printed name)..........Bob Jacobs, Ph.D..........



(signature).......   ....

References cited

Bahar, A., Kasimi, N. H. A., & Hambali, K. (2018). Home range and movement patterns of Asian elephant (*Elephas maximus*) in Gua Musang, Kelantan, Malaysia. *Malayan Nature Journal, 70*, 221-232.

Banihashemi, L., Wallace, M.L., Peng, C.W., Stinley, M.M., Germain, A., & Herringa, R.J. (2020). Interactions between childhood maltreatment and combat exposure trauma on stress-related activity within the cingulate cortex: A pilot study. *Mil. Psychol., 32*, 176-185. http://doi.org/10.1080/08995605.2019.1702831.

Barasa, A., & Shochatovitz, A. (1961). Grandezza e densità della cellule nervose della corteccia cerebrale de *Elephas indicus*. *Rendiconti Accademia Nazionale dei Lincei, 30*, 246-249.

Basso, J.C., & Suzuki, W.A. (2017). The effects of acute exercise on mood, cognition, neurophysiology, and neurochemical pathways: A review. *Brain Plasticity, 2*, 127 – 152. http://dx.doi.org/10.3233/BPL-160040

Boorer, M.K. (1972). Some aspects of stereotyped patterns of movement exhibited by zoo animals. Internat. *Zoo Yb., 12*, 164-168. https://doi.org/10.1111/j.1748-1090.1972.tb02312.x.

Bos, K.J., Zeanah, C.H., Smyke, A.T., Fox, N.A., & Nelson, C.A. (2010). Stereotypies in children with a history of early institutional care. *Arch. Pediatr. Adolesc. Med., 164*, 406-411. https://doi.org/10.1001/archpediatrics.2010.47.

Bouley, D.M., Alarcón, C.N., Hildebrandt, T., O'Connell-Rodwell, C.E. (2007). The distribution, density and three-dimensional histomorphology of Pacinian corpuscles in the foot of the Asian elephant (*Elephas maximus*) and their potential role in seismic communication. *Journal of Anatomy, 4*, 428-35. https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2375831/.

Brown, J.L., Carlstead, K., Bray, J.D., Dickey, D., & Farin, C. (2019). Individual and environmental risk factors associated with fecal glucocorticoid metabolite concentrations in zoo-housed Asian and African elephants. *PLOS One, 14*, e0217326. https://doi.org/10.1371/journal.pone.0217326.

Buckley, C. (2009). Sanctuary: A fundamental requirement of wildlife management. In D. L. Forthman, L. F. Kane, D. Hancocks, P. F. Waldau. (Eds.), An elephant in the room: The science and well-being of elephants in captivity (pp. 191-197). Center for Animals and Public Policy. North Grafton, MA: Tufts University.

Buckwalter, J.A., Anderson, D.D., Brown, T.D., Tochigi, Y., & Martin J. (2013). The roles of mechanical stresses in the pathogenesis of osteoarthritis: Implications for treatment of joint injuries. *Cartilage, 4*, 286-294. https://doi.org/10.1177/1947603513495889.

Cabib, S. (2006). The neurobiology of stereotypy II: The role of stress. In: Mason, G., Rushen, J. (Eds.). Stereotypic Animal Behavior: Fundamentals and Applications to welfare, 2nd ed. CABI, Cambridge, MA., pp. 227-255.

Capuron, L., & Miller, A.H. (2011). Immune system to brain signaling: Neuropsychopharmacological implications. *Pharmacol. Ther., 130*, 226-238. https://doi.org/10.1016/j.pharmthera.2011.01.014.

Chugani, H.T., Behen, M.E., Muzik, O., Juhász, C., Nagy, F., & Chugani, D.C. (2001). Local brain functional activity following early deprivation: A study of postinstitutionalized Romanian orphans. *NeuroImage, 14*, 1290-1301. https://doi.org/10.1006/nimg.2001.0917.

de Silva, S., Ranjeewa, S.D.G., & Kryazhimskiy, S. (2011). The dynamics of social networks among female Asian elephants. *BMC Ecology, 11*, 17. https://doi.org/10.1186/1472-6785-11-17.

Derby, P. (2009). Changes in social and biophysical environment yield improved physical and psychological health for captive elephants. In D. L. Forthman, L. F. Kane, D. Hancocks, P. F. Waldau. (Eds.), An elephant in the room: The science and well-being of elephants in captivity (pp. 198-207). Center for Animals and Public Policy. North Grafton, MA: Tufts University.

Diamond, M.C. (2001). Response of the brain to enrichment. *Anais da Academia Brasileira de Ciências*, *73*, 211-220. https://doi.org/10.1590/S0001-37652001000200006.

Diamond, M.C., Krech, D., & Rosenzweig, M.R. (1964). The effects of an enriched environment on the histology of the rat cerebral cortex. *Journal of Comparative Neurology, 123,* 111-119. https://doi.org/10.1002/cne.901230110.

Dierenfeld, E. S. (2006). Nutrition. In M. E. Fowler & S. K. Mikota (Eds.), *Biology, medicine, and surgery of elephants* (pp. 57-65). Ames, IA: Blackwell Publishing.

Doyle, C., Rally, H., O'Brien, L., Tennison, M., Marino, L. & Jacobs, B. (2024). Continuing challenges of elephant captivity (with a focus on Western facilities). *PeerJ. 12*:e18161. https://doi.org/10.7717/peerj.18161

Edwards, K.L., Edes, A.N., & Brown, J.L. (2019). Stress, well-being and reproductive success In: Holt, W.V., Brown, J.L., Comizzoli, P. (Eds.). Reproductive Sciences in Animal Conservation, 2nd ed. Springer, New York, pp. 91-162.

Fernando, P., Wikramanayake, E. D., Janaka, H. K., Jayasinghe, L. K. A., Gunawardena, M., Kotagama, S. W., Weerakoon, D., & Pastorini, J. (2008). Ranging behavior of the Asian elephant in Sri Lanka. *Mammalian Biology, 73*, 2-13. https://doi.org/10.1016/j.mambio.2007.07.007.

Greco, B.J., Meehan, C.L., Heinsius, J.L., & Mench, J.A. (2017). Why pace? The influence of social, housing, management, life history, and demographic characteristics on locomotor stereotypy in zoo elephants. Applied Animal Behviour Science, 194, 104-111.

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

Hammack, S.E., Cooper, M.A., & Lexak, K.R. (2012). Overlapping neurobiology of learned helplessness and conditioned defeat: Implications for PTSD and mood disorders. *Neuropharmacology, 62,* 565-575. https://doi.org/10.1016/j.neuropharm.2011.02.024.

Hart, B.L., Hart, L.A., & Pinter-Wollman, N. (2008). Large brains and cognition: Where do elephants fit in? *Neuroscience and Biobehavioral Reviews, 32*, 86-98.

Holdgate, M.R., Meehan, C.L., Hogan, J.N., Miller, L.J., Soltis, J., Andrews, J., & Shepherdson, D.J. (2016). Walking behavior of zoo elephants: Associations between GPS-measured daily walking distances and environmental factors, social factors, and welfare indicators. *PLoS ONE 11*. https://doi.org/10.1371/journal.pone.0150331.

Horowitz, A.M., Fan, X. Bieri, G., Smith, L.K., Sanchez-Diaz, C. I., Schroer, A.B., Gontier, G., Casaletto, K.B., Kramer, J.H., Williams, K.E., & Villeda, S.A. (2020). Blood factors transfer beneficial effects of exercise on neurogenesis and cognition to the aged brain. *Science, 369*, 167-173**.** http://dx.doi.org/10.1126/science.aaw2622.

Issa, R.I., & Griffin, T.M. (2012). Pathobiology of obesity and osteoarthritis: Integrating biomechanics and inflammation. *Pathobiology of Aging & Age-Related Diseases, 2*, 1. https://doi.org/10.3402/pba.v2i0.17470.

Jacobs, B., Lubs, J., Hannan, M., Anderson, K., Butti, C., Sherwood, C.C., Hof, P.R., & Manger, P.R. (2011). Neuronal morphology in the African elephant (*Loxodonta africana*) neocortex. *Brain Structure and Function, 215*, 273-298. http://dx.doi.org/10.1007/s00429-010-0288-3.

Jacobs, B., Rally, H., Doyle, C., O'Brien, L., Tennison, M., & Marino, L. (2021). Putative neural consequences of captivity for elephants and cetaceans: *Reviews in the Neurosciences*, *33 (4),* 439-465. https://doi.org/10.1515/revneuro-2021-0100

Jacobs, B., Schall, M., & Scheibel, A.B. (1993). A quantitative dendritic analysis of Wernicke's area in humans. II. Gender, Hemispheric, and Environmental Factors. *Journal of Comparative Neurology, 327*, 97-111. http://dx.doi.org/10.1002/cne.903270108.

Koenigs, M., & Grafman, J. (2009). Posttraumatic stress disorder: The role of medial prefrontal cortex and amygdala. *The Neuroscientist, 15*, 540-548. http://dx.doi.org/10.1177/1073858409333072.

Kozorovitskiy, Y., Gross, C. G., Kopil, C., Battaglia, L., McBreen, M., Stranahan, A. M., &Gould, E. (2005). Experience induces structural and biochemical changes in the adult primate brain. *Proceedings of the National Academy of Sciences, 102*, 17478-17482; HTTP://DX.DOI.ORG/10.1073/pnas.0508817102.

Lambert, K., Hyer, M., Bardi, M., Rzucidlo, A., Scott, S., Terhune-Cotter, B., Hazelgrove, A., Silva, I., Kinsley, C. (2016). Natural-enriched environments lead to enhanced environmental engagement and altered neurobiological resilience. *Neuroscience, 330*, 386-394. https://doi.org/10.1016/j.neuroscience.2016.05.037.

Lambert, K.G., Nelson, R.J., Javanovic, T., Cerdá, M. (2015). Brains in the city: Neurobiological effects of urbanization. *Neuroscience and Biobehavioral Reviews, 58*, 107-122. https://doi.org/10.1016/j.neubiorev.2015.04.007.

Langen, M., Kas, M. J.H., Staal, W.G., van Engeland, H., & Durston, S. (2011). The neurobiology of repetitive behavior: Of mice… *Neuroscience & Biobehavioral Reviews, 35*, 345-355. https://doi.org/10.1016/j.neubiorev.2010.02.004.

Latham, N.R., Mason, G. (2010). Frustration and perseveration in stereotypic captive animals: Is a taste of enrichment worse than none at all? *Behavior and Brain Research, 211*, 96-104. https://doi.org/10.1016/j.bbr.2010.03.018.

Lecorps, B., Weary, D.M., & von Keyserlingk, M.A.G. (2021). Captivity-induced depression in animals. *Trends Cogn. Sci.* https://doi.org/10.1016/j.tics.2021.03.010.

Leszek, J., Barreto, G.E., Gasiorowski, K., Koutsouraki, E., Avila-Rodrigues, M., & Aliev, G. (2016). Inflammatory mechanisms and oxidative stress as key factors responsible for progression of neurodegeneration: Role of brain innate immune system. *CNS Neurol. Disord. Drug Targets, 15*, 329-336. https://pubmed.ncbi.nlm.nih.gov/26831258/.

Maier, S.F., & Seligman, M.E.P. (2016). Learned helplessness at fifty: Insights from neuroscience. *Psychological Review, 123*, 349–367. https://doi.org/10.1037/rev0000033.

Maier, S.F., & Watkins, L.R. (2005). Stressor controllability and learned helplessness: The roles of the dorsal raphe nucleus, serotonin, and corticotropin-releasing factor. *Neuroscience & Biobehavioral Reviews, 29*, 829-841. https://doi.org/10.1016/j.neubiorev.2005.03.021.

Markowitz, H. (1982). Behavioral enrichment in the zoo. Van Nostrand- Reinhold, New York.

Martin, L.J., Spicer, D.M., Lewis, M.H., Gluck, J.P., &Cork, L.C. (1991). Social deprivation of infant rhesus monkeys alters the chemoarchitecture of the brain: I. Subcortical regions. *J. Neurosci., 11*, 3344-3358 https://doi.org/10.1523/JNEUROSCI.11-11-03344.1991.

Maseko, B. C., Jacobs, B., Spocter, M.A., Sherwood, C.C., Hof, P.R., & Manger, P.R. (2012). Qualitative and qualitative aspects of the microanatomy of the African elephant cerebellar cortex. *Brain, Behavior & Evolution, 81*, 40-55. http://dx.doi.org/ 10.1159/000345565.

Mason, G. J., & Veasey, JS. (2010). What do population-level welfare indices suggest about the well-being of zoo elephants? *Zoo Biology, 29*, 256-273. https://doi.org/10.1002/zoo.20303.

Mason, G.J., & Latham, N.R. (2004). Can't stop, won't stop: Is stereotypy a reliable animal welfare indicator? *Animal Welfare, 13* (Suppl), S57-S69.

McBride, S.D., & Hemmings, A. (2005). Altered mesoaccumbens and nigro-striatal dopamine physiology is associated with stereotypy development in a non-rodent species. *Behav. Brain Res., 159*, 113-118. https://doi.org/10.1016/j.bbr.2004.10.014.

McBride, S.D., & Parker, M.O. (2015). The disrupted basal ganglia and behavioural control: An integrative cross-domain perspective of spontaneous stereotypy. *Behavioural Brain Research, 276*, 45-58. https://doi.org/10.1016/j.bbr.2014.05.057.

McEwen, B., Nasca, C. & Gray, J. Stress Effects on Neuronal Structure: Hippocampus, Amygdala, and Prefrontal Cortex. *Neuropsychopharmacol* 41, 3–23 (2016). https://doi.org/10.1038/npp.2015.171.

McEwen, B.S., Bowles, N.P., Gray, J.D., Hill, M.N., Hunter, R.G., Karatsoreos, I.N., & Nasca, C. (2015). Mechanisms of stress in the brain. *Nat. Neurosci., 18*, 1353-1363. https://doi.org/10.1038/nn.4086.

McLeod, T.M., Lopez-Figueroa, A.L., & Lopez-Figueroa, M.O. (2001). Nitric oxide, stress, and depression. *Psychopharmacol. Bull., 35*, 24-41.

Maier, S.F. & Seligman, M.E.P. (2016). Learned helplessness at fifty: insights from neuroscience. Psychol. Rev. 123: 349–367, https://doi.org/10.1037/rev0000033.

Miller, M. A., Hogan, J. N., & Meehan, C. L. (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*, e0155223. https://doi.org/10.1371/journal.pone.0155223.

Miura, H., Qiao, H., & Ohta, T. (2002). Attenuating effects of the isolated rearing condition on increased brain serotonin and dopamine turnover elicited by novelty stress. *Brain Res., 926*, 10-17. https://doi.org/10.1016/S0006-8993(01)03201-2.

Morfeld, K.A., Lehnhardt, J., Alligood, C., Bolling, J., & Brown, J.L. (2014). Development of a body condition scoring index for female African elephants validated by ultrasound measurements of subcutaneous fat. *PLoS One, 9*, e93802. https://doi.org/10.1371/journal.pone.0093802.

Mortimer, B., Walker, J.A., Lolchuragi, D.S., Reinwald, M. & Daballen, D. (2021) Noise matters: elephants show risk-avoidance behaviour in response to human-generated seismic cuesProc. R. Soc. B.2882021077420210774 http://doi.org/10.1098/rspb.2021.0774.

Nikolova, Y.S., Misquitta, K.A., Rocco, B.R., Prevot, T.D., Knodt, A.R., Ellegood, J., Voineskos, A.N., Lerch, J.P., Hariri, A.R., Sibille, E., & Banasr, M. (2018). Shifting priorities: highly conserved behavioral and brain network adaptations to chronic stress across species. *Translational Psychiatry, 8*, 26. https://doi.org/10.1038/s41398-017-0083-5.

Panagiotopoulou O, Pataky TC, Day M, Hensman MC, Hensman S, Hutchinson JR, Clemente C J. (2016). Foot pressure distributions during walking in African elephants (*Loxodonta africana*) *Royal Society Open Science* 3(10):160303

Plotnik, J.M., de Waal, F.B.M., & Reiss, D. (2006). Self-recognition in an Asian elephant. *Proceedings of the National Academy of Sciences (USA), 103*, 17053-17057.

Poirier, C., & Bateson, M. (2017). Pacing stereotypies in laboratory rhesus macaques: Implications for animal welfare and the validity of neuroscientific findings. *Neuroscience & Biobehavioral Reviews, 83*, 508-515. https://doi.org/10.1016/j.neubiorev.2017.09.010.

Poole, J. H., & Granli, P. (2009). Mind and movement: Meeting the interests of elephants. In D. L. Forthman, L. F. Kane, D. Hancocks, P. F. Waldau. (Eds.), *An elephant in the room: The science and well-being of elephants in captivity* (pp. 2-21). Center for Animals and Public Policy. North Grafton, MA: Tufts University.

Poole, J.H., & Moss, C.J. (2008). Elephant sociality and complexity. In C. Wemmer, & C. A. Christen (Eds.), Elephants and ethics (pp. 69-100). Baltimore, MD: Johns Hopkins University Press.

Reisinger, R.R., Keith, M., Andrews, R.D., & de Bruyn, P.J.N. (2015). Movement and diving of killer whales (Orcinus orca) at a Southern Ocean archipelago. *Journal of Experimental Marine Biology and Ecology, 473*, 90-102. https://doi.org/10.1016/j.jembe.2015.08.008.

Riddle, H., & Stremme, C. (2011). Captive elephants - an overview. *Journal of Threatened Taxa*, *3*, 1826-1836. https://doi.org/10.11609/JoTT.o2620.1826-36.

Rosenzweig, M.R., & Bennett, E.L. (1969). Effects of differential environments on brain weights and enzyme activities in gerbils, rats, and mice. *Developmental Psychobiology, 2*, 87-95. https://doi.org/10.1002/dev.420020208.

Sapolsky, R.M. (2012). Physiological benefits of leadership. *Proceedings of the National Academy of Sciences, 109*, 17730-17731. http://dx.doi.org/10.1073/pnas.1215502109.

Sapolsky, R.M. (1996). Stress, glucocorticoids, and damage to the nervous system: The current state of confusion. *Stress, 1*, 1-19. http://dx.doi.org/10.3109/10253899609001092.

Sapolsky, R.M. (2005). The influence of social hierarchy on primate health. *Science, 29,* 648-652.

Sapolsky, R.M. (2017). *Behave: The biology of human at our best and worst.* New York: Penguin Press.

Sapolsky, R.M., Uno, H., Rebert, C.S., & Finch, C.E., (1990). Hippocampal damage associated with prolonged glucocorticoid exposure in primates. *Journal of Neuroscience, 10,* 2897-2902. https://pubmed.ncbi.nlm.nih.gov/2398367/.

Schedlowski, M., & Schmidt, R.E. (1996). Streß und Immunsystem [Stress and the immune system]. *Sci. Nat., 83*, 214-220. https://doi.org/10.1007/BF01143326.

Schmid, J., Heisterman, M., Gansloßer, U., & Hodges, J.K. (2001). Introduction of foreign female Asian elephants (Elephas maximus) into an existing group: Behavioral reactions and changes in cortisol levels. *Anim. Welf., 10*, 357-372.

Shoshani J. (1998). Understanding proboscidean evolution: a formidable task. Trends in Ecology and Evolution 13(12):480-487

Shoshani, J., Kupsky, W.J., & Marchant, G.H. (2006). Elephant brain part I: Gross morphology, functions, comparative anatomy, and evolution. *Brain Research Bulletin, 70*, 124-157.

Turner, C.A., Yang, M.C., &Lewis, M.H. (2002). Environmental enrichment: effects on stereotyped behavior and regional neuronal metabolic activity. *Brain Res., 938*, 15-21. https://doi.org/10.1016/S0006-8993(02)02472-1.

van Praag, H., Kempermann, G., & Gage, F.H. (2000). Neural consequences of environmental enrichment. *Nature Reviews Neuroscience, 1*, 191-198.

Vance, E.A., Archie, E.A., & Moss, C.J. (2009). Social networks in African elephants. *Computational and Mathematical Organizational Theory, 15*, 273. https://doi.org/10.1007/s10588-008-9045-z.

Veasey, J. (2006). Concepts in the care and welfare of captive elephants. *International Zoo Yearbook, 40,* 63-79. https://doi.org/10.1111/j.1748-1090.2006.00063.x.

Vyas, S., Rodrigues, A.J., Silva, J.M., Tronche, F., Osborne, F.X., Almeida, O.F.X., Sousa, N., & Sotiropoulos, I. (2016). Chronic Stress and Glucocorticoids: From Neuronal Plasticity to Neurodegeneration. *Neural Plasticity, 2016*. https://doi.org/10.1155/2016/6391686.

Wall, J., Wittemyer, G., Klinkenberg, B., LeMay, V., & Douglas-Hamilton, I. (2013). Characterizing properties and drivers of long distance movements by elephants

(Loxodonta africana) in the Gourma, Mali. *Biological Conservation, 157*, 60-68. https://doi.org/10.1016/j.biocon.2012.07.019.

Zhang, X., Ge, T. T., Yin, G., Cui, R., Zhao, G., & Yang, W. (2018). Stress-induced functional alterations in amygdala: Implications for neuropsychiatric diseases. *Frontiers in Neuroscience, 12*. https://doi.org/10.3389/fnins.2018.00367.