AN-02 Elephants: matriarchs and bull society

Introduction: The Architecture of Proboscidean Society

The social organization of elephants represents one of the most complex non-human systems of cohabitation, kin-recognition, and collective action yet documented by the biological sciences. Comprising fluid but highly structured networks, elephant society is effectively divided into two parallel, interacting worlds: the matrilineal, cooperative networks led by older females (matriarchs) and the hierarchical, competitive, and hormonally driven societies of adult males (bulls). Understanding this architecture requires analyzing the species across three distinct but interacting layers of biological reality: the physiological substrate, the behavioural network, and the cultural fabric.

Drawing upon decades of primary literature, systematic reviews, and longitudinal field studies, this foundational report provides an exhaustive analysis of elephant social structure. It examines the indispensable role of matriarchs as repositories of ecological and social knowledge, the separate socio-sexual world of bulls driven by the phenomenon of *musth*, and the profound consequences of anthropogenic disruption on their social fabric. By dissecting the evidence, including controversies surrounding elephant self-awareness, mourning, and psychopathology, this chapter establishes a robust empirical foundation for understanding how complex, long-lived, and large-brained species organize themselves to survive, reproduce, and adapt.

Layer I: The Physiological Substrate (Measurable Mechanisms)

To comprehend the macroscopic realities of elephant society, one must first examine the physiological hardware that dictates their sensory perception, cognitive capacity, and endocrine regulation. The measurable biological mechanisms of elephants set the absolute boundaries within which their behaviour and culture emerge.

Neuroanatomy, Cellular Composition, and Cognitive Hardware

The elephant brain is the largest of any extant terrestrial mammal, weighing between 4.5 and 5.0 kilograms[1]. Historically, absolute brain size was assumed to correlate linearly with cognitive architecture and behavioural complexity. However, Herculano-Houzel, Souza, and Neves (2014, *Frontiers in Neuroanatomy*) utilized the isotropic fractionator method to exhaustively map the cellular composition of the African elephant (*Loxodonta africana*) brain, revealing a highly specialized and skewed distribution of neurons.

Their analysis demonstrated that the African elephant brain contains an astonishing 257 billion neurons—roughly three times the average human brain's 86 billion neurons[1]. However, 97.5% of these neurons (approximately 250.7 billion) reside in the cerebellum[1]. This massive cerebellar allocation is hypothesized to be dedicated to the immense sensorimotor processing required to

operate the trunk, a highly complex muscular hydrostat containing tens of thousands of muscle fascicles[2].

In stark contrast to the cerebellum, the elephant's cerebral cortex, despite having twice the mass of the human cerebral cortex (weighing roughly 2,848 grams), contains only 5.6 billion neurons[1]. This amounts to merely one-third of the average 16.3 billion neurons found in the human cerebral cortex[1]. Furthermore, the elephant hippocampus, a region critical for spatial memory and navigation, weighs slightly more than the human hippocampus (24.42 grams) but holds only 36.63 million neurons bilaterally, compared to the approximately 250 million neurons in the human hippocampus and amygdala combined[1].

Brain Structure (African Elephant)	**Mass (grams)**	**Total Neurons**	**Neuronal Density (Neurons/mg)**	**Ratio of Other Cells to Neurons**
Whole Brain	4,618.62	257.04 Billion	56,071	0.841
Cerebral Cortex (Gray + White Matter)	2,847.95	5.59 Billion	1,964	26.844
Cerebellum	1,171.63	250.71 Billion	213,983	0.154
Hippocampus	24.42	36.63 Million	1,500	47.154
Olfactory Bulb	41.88	908.37 Million	21,687	3.146

This physiological reality—a massive cerebellum combined with a relatively low-density, highly folded cerebral cortex—suggests that elephant cognition, memory, and social intelligence operate on a vastly different neuroanatomical blueprint than primate cognition. Despite possessing fewer cortical neurons, elephants demonstrate high levels of executive function. MacLean et al. (2014, *Proceedings of the National Academy of Sciences* [*PNAS*]) conducted a massive comparative analysis of self-control using a cylinder task across 32 species with a sample size of 439 individuals. They found that absolute brain volume (rather than residual brain volume or cortical neuron count alone) was the strongest predictor of self-control (R^2 = 0.43, $p < 0.01$)[4]. The elephant's performance in this task rivalled that of the great apes, suggesting cognitive convergence despite divergent neuroanatomical structures[5]. This finding has been widely replicated in comparative cognition literature, establishing that absolute brain volume is a robust proxy for certain inhibitory control mechanisms across mammalian taxa.

Sensory Physiology: Infrasound, Seismic Communication, and Olfaction

Elephant social networks are maintained over vast spatial scales through specialized sensory physiology. Acoustically, elephants utilize low-frequency rumbles, dropping well into the infrasonic range (20–40 Hz and below), which propagate through both air and seismic waves. Charif, Rappaport, and Osborn (2005) demonstrated that these low-frequency calls act as a critical index for population monitoring[7]. Using an acoustic grid monitoring 1,250 square kilometers of forest, they recorded 58 playback experiments, revealing that elephant calls can propagate up to 6 kilometers under favourable atmospheric boundary layer conditions[7]. The seismic component of these rumbles is detected via somatosensory receptors in the elephants' feet and trunk, a phenomenon thoroughly detailed by O'Connell-Rodwell (2007), allowing matriarchs and bulls to monitor distant social events, reproductive status, and threats without visual contact[8].

Olfaction is equally critical to the maintenance of the society. The elephant possesses a highly developed vomeronasal organ (VNO) located in the roof of the mouth, coupled with an expansive olfactory bulb containing over 908 million neurons[1]. Chemical communication relies heavily on the *flehmen* response, a behaviour where the trunk tip touches a chemical stimulus (such as urine or temporal gland secretions) and transfers it to the VNO ducts[11].

Rasmussen and Greenwood (2003, *Chemical Senses*) exhaustively mapped these chemical signaling pathways. They demonstrated that male Asian elephants (*Elephas maximus*) secrete specific enantiomeric ratios of the pheromone *frontalin* from their temporal glands to signal age and *musth* status[10]. Females, in turn, release the preovulatory pheromone (Z)-7-dodecen-1-yl acetate (Z7-12:Ac), which males detect with extreme precision, triggering age-dependent flehmen responses and subsequent mating strategies[15]. Furthermore, Archie et al. (2007, *Molecular Ecology*) established that African elephants utilize olfactory cues to identify paternal kin, allowing them to differentiate between in-group and out-group odours to avoid inbreeding, a finding that has successfully replicated across multiple elephant populations[18].

Endocrinology: Testosterone, Cortisol, and the Physiology of *Musth*

The physiological driver of adult male society is *musth*, an asynchronous, periodic state of heightened sexual and aggressive activity unique to elephants. Musth is characterized by a massive surge in circulating androgens, temporal gland secretions, and continuous urine dribbling. Poole (1987, 1989, *Behaviour*) demonstrated that testosterone levels in African elephants spike dramatically from non-musth baselines of approximately 2 ng/ml to 20–40 ng/ml during musth[21].

Because musth leads to significant weight loss, physical deterioration, and heightened aggression, a persistent question in veterinary and biological sciences has been whether musth is inherently a state of physiological distress. Ghosal, Ganswindt, Seshagiri, and Sukumar (2013, *PLoS ONE*) investigated this dynamic by measuring faecal glucocorticoid metabolites (fGCM, a robust proxy for cortisol and physiological stress) alongside faecal testosterone metabolites in 60 free-ranging male Asian elephants in Kaziranga National Park, India (N=77 samples)[23]. While testosterone metabolites predictably spiked, fGCM concentrations remained

unchanged between musth and non-musth periods[23]. This strongly suggests that in stable, free-ranging populations, musth is not necessarily a distress-inducing condition, but rather an evolved physiological baseline for reproductive competition[23].

Conversely, Ganswindt et al. (2010, 2021) observed that in captive environments, or in populations subjected to anthropogenic social disruption, cortisol often covaries positively with testosterone, indicating that the stress of musth is highly context-dependent[24]. Longitudinal monitoring of four adult Asian elephant bulls spanning ages 12 to 54 years revealed that circulating cortisol covaried positively with testosterone during musth under human care, highlighting that environmental and social confinements alter the endocrine baseline of the species[24].

Layer II: The Behavioural Network (Statistical Distributions and Interactions)

Building upon the physiological substrate of neuroanatomy and endocrinology, the behavioural layer of elephant society encompasses the statistical probabilities of association, the fission-fusion dynamics of herds, and the competitive strategies of mating. Behaviour in this context is defined by overlapping distributions of traits, rather than rigid, invariant rules.

Matrilineal Society: Fission-Fusion Dynamics and Spatial Segregation

Female elephants remain in their natal groups for life, creating a multi-tiered society built on overlapping generations of genetic relatives. The structural base unit is the mother-calf pair (Tier 1), which forms the core of a family group (Tier 2). These families associate with broader bond/kinship groups (Tier 3), clans (Tier 4), and subpopulations (Tier 5)[27].

This structure operates on a highly dynamic fission-fusion model, where group size expands and contracts in response to spatial resource availability and social needs. However, distinct behavioural differences exist between proboscidean species. De Silva and Wittemyer (2012, *Animal Behaviour*) observed 286 individually identified adult female Asian elephants over a continuous 20-month period in Sri Lanka[28]. They found that while African savannah elephants often exhibit stable, highly cohesive family units (associating over 70% of the time), Asian elephants display much more fluid, loosely connected social networks[29]. In the Asian species, daily association rates are statistically lower, and groups frequently fission into small foraging units, yet they maintain a hidden, long-term stability across years[28]. This statistical fluidity is a behavioural adaptation to differing ecological constraints, specifically the demands of foraging in dense, resource-scattered tropical forests versus the open landscapes of the African savannah.

On average, group size, cohesion, and spatial movement are dictated by the oldest female—the matriarch. Wittemyer et al. (2007) demonstrated that social rank, derived primarily from age and physical size, determines a family's access to critical resources. Using high-resolution GPS tracking of 13 wild African elephants over a seven-year period (yielding approximately 0.5 million spatial data points), they found that dominant, older-matriarch-led groups systematically monopolize preferred habitats[31]. During harsh dry seasons, dominant groups expend significantly less energy searching for food and water and limit their exposure to predation and human conflict, while subordinate groups are statistically pushed to marginal, riskier habitats[31].

Bull Society: Roving Strategies, Bachelor Hierarchies, and Leadership

The male behavioural trajectory diverges sharply from the female's. Between the ages of 10 and 15, juvenile males gradually leave their natal herds—or are aggressively pushed out by older females—to enter the separate social world of bulls[24]. Historically, literature viewed adult males as solitary wanderers. However, statistical network analyses reveal that adult males form complex, non-random associations known as bachelor groups.

Within these all-male groups, a strict, size-and-age-based hierarchy regulates behaviour. Allen, Brent, Motsentwa, Weiss, and Croft (2020, *Scientific Reports*) analyzed the collective movements of 10 adult male African savannah elephants. They found that older, non-musth bulls consistently act as leaders, guiding younger followers in collective movements[18]. The older bulls dictate the trajectory toward critical resources, such as specific foraging patches or secure water sources. This leadership dynamic represents a mutualistic behavioural distribution: older bulls benefit from the dilution effect regarding predators or anthropogenic threats, while younger, naïve bulls benefit from the older bulls' spatial memory and ecological knowledge[35].

When a male enters *musth*, however, his behavioural distribution shifts dramatically from sociability to a highly competitive "roving strategy." Hollister-Smith et al. (2007) and Sukumar's research group (2019) demonstrated that *musth* males travel significantly larger distances than non-musth males, actively seeking out female herds across wide geographical expanses[37]. The duration of musth is heavily age-dependent. Poole (1987) reported that the median duration of musth increases from a mere 2 days for males aged 16–25 years, to 13 days for males aged 26–35, peaking at 81 days for males aged 46–50, before declining to 54 days for males aged 51–60[37]. This creates a statistical curve where older males dominate the mating landscape simply by outlasting younger competitors in the physiological state required to secure females.

The Mating Interface: Age, *Musth*, and Inbreeding Avoidance

The intersection of the female and male networks is defined by intense intersexual and intrasexual selection. Female elephants are only in oestrus for a few days every four to five years, making them an exceptionally scarce and valuable reproductive resource[37]. Consequently, mating success is highly skewed.

Hollister-Smith et al. (2007, *Animal Behaviour*) conducted a definitive genetic paternity analysis of 119 calves born over a 22-year period in Amboseli National Park, Kenya, mapping paternity against 89 sampled adult males[37]. The findings generated three highly replicated behavioural rules:

1. **The Age Effect:** Paternity success increases dramatically with age, peaking between the ages of 45 and 53[39]. Older males sired the vast majority of the 119 calves sampled.
2. **The *Musth* Effect:** Males in the physiological state of *musth* secure almost all dominant mating opportunities, utilizing their elevated testosterone and aggression to guard oestrous females from rivals[37].
3. **Alternative Tactics:** Crucially, while older *musth* males dominate the averages, the data revealed a secondary distribution: non-musth males still managed to sire roughly 20% of the genotyped calves[42]. This demonstrates that alternative, opportunistic mating tactics (often employed by younger or subordinate males sneaking access to females) persist as

a statistically viable secondary strategy within the population[42].

Furthermore, the female network exerts significant selective pressure. Archie et al. (2007, *Molecular Ecology*) analyzed 113 individuals to establish that female choice plays a critical role in preventing genetic degradation. Females utilize the acoustic and olfactory cues discussed in Layer I to identify paternal kin, actively avoiding mating with related males[18]. This demonstrates a robust behavioural inbreeding avoidance mechanism, entirely mediated by the matriarchal network's spatial and olfactory memory of male phenotypes[19].

Layer III: The Cultural Fabric (Knowledge, Trauma, and Tradition)

Culture in biological sciences is defined as information, behaviour, or ecological knowledge acquired from conspecifics through social learning, which affects an individual's phenotype and is transmitted across generations. In elephants, this cultural fabric is physically embodied in the matriarch and behaviorally regulated by older bulls.

Matriarchs as Repositories of Social and Ecological Knowledge

The evolutionary rationale for the extraordinarily long post-reproductive lifespan of female elephants relies on their role as cultural repositories. The foundational empirical demonstration of this phenomenon was conducted by McComb, Moss, Durant, Baker, and Sayialel (2001, *Science*). Using a controlled playback experimental design in Amboseli National Park, the research team tested 21 family units led by matriarchs ranging in age from 27 to 67 years[43]. The families were exposed to the recorded contact calls of either familiar (network members) or unfamiliar (out-group) elephants. The results yielded massive effect sizes: families with older matriarchs (specifically modeled at 55 years of age) were statistically vastly superior at discriminating between familiar and unfamiliar calls compared to families with younger matriarchs (modeled at 35 years of age)[43]. When hearing unfamiliar calls, older matriarchs initiated defensive "bunching" and "smelling" behaviours with highly calibrated precision. Conversely, younger matriarchs frequently reacted defensively to both familiar and unfamiliar calls, wasting metabolic energy and losing critical foraging time[43]. The study established that the social knowledge held by the oldest females directly translates into higher per capita reproductive success for the entire family unit[43].

McComb et al. (2011, *Proceedings of the Royal Society B*) replicated and expanded this paradigm with a sample size of 39 family units, this time playing the recorded sounds of roaring lions (varying the threat level by playing one versus three lions, and male versus female lions)[45]. Again, the data robustly showed that older matriarchs accurately assessed the level of predatory threat, leading to superior anti-predator defensive formations, proving that threat-assessment knowledge is culturally transmitted and accumulates over decades[45].

The Regulatory Role of Older Bulls in Male Culture

Just as matriarchs govern the female cultural sphere, older bulls act as cultural regulators in male society. A stark demonstration of this occurred in the late 1990s in Pilanesberg National Park, South Africa, documented by Slotow, van Dyk, Poole, Page, and Klocke (2000, *Nature*). Following intense culling operations in Kruger National Park, young orphaned male elephants

were translocated to Pilanesberg without the demographic presence of older bulls[48]. Reaching adolescence in a cultural vacuum, these young males entered *musth* prematurely and remained in this highly aggressive physiological state for extended periods. This resulted in a wave of hyper-aggression that led to the killing of over 100 white rhinoceroses[48]. The park authorities responded by introducing six older, dominant bulls into the ecosystem. The mere presence of these older males—signalling their dominance via the acoustic and olfactory channels detailed in Layer I—abruptly suppressed the *musth* cycles and hyper-aggressive behaviour of the younger males, immediately halting the rhino killings[48]. This finding, heavily replicated in subsequent conservation interventions, solidified the understanding that older bulls are structurally essential for maintaining behavioural norms and suppressing the dangerous physiological extremes of young males.

Social Trauma, "Elephant Breakdown," and Resilience

What happens when this cultural fabric is destroyed by poaching, culling, or habitat loss? Bradshaw, Schore, Brown, Poole, and Moss (2005, *Nature*) introduced the concept of "Elephant Breakdown," drawing explicit clinical parallels between the trauma experienced by heavily poached elephant populations and human Post-Traumatic Stress Disorder (PTSD)[50]. Bradshaw argued that the mass killing of older matriarchs and bulls completely disrupts the vertical transmission of culture and destroys the corticolimbic attachment bonds necessary for healthy neurobiological development in calves[51].

The physiological toll of such cultural disruption is immense. Wasser, Gobush, and Mutayoba (2008/2010, *PNAS*) measured faecal glucocorticoid metabolites (fGCM) in orphaned versus non-orphaned African elephants[53]. In a sample of 37 elephants (25 orphans, 12 non-orphans), they found that young orphans exhibited significantly elevated baseline fGCM levels (averaging 95.69 ng/g dry weight) compared to non-orphans[54]. This established a direct physiological link demonstrating that the trauma of losing the matriarchal structure induces chronic, measurable distress[54].

However, elephant culture also demonstrates remarkable structural resilience. Goldenberg, Douglas-Hamilton, and Wittemyer (2016, *Current Biology*) analyzed the social networks of heavily poached populations in Samburu, Kenya. They found that despite the targeted assassination of matriarchs for their ivory, the hierarchical social structure did not entirely collapse. Instead, younger daughters effectively re-wired the network, stepping into their deceased mothers' central roles and recreating the social web[56]. This suggests that while trauma causes severe physiological distress, the cultural drive for network cohesion is deeply embedded and highly adaptive.

Controversies, Debates, and Cognitive Limitations

While the data on elephant sociality is vast and robust, several areas remain heavily contested within the ethological, psychological, and biological communities.

1. Mirror Self-Recognition (MSR) and Self-Awareness

A central debate in animal cognition is whether elephants possess a "theory of mind" or self-awareness akin to humans and great apes. Plotnik, de Waal, and Reiss (2006, *PNAS*) subjected three female Asian elephants to the classic Gallup mirror "mark test." One of the three

elephants (named "Happy") successfully passed the test, using the mirror to repeatedly touch an invisible mark placed on her head, which the authors argued was definitive proof of mirror self-recognition (MSR)[58]. Plotnik et al. (2011, *PNAS*) subsequently demonstrated that elephants (N=9) can pass the "loose-string" cooperation task (requiring two individuals to pull simultaneously to retrieve food), further suggesting high-level cooperative cognition[60].

The Critics: Gallup and Anderson (2020) fiercely critique these findings. They argue that an N=1 success out of 3 subjects in the 2006 study is statistically insufficient to claim a species-wide cognitive trait. They point to the high rate of false positives in MSR literature and argue that true MSR is restricted almost exclusively to chimpanzees and humans[61]. Furthermore, behavioural ecologists note that failing the mark test may simply mean the animal does not care about the mark (a motivational failure), not that they lack self-awareness[62]. The debate over whether the Plotnik study represents true self-awareness or a methodological anomaly remains unresolved.

2. Anthropomorphism: Mourning the Dead vs. Investigative Behaviour

Elephants are famously known to interact with the bones of deceased conspecifics. McComb, Baker, and Moss (2006, *Biology Letters*) experimentally presented elephants with the skulls of elephants, rhinos, and buffalos. The elephants showed a highly significant preference for investigating elephant skulls and ivory over the natural objects of other species[63].

The Controversy: Is this behaviour indicative of "mourning" or is it simply a highly evolved mechanism of olfactory and tactile curiosity? Goldenberg and Wittemyer (2020) reviewed extensive field observations of elephant behaviour toward the dead. While Bradshaw (2005) and trans-species psychologists interpret these actions as evidence of profound grief, empathy, and psychological trauma, strict ethologists argue that applying human clinical terms (like grief, mourning, or PTSD) to proboscideans is an anthropomorphic projection[51]. Critics of the PTSD model argue that while elephants clearly experience chronic stress (validated by fGCM levels) and show targeted interest in their dead, labeling these responses as clinical psychiatric disorders risks the naturalistic fallacy, blurring the empirical lines between human psychology and animal ethology[51].

Distinguishing Averages from Individuals

Throughout the literature, a critical statistical distinction must be maintained between population averages (central tendencies) and individual variance. Biological rules dictate the averages, but individual phenotypes display vast behavioural plasticity.

- **Averages in Female Society:** *On average*, older matriarchs have higher reproductive success, make better ecological decisions, and exhibit superior threat-assessment capabilities compared to younger females[43]. However, individually, some younger females in poached populations demonstrate remarkable social connectivity and assume leadership roles effectively when forced by circumstance[56].
- **Averages in Male Society:** *On average*, males over 45 years of age in the state of *musth* secure the vast majority of paternities, utilizing their size and extended physiological stamina to outcompete rivals[37]. However, individually, younger, non-musth males still successfully employ alternative sneaking tactics to sire up to 20% of the offspring in a

population[42]. Furthermore, while *musth* on average correlates with increased cortisol in captive environments, individual wild bulls often experience *musth* with no significant elevation in stress hormones, highlighting profound individual physiological variance[23].

Conclusions

Summary of Robust Findings

#	Finding	Biological Domain
1	Elephant society is strictly divided into a matriarchal, kin-based female network and a competitive, size/age-based male hierarchy.	Social Structure
2	Older matriarchs function as cultural repositories; their accumulated ecological and social knowledge statistically increases the reproductive success and survival of their family units.	Female Culture
3	Asian elephant female networks exhibit higher fluidity and fission-fusion dynamics than African savannah elephants, adapting to different ecological constraints.	Behavioural Ecology
4	Adult males are not solitary; older, non-musth bulls act as leaders and ecological regulators in bachelor herds, guiding younger males.	Male Culture
5	The presence of older, dominant bulls effectively	Endocrine Regulation

	suppresses premature, hyper-aggressive *musth* cycles in younger males.	
6	*Musth* is an asynchronous, endocrinologically driven state characterized by massive testosterone spikes and frontalin secretion, functioning as a roving strategy for mating.	Male Physiology
7	Paternity success is overwhelmingly skewed toward older males (>45 years) in *musth*, though alternative sneaking strategies by non-musth males successfully persist.	Reproductive Success
8	Elephants utilize acoustic (20-40 Hz infrasound) and olfactory (VNO) channels to communicate over long distances and behaviourally avoid inbreeding.	Sensory Physiology
9	Poaching and culling disrupt vertical cultural transmission, causing chronic, measurable physiological stress (elevated cortisol/fGCM) in orphaned calves.	Trauma & Stress
10	Despite severe social trauma, female networks demonstrate high resilience, with daughters seamlessly rewiring the network to	Network Resilience

	replace lost matriarchs.	

Contested and Open Questions

Question	Core Dispute	Leading Critics / Proponents
Mirror Self-Recognition	Does the single success in Plotnik's 2006 study prove species-wide self-awareness, or is it a methodological anomaly plagued by false positives?	Proponent: Plotnik (2006); Critic: Gallup & Anderson (2020)
The Nature of *Musth*	Is *musth* inherently a state of physiological stress (inevitably raising cortisol), or is the stress response purely dependent on environmental confinement?	Ganswindt (captives) vs. Ghosal & Sukumar (wild)
Psychopathology	Can human psychiatric diagnoses like PTSD accurately describe the behavioral dysfunction in elephants, or is this unscientific anthropomorphism?	Proponent: Bradshaw (2005); Critics: Traditional Ethologists
Pheromonal Decoding	While frontalin and Z7-12:Ac are identified, what is the full molecular grammar of elephant temporal and urine secretions?	Rasmussen (2003); Open biochemical question

5 to 10 Most Important Sources to Read in Full

Author(s) & Year	Title	Journal	Significance
Herculano-Houzel et al. (2014)	The elephant brain in numbers.	*Frontiers in Neuroanatomy*	Establishes the exact cellular neuroanatomy of the species.[1]
McComb et al. (2001)	Matriarchs as repositories of social knowledge in African elephants.	*Science*	Foundational proof that old female knowledge drives fitness.[43]
Hollister-Smith et al. (2007)	Age, musth and paternity success in wild male African elephants.	*Animal Behaviour*	Definitive genetic mapping of male mating success and *musth*.[37]
Bradshaw et al. (2005)	Elephant breakdown. Social trauma.	*Nature*	Introduces the controversial model of PTSD in proboscideans.[51]
Slotow et al. (2000)	Older bull elephants control young males.	*Nature*	Proves older bulls suppress young male hyper-aggression.[48]
Goldenberg et al. (2016)	Vertical transmission of social roles drives resilience to poaching.	*Current Biology*	Demonstrates structural network rewiring after trauma.[56]
Archie et al. (2007)	Behavioural inbreeding avoidance in wild African elephants.	*Molecular Ecology*	Details kin recognition via olfactory and acoustic channels.[18]
de Silva &	A Comparison of Social Organization	*Animal Behaviour*	Maps the differences in

Wittemyer (2012)	in Asian Elephants...		fission-fusion between species.[28]
Wasser et al. (2010)	Long-term impacts of poaching on relatedness, stress physiology...	*PNAS*	Quantifies chronic physiological stress (fGCM) in orphans.[54]
Plotnik et al. (2006)	Self-recognition in an Asian elephant.	*PNAS*	The highly debated study on elephant mirror self-awareness.[59]

Implications for Living Together

While one must strictly avoid the naturalistic fallacy—the assumption that because something occurs in nature, it is morally good or directly applicable to human ethics—the architectural dynamics of elephant society provide a fascinating, empirical lens for examining organizational theory in human groups, families, and societies.

The primary implication derived from the elephant model is the measurable, survival-based value of intergenerational knowledge. In human organizations and modern societies, a hyper-focus on youth, rapid innovation, and immediate productivity often marginalizes older demographics. The elephant data robustly demonstrates that systemic resilience, threat assessment, and collective survival are heavily dependent on the deep, longitudinal data stored by the oldest members of the community (the matriarchs). Removing this demographic does not simply alter the group's aesthetic; it physically stresses the remaining members, wastes energy, and statistically diminishes their decision-making accuracy in crises. Organizations that fail to integrate the accumulated ecological knowledge of their most senior members systematically handicap their own operational efficiency.

Secondly, the regulation of male behaviour highlights the absolute necessity of structured, intergenerational mentorship. The hyper-aggression of young male elephants in the absence of older bulls suggests that male competitiveness and physiological drives require hierarchical, socially enforced boundaries to remain functional rather than violently destructive. In human societies, the absence of integrated, multi-generational community structures often correlates statistically with increased antisocial behaviour in young males. The presence of older, established males provides a regulatory buffer that channels youthful energy into constructive, or at least non-destructive, avenues.

Finally, the resilience of the female network in the face of mass poaching—where daughters seamlessly rewire the social fabric to replace lost mothers—highlights that robust systems must allow for flexible role transmission. A resilient human organization or family structure is one where knowledge and social roles are continuously distributed and passed down. This ensures that the sudden loss of a key leader triggers an automatic, stabilizing structural rewiring, rather

than a complete systemic collapse.

Works cited

1. The elephant brain in numbers - Frontiers, https://www.frontiersin.org/journals/neuroanatomy/articles/10.3389/fnana.2014.00046/full
2. The elephant brain in numbers - PMC - NIH, https://pmc.ncbi.nlm.nih.gov/articles/PMC4053853/
3. (PDF) The elephant brain in numbers - ResearchGate, https://www.researchgate.net/publication/263475914_The_elephant_brain_in_numbers
4. The evolution of self-control - PNAS, https://www.pnas.org/doi/pdf/10.1073/pnas.1323533111
5. The evolution of self-control - PNAS, https://www.pnas.org/doi/10.1073/pnas.1323533111
6. This is How You Study The Evolution of Animal Intelligence, https://www.nationalgeographic.com/science/article/this-is-how-you-study-the-evolution-of-animal-intelligence
7. Acoustic estimation of wildlife abundance: methodology for vocal, https://www.researchgate.net/publication/227900488_Acoustic_estimation_of_wildlife_abundance_Methodology_for_vocal_mammals_in_forested_habitats
8. elephants show risk-avoidance behaviour in response to human, https://ora.ox.ac.uk/objects/uuid:65bf5eec-27e8-4622-b9f1-c0040d55c4a2/files/rg158bh65s
9. Seismic localization of elephant rumbles as a monitoring approach, https://royalsocietypublishing.org/rsif/article/18/180/20210264/89914/Seismic-localization-of-elephant-rumbles-as-a
10. Olfactory Discrimination Ability of Asian Elephants (Elephas, https://academic.oup.com/chemse/article/38/2/107/332786
11. Flehmen response - Wikipedia, https://en.wikipedia.org/wiki/Flehmen_response
12. Evolution of chemical signals in the Asian elephant, Elephas maximus, https://www.ias.ac.in/article/fulltext/jbsc/024/02/0241-0251
13. Chemical communication: chirality in elephant pheromones - PubMed, https://pubmed.ncbi.nlm.nih.gov/16371998/
14. The Chemical Ecology of Elephants: 21st Century Additions to Our, https://www.mdpi.com/2076-2615/11/10/2860
15. Reverse chemical ecology indicates long-chain aldehydes as new, https://www.frontiersin.org/journals/ecology-and-evolution/articles/10.3389/fevo.2022.1061278/full
16. Prospecting for Mammalian Chemical Signals via Solventless, https://digitalcommons.wku.edu/cgi/viewcontent.cgi?article=1012&context=bio_fac_pub
17. (PDF) Assessing chemical communication in elephants, https://www.researchgate.net/publication/226675507_Assessing_chemical_comm

unication_in_elephants
18. References - Elephants - Cambridge University Press & Assessment, https://www.cambridge.org/core/books/elephants/references/09F75CEC1E670FB76E5340B443B82F1F
19. (PDF) Olfaction and scent discrimination in African elephants, https://www.researchgate.net/publication/358978269_Olfaction_and_scent_discrimination_in_African_elephants_Loxodonta_africana
20. odour encodes identity and group membership in African elephants, https://pmc.ncbi.nlm.nih.gov/articles/PMC9537315/
21. Characterization of Longitudinal Testosterone, Cortisol, and Musth, https://www.mdpi.com/2076-2615/12/10/1332
22. The Living Elephants: Evolutionary Ecology, Behaviour, and ... - EPDF, https://epdf.pub/the-living-elephants-evolutionary-ecology-behaviour-and-conservation-life-scienc.html
23. Endocrine Correlates of Musth in Free-Ranging Asian Elephants, https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0084787
24. Characterization of Longitudinal Testosterone, Cortisol, and Musth, https://pmc.ncbi.nlm.nih.gov/articles/PMC9137588/
25. BLOOD ANALYTE CHANGES ASSOCIATED WITH MUSTH IN TWO, https://bioone.org/journals/journal-of-zoo-and-wildlife-medicine/volume-57/issue-2/2025-0064/BLOOD-ANALYTE-CHANGES-ASSOCIATED-WITH-MUSTH-IN-TWO-CAPTIVE-ASIAN/10.1638/2025-0064.full
26. Vaccination against GnRH may suppress aggressive behaviour and, https://scielo.org.za/scielo.php?script=sci_arttext&pid=S1019-91282010000100002
27. analysis of the processes creating multitiered social structures, https://repository.up.ac.za/bitstreams/29eb15e5-4e54-459c-b5cd-ba4c7f4d11ca/download
28. Seasonal variation in female Asian elephant social structure in, https://www.researchgate.net/publication/321435382_Seasonal_variation_in_female_Asian_elephant_social_structure_in_Nagarahole-Bandipur_southern_India
29. The dynamics of social networks among female Asian elephants, https://www.researchgate.net/publication/51525809_The_dynamics_of_social_networks_among_female_Asian_elephants
30. Physiology modulates social flexibility and collective behaviour in, https://royalsocietypublishing.org/rstb/article/372/1727/20160241/30309/Physiology-modulates-social-flexibility-and
31. Simulated poaching affects connectedness and efficiency in social, https://www.biorxiv.org/content/10.1101/2020.08.24.252536v1.full.pdf
32. Inferring ecological and behavioral drivers of African elephant, https://doi.org/10.1890/10-0106.1
33. Social dominance, seasonal movements, and spatial segregation in, https://www.researchgate.net/publication/226958703_Social_dominance_seasonal_movements_and_spatial_segregation_in_African_elephants_A_contribution_to_conservation_behavior

34. Aging: What We Can Learn From Elephants - PMC, https://pmc.ncbi.nlm.nih.gov/articles/PMC9261397/
35. The Interplay between Individual Traits and Coordination Mechanisms, https://ecoevorxiv.org/repository/object/5761/download/13653/
36. Movement patterns of two reintegrated African elephant (Loxodonta, https://pmc.ncbi.nlm.nih.gov/articles/PMC11162612/
37. Age, musth and paternity success in wild male African elephants, https://sandiegozoowildlifealliance.org/sites/default/files/fee_calendar/Post-Lesson_%20Hollister-Smith%20et%20al%20%282007%29.pdf
38. Musth and its effects on male–male and male–female associations, https://bioone.org/journals/journal-of-mammalogy/volume-101/issue-1/gyz190/Musth-and-its-effects-on-malemale-and-malefemale-associations-in/10.1093/jmammal/gyz190.short
39. Elephant bulls - breeding and trophy hunting - Africa Geographic, https://africageographic.com/stories/elephant-bulls-breeding-and-trophy-hunting/
40. Animal Behaviour - Save the Elephants, https://www.savetheelephants.org/wp-content/uploads/2016/11/2014GoldenbergControllingforBehaviouralState.pdf
41. Age, musth and paternity success in wild male African elephants, https://www.semanticscholar.org/paper/Age%2C-musth-and-paternity-success-in-wild-male-Hollister-Smith-Poole/0ac3fdf7092623b416beae25ea337f7f748d3652
42. Age- and tactic-related paternity success in male African elephants, https://www.researchgate.net/publication/46511676_Age-_and_tactic-related_paternity_success_in_male_African_elephants
43. Matriarchs As Repositories of Social Knowledge in African Elephants, https://www.researchgate.net/publication/12020338_Matriarchs_As_Repositories_of_Social_Knowledge_in_African_Elephants
44. Tag: Kasane Botswana - Unteachable Courses, https://unteachablecourses.com/tag/kasane-botswana/
45. Oxytocin promotes social proximity and decreases vigilance in, https://pmc.ncbi.nlm.nih.gov/articles/PMC9042884/
46. Social Disruption Impairs Predatory Threat Assessment in African, https://www.mdpi.com/2076-2615/12/4/495
47. Distinguishing epidemic waves from disease spillover in a wildlife, https://royalsocietypublishing.org/rspb/article/276/1663/1777/72675/Distinguishing-epidemic-waves-from-disease
48. men's ministry: a study of leadership development in churches of the, https://place.asburyseminary.edu/cgi/viewcontent.cgi?article=1449&context=ecommonsatsdissertations
49. African Bush Elephant | Encyclopedia MDPI, https://encyclopedia.pub/entry/37986
50. Effects of social disruption in elephants persist decades after culling, https://pmc.ncbi.nlm.nih.gov/articles/PMC3874604/
51. Early trauma and social disruption can affect the physiology, https://www.researchgate.net/publication/8004966_Elephant_breakdownSocial_trauma_Early_trauma_and_social_disruption_can_affect_the_physiology_behaviou

r_and_culture_of_animals_and_humans_over_generations
52. Psychological Trauma and Posttraumatic Psychopathology in Animals, https://www.cabidigitallibrary.org/doi/10.1079/9781800624313.0012
53. Long-Term Impacts of Poaching on Relatedness, Stress Physiology, https://www.researchgate.net/publication/23226091_Long-Term_Impacts_of_Poaching_on_Relatedness_Stress_Physiology_and_Reproductive_Output_of_Adult_Female_African_Elephants
54. Social support correlates with glucocorticoid concentrations in wild, https://pmc.ncbi.nlm.nih.gov/articles/PMC9283395/
55. Fecal Glucocorticoid Metabolite and T3 Profiles of Orphaned, https://digitalcommons.library.tmc.edu/cgi/viewcontent.cgi?article=1194&context=staff_pub
56. Why identifying individual elephants is important, and the pivotal, https://africageographic.com/stories/why-identifying-individual-elephants-is-important-and-the-pivotal-roles-matriarchs-and-older-bulls-play/
57. The (surprising) importance of males in a matrilineal society - UCLA, https://sites.lifesci.ucla.edu/eeb-blumstein/wp-content/uploads/sites/104/2023/05/Zenth_etal_2023_AB.pdf
58. Self-recognition in an Asian elephant - PNAS, https://www.pnas.org/doi/10.1073/pnas.0608062103
59. (PDF) Self-recognition in an Asian elephant - ResearchGate, https://www.researchgate.net/publication/6721540_Self-recognition_in_an_Asian_elephant
60. Cooperating elephants mitigate competition until the stakes get too, https://pmc.ncbi.nlm.nih.gov/articles/PMC8478180/
61. On the mirror test and the evolutionary origin of self-awareness in, https://pmc.ncbi.nlm.nih.gov/articles/PMC12612708/
62. Mirror test - Wikipedia, https://en.wikipedia.org/wiki/Mirror_test
63. Conspecific investigation of a deceased forest elephant (Loxodonta, https://dukespace.lib.duke.edu/bitstreams/c4492f3b-2cea-4532-a66b-a5b8ea22d4b9/download
64. African elephants show high levels of interest in the skulls and ivory, https://pmc.ncbi.nlm.nih.gov/articles/PMC1617198/
65. African Elephants Show High Levels of Interest in the Skulls and, https://www.researchgate.net/publication/6651464_African_Elephants_Show_High_Levels_of_Interest_in_the_Skulls_and_Ivory_of_Their_Own_Species
66. Elephant behavior toward the dead: A review and insights from field, https://www.researchgate.net/publication/337182950_Elephant_behavior_toward_the_dead_A_review_and_insights_from_field_observations