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Reports of the Taxonomic Sub-Groups: Elephants

Species and status

There are currently three recognised elephant species: African savannah (*Loxodonta africana*) and forest (*Loxodonta cyclotis*) elephants, and the Asian elephant (*Elephas maximus*). Globally, populations of all species are declining, and they are listed as endangered (*Elephas* and *L. africana*) and critically endangered (*L. cyclotis*) (Gobush et al. 2021; 2022; Williams et al. 2020). The Indian sub-species of *Elephas* is listed on CMS Appendix I, and both *Loxodonta* species are on CMS Appendix II.

Elephants are the world's largest terrestrial animals and can live up to 60-70 years. They are considered ecosystem engineers and thereby have considerable short- and long-term effects on vegetation structure and composition across the wide range of habitats they occupy (Bunney et al. 2017; Campos-Arceiz & Blake 2011; Guldemond et al. 2017). All elephant species move long distances when unimpeded by human activity or infrastructure (Lindsay et al. 2017), with range sizes varying greatly dependent on habitat type and productivity, water availability, human presence, and individual strategy.

Evidence for elephant culture

Much of the evidence relating to elephant culture is derived from studies of savannah elephants, with equivalent behaviour in forest and Asian elephants less studied and documented. In this report unless clearly stated otherwise, information relates to savannah elephants. Ongoing ethnographic survey suggests savannah elephant populations do exhibit different cultures (L. Bates et al. *in prep.*) but more work on all species is required. Additionally, elephants occupy extensive habitat gradients from lush afro-montane to arid-desert. Each environment presents different challenges and drives a need for specialised behavioural adaptations for finding sufficient food and water while minimising risk (e.g. predation) (Wall et al. 2021). It is highly plausible that the broad niche elephants can occupy is underpinned by their capacity for social learning.

Opportunities for social learning – a building block of culture

Elephant social systems across all three species provide extensive opportunities for social learning.

All elephant species live in multi-tiered fission-fusion societies (Goldenberg et al. 2021; de Silva & Wittemyer 2012; Nandini et al. 2018; Wittemyer et al. 2005), with layers of familiarity, competition and association that are influenced by species, habitat type, and possibly by population tendencies, shaped by the risks and rewards and history different populations experience. Savannah elephants are the most social species, with females usually remaining in

their natal family for life, alongside their mother, grandmother, sisters, daughters, aunts, cousins, and nieces (Buss 1961; Moss & Lee 2011). These close-knit family units are led by a matriarch (usually the oldest female) and are characterised by persistent and strong social bonds, although families don't spend all their time together, breaking into smaller groups to forage for hours or days before reuniting. Savannah elephants have friendships they maintain outside the family, creating a tier known as the bond group, or clan (Archie et al. 2006; Wittemyer et al. 2005; 2009). Males disperse from the family as teenagers, establishing themselves in male society and developing friendships and competitive relationships that last for lifetimes (Evans & Harris 2008; Lee et al. 2011). In forest elephants, both females and males disperse from the family (Turkalo et al. 2018), and the closest female friendships may be less tied to relatives than savannah elephants (Brand et al. 2020). Although forest elephants may range in small groups, they associate in large numbers at forest clearings, where they maximise social opportunities rather than minimise competition (Fishlock & Lee 2013). Asian elephants are usually found in much smaller groups than savannah elephants, which appears to be a result of higher rates of fission and fusion among social affiliates (de Silva & Wittemyer 2012), although this may be an effect of historical human impacts on populations (Nandini et al. 2018).

These complex societies are built on individual recognition: Elephant communication is multimodal, employing chemical and vocal modes that also encode identity (Poole & Granli 2011). Elephants can therefore recognise and respond appropriately to many other individuals from their family, bond group, other bond groups and sub-populations (Bates et al. 2008; McComb et al. 2000; 2001;). Experimental and observational studies have shown that elephants are empathic, and understand the goals, desires, and perhaps minds of other individuals as well as of themselves (Bates et al. 2008; Plotnik & de Waal 2014; Smet & Byrne 2013), with evidence from an Asian elephant demonstrating that species has the capacity for self-awareness (Plotnik et al. 2006).

Calf survival is greatly increased by the presence of extra females in the family unit, and particularly by having older females present in both savannah and Asian elephants (Gobush, et al. 2008; Goldenberg and Wittemyer, 2017, 2018; Lahdenpera et al. 2016; Lee, 1987; Lee et al. 2016; Moss and Lee 2011). The long-life spans and extended period of maternal care in elephants likely provide many opportunities for transmission of vital ecological and social information. Additionally, savannah elephant families led by older matriarchs display greater social knowledge (McComb et al. 2001; Shannon et al. 2013), more appropriate behaviour in response to threats and predators (McComb et al. 2011; Shannon et al. 2022) and greater calf survival in times of drought (Foley et al. 2008). Younger elephants of both sexes thereby benefit from the presence of older, more experienced females. For forest and Asian elephants, matriarchs may be less central social hubs (Goldenberg et al. 2021, de Silva et al. 2017) but they nonetheless learn by associating with others from a young age.

Adolescent males (aged 10 to 18 years) gradually gain their independence by spending longer periods away from the family before leaving permanently. Young independent males preferentially seek out the company of older males (Evans & Harris 2008; Chiyo et al. 2011; Lee et al. 2011; O'Connell-Rodwell et al. 2011), learning the rules of male dominance hierarchies that are based on sexual status, physical size and strength and personality. These older males also take active leadership roles in the collective movements of all-male groups (Allen et al. 2020). As they age, males enter annual 'musth' phases - periods of greatly heightened testosterone that can last several months - that signal social and sexual maturity (Poole & Moss, 1981). During musth, males range widely in search of sexually receptive females (Poole, 1987; 1989a), and compete fiercely for access (Evans & Harris 2008; Lee et al. 2011; O'Connell-Rodwell et al. 2011; Poole 1989b). However, most of the year when not in musth, adult males are more sociable and can

often be found in relatively stable all-male groups (Murphy et al. 2019; Taylor et al. 2019). Their ranging behaviour is influenced by these social contexts as well as resource availability (Wiśniewska et al. *in prep.*). The presence of mature adult males appears important for younger males to learn appropriate behaviour and to suppress premature musth (Slotow et al. 2000). Without elder males, socially immature bulls in musth can exhibit extremely aggressive and destructive behaviour (Slotow et al. 2001).

For elephants, multi-generational social interactions, characterised by a high degree of social tolerance likely facilitates vertical, horizontal, and oblique transmission of information.

Evidence for social learning in elephants

Most evidence for social learning is indirect.

The evidence for social function and the key role of knowledgeable elders in elephants is strong and seems to be a central elephant tenet: Older individuals add considerable adaptive value to elephant society. However, whilst it seems extremely likely that such a long-lived and highly social species would learn from observing others, direct evidence that younger elephants acquire knowledge from their elders is lacking, with only scarce examples of transmission of knowledge or social roles down or across generations. Familial social network positions are likely socially learned, with young females actively seeking to maintain the traditional place of their family in the wider social network when older individuals were lost to poaching (Goldenberg et al. 2016). Elephants travel well-established paths to resources which appear to be traditional, with spatial knowledge likely transmitted from older relatives to younger individuals (e.g. Fishlock et al. 2016).

Expanding our premise to include indicators of social learning (Schuppli and van Schaik 2019), rather than direct records, close proximity of calves to elders (mothers or babysitters) is a given in elephant societies (Lee 1986; Lee & Moss 2011). Although it has not yet been validated as such, this proximity may be functionally equivalent to the peering behaviour of immature primates, which serves as an index of their social learning (Schuppli and van Schaik 2019). Thus, the proximity of immature elephants to more knowledgeable elders may also indicate a propensity for social learning. Elephants also tend to aggregate wherever resources permit (Fishlock et al. 2016), creating lifelong opportunities for learning and social exchange.

Experimental work exploring elephant cognition has been somewhat limited by their size and power, however some enterprising researchers have succeeded in working with captive or semi-wild individuals. Captive savannah elephants presented with a classic “two-action” feeding apparatus did not copy a demonstrator, but results provided experimental evidence of local enhancement or observational conditioning (Greco et al. 2013). Asian elephants, meanwhile, learn to cooperate in experimental tasks (Plotnik et al. 2011) and mitigate competition until the stakes get too high (Li et al. 2021). There is also evidence of vocal imitation in both savannah and Asian elephants (Poole et al. 2005; Stoeger et al. 2012). Observational data from the wild suggests that although elephant mating is usually a highly social affair where learning opportunities are maximised (Moss 1983; Moss & Lee 2011), older female elephants might actively teach and correct naive females how to behave when they come into oestrous for the first time (Bates et al. 2010).

Elephant culture and conservation

Loss of mature elephants and their accumulated knowledge negatively impacts reproduction and survival across generations.

Older elephants are considered 'repositories of knowledge' (McComb et al. 2001), and experienced matriarchs improve calf survival for all family members (McComb et al. 2011; Foley et al. 2008). The loss of these mature individuals therefore results in a loss of knowledge, and profoundly impacts remaining elephants. Populations that have lost older matriarchs are less cohesive and more prone to behave erratically (Gobush & Wasser 2009), and survivors can display maladaptive responses to threats (Shannon et al 2013; 2022) and struggle to raise calves successfully (Gobush et al. 2008, Goldenberg & Wittemyer 2018). These effects are multigenerational (Goldenberg & Wittemyer 2017; 2018; Shannon et al. 2013), where young elephants struggle when they do not have elders to guide them (Parker et al. 2021) and have implications for population structure and survival (Brakes et al. 2019; 2021; de Silva & Leimgruber 2019).

Elephant populations are not functionally equivalent, and numbers alone tell a limited story.

Population numbers alone are not sufficient to draw conclusions about how elephants are faring: social structure and behaviour must be taken into account. Even where elephant numbers are locally increasing, elephants may not be especially well-adapted for the long-term if they lack the appropriate social structure to have acquired detailed local knowledge (e.g. Shannon et al. 2013; 2022). Maintaining suitable social structures with knowledgeable elders is critical for elephant flexibility and survival. Elders can empower resilience in the face of climate and anthropogenic change (e.g., finding water sources in periods of drought, or accessing areas when common pathways are blocked), and when faced with conservation interventions or other human actions at the human-elephant interface (e.g., translocations, fences or habitat transformation).

The habitat range and probable knowledge diversity of savannah elephants also means that populations across Africa are not functionally equivalent. Individuals spend decades learning about resources and risks within their environments (Bates et al. 2007; McComb et al. 2014) and developing strategies based on that knowledge: An elephant from Amboseli, used to year-round access to water, would be highly unlikely to survive in the deserts of Namibia or Mali. This diverse local knowledge suggests elephants form culturally significant units, each of which should be conserved and managed in its own right and context. Translocations for both savannah and Asian elephants have high costs and limited success with elephants dying or attempting to return to their natal area (and causing damage as they do so) (Fernando et al 2012; Pinter-Wollman et al. 2009; Tiller et al. 2022; Viljoen et al. 2008; 2015). This lack of success likely stems at least in part from moving elephants between ecological and/or cultural zones where they lack social functionality (Goldenberg et al. 2019, 2022). Perturbations to elephant social groups that interfere with knowledge transfer and normal social function can result in aberrant or dangerous behaviour which can have negative impacts on people living alongside elephants.

Elephants are vulnerable to human-induced environmental change, and appropriately managing interactions between people and elephants depends on local contexts.

Across most of their range, elephants share space with humans, who increasingly transform habitats with profound consequences for elephant ranging and survival (Boult et al. 2019). Costly management strategies focus on problems such as crop depredation, influencing how elephants are permitted to inhabit landscapes according to policies developed largely to serve human needs (Evans & Adams 2015). Without considering how elephants may respond to or resist such strategies (Mumby & Plotnik 2018), or how their flexible decision-making promotes their ability to adapt to fluid human behaviour (Evans & Adams 2018; Plotnik & Jacobson 2022), it becomes

difficult to effectively allocate conservation resources. More worryingly, managers risk perverse outcomes such as the social transmission of problem behaviour to naïve populations, that may be difficult to reverse once established. Unfortunately, human bias also limits how we study and document elephant responses. For example, fence breaking by elephants or crop depredations are strongly suspected to have personality and social components, but the working group authors find these papers are difficult to publish, frequently rejected as being "case-studies" anecdotal, or unsystematic. As long as evidence is difficult to share in this way, a systematic multi-species review of the social learning opportunities and how these impact management seems distant. Yet elephants remain deeply affected by ecologically arbitrary shifts in human behaviour: e.g. a cryptic and human-averse population of elephants in Southern India experienced hugely escalated conflict with their human neighbours when increased coffee prices encouraged producers to pay overtime, minimising the window in which elephants were free to feed in coffee plantations (Narayana 2015). Culture is composed not only of observable active behaviour but also of unobservable behaviour (i.e., not doing something). For elephants, there is a grave and urgent danger that relatively cryptic and conflict-avoiding populations will either be extirpated or grow more behaviourally conflict-prone as a result of human activity.

Recommendations

No assessments of evolutionary or culturally significant units of elephants have yet been undertaken. This is imperative, given the extensive habitat diversity in which elephants exist. For example, it is highly likely that savannah elephants occupying the deserts of Namibia or Mali are behaviourally and thus culturally distinct from those occupying the comparatively much wetter areas of Gorongosa, Mozambique or Mount Elgon, Kenya. Overlooking cultural diversity ignores the potential to harness elephant flexibility and responsiveness in ways that promote coexistence and conservation across their range for human and elephant generations to come. It is imperative that assessments of evolutionary and culturally significant units (ESUs and CSUs) are undertaken and incorporated into future management strategies, designation of protected areas, and drafting of national and international threat classifications and biodiversity strategies.

References

Allen, C. R., Brent, L. J., Motsentwa, T., Weiss, M. N., & Croft, D. P. (2020). Importance of old bulls: leaders and followers in collective movements of all-male groups in African savannah elephants (Loxodonta africana). Scientific Reports, 10(1), 13996. doi: 10.1038/s41598-020-70682-y

Archie, E. A. Moss, C. J. and Alberts, S. C. (2006) 'The ties that bind : genetic relatedness predicts the fission and fusion of social groups in wild African elephants', Proceedings of the Royal Society, Series B, 273, , pp. 513–522. doi: 10.1098/rspb.2005.3361.

Bates, L. A., Sayialel, K. N., Njiraini, N. W., Moss, C. J., Poole, J. H., & Byrne, R. W. (2007). Elephants classify human ethnic groups by odor and garment color. *Current Biology*, *17*(22), 1938-1942. doi: 10.1016/j.cub.2007.09.060

Bates, L. A., Sayialel, K. N., Njiraini, N. W., Poole, J. H., Moss, C. J., & Byrne, R. W. (2008). African elephants have expectations about the locations of out-of-sight family members. Biology Letters, 4(1), 34-36. doi: 10.1098/rsbl.2007.0529

Byrne, R., Lee, P. C., Njiraini, N., Poole, J. H., Sayialel, K., Sayialel, S., ... & Moss, C. J. (2008). Do elephants show empathy? Journal of Consciousness Studies, 15(10-11), 204-225.

Bates, L. A., Handford, R., Lee, P. C., Njiraini, N., Poole, J. H., Sayialel, K., ... & Byrne, R. W. (2010). Why do African elephants (Loxodonta africana) simulate oestrus? An analysis of longitudinal data. PLoS One, 5(4), e10052. doi: 10.1371/journal.pone.0010052

Boult, V. L., Fishlock, V., Quaife, T., Hawkins, E., Moss, C., Lee, P. C., & Sibly, R. M. (2019). Human-driven habitat conversion is a more immediate threat to Amboseli elephants than climate change. Conservation Science and Practice, 1(9), e87. doi: 10.1111/csp2.87

Brand, C. M., Johnson, M. B., Parker, L. D., Maldonado, J. E., Korte, L., Vanthomme, H., ... & Ting, N. (2020). Abundance, density, and social structure of African forest elephants (Loxodonta cyclotis) in a human-modified landscape in southwestern Gabon. Plos one, 15(4), e0231832. doi: 10.1371/journal.pone.0231832

Brakes, P., Dall, S. R., Aplin, L. M., Bearhop, S., Carroll, E. L., Ciucci, P., ... & Rutz, C. (2019). Animal cultures matter for conservation. Science, 363(6431), 1032-1034. doi: 10.1126/science.aaw3557

Brakes, P., Carroll, E. L., Dall, S. R., Keith, S. A., McGregor, P. K., Mesnick, S. L., ... & Garland, E. C. (2021). A deepening understanding of animal culture suggests lessons for conservation. Proceedings of the Royal Society B, 288(1949), 20202718.

Buss, I. O. (1961). Some observations on food habits and behavior of the African elephant. The Journal of Wildlife Management, 25, 131–148. doi: 10.2307/3798671

Bunney, K., Bond, W. J., & Henley, M. (2017). Seed dispersal kernel of the largest surviving megaherbivore—the African savanna elephant. Biotropica, 49(3), 395-401. doi: 10.1111/btp.12423

Campos-Arceiz, A., & Blake, S. (2011). Megagardeners of the forest–the role of elephants in seed dispersal. Acta Oecologica, 37(6), 542-553. doi: 10.1016/j.actao.2011.01.014

Chiyo, P. I., Archie, E. A., Hollister-Smith, J. A., Lee, P. C., Poole, J. H., Moss, C. J., & Alberts, S. C. (2011). Association patterns of African elephants in all-male groups: the role of age and genetic relatedness. Animal Behaviour, 81(6), 1093-1099. doi: 10.1016/j.anbehav.2011.02.013.

de Silva, S., & Wittemyer, G. (2012). A comparison of social organization in Asian elephants and African savannah elephants. International Journal of Primatology, 33, 1125-1141. doi: 10.1007/s10764-011-9564-1

de Silva, S., Schmid, V., & Wittemyer, G. (2017). Fission–fusion processes weaken dominance networks of female Asian elephants in a productive habitat. *Behavioral Ecology*, *28*(1), 243-252. doi: 10.1093/beheco/arw153

de Silva, S., & Leimgruber, P. (2019). Demographic tipping points as early indicators of vulnerability for slow-breeding megafaunal populations. *Frontiers in Ecology and Evolution*, *7*, 171. doi: 10.3389/fevo.2019.00171

Evans, K. E. Y Harris, S. (2008) 'Adolescence in male African elephants, Loxodonta africana, and the importance of sociality', Animal Behaviour, 76(3), pp. 779–787. doi: 10.1016/j.anbehav.2008.03.019.

Evans, L. A., & Adams, W. M. (2016). Fencing elephants: The hidden politics of wildlife fencing in Laikipia, Kenya. Land Use Policy, 51, 215-228. doi: 10.1016/j.landusepol.2015.11.008

Evans, L. A., & Adams, W. M. (2018). Elephants as actors in the political ecology of human–elephant conflict. Transactions of the Institute of British Geographers, 43(4), 630-645. doi: 10.1111/tran.12242

Fernando, P., Leimgruber, P., Prasad, T., & Pastorini, J. (2012). Problem-elephant translocation: translocating the problem and the elephant?. PloS one, 7(12), e50917. doi: 10.1371/journal.pone.0050917

Fishlock, V., & Lee, P. C. (2013). Forest elephants: fission–fusion and social arenas. Animal Behaviour, 85(2), 357-363. doi: 10.1016/j.anbehav.2012.11.004

Fishlock, V. Caldwell, C. and Lee, P. C. (2016) 'Elephant resource-use traditions', Animal Cognition, 19(2), pp. 429–433. doi: 10.1007/s10071-015-0921-x.

Foley, C. PettorelliI, N. and Foley, L. (2008) 'Severe drought and calf survival in elephants.', Biology Letters, 4(5), pp. 541–544. doi: 10.1098/rsbl.2008.0370.

Gobush, K. S. Mutayoba, B. M. and Wasser, S. K. (2008) 'Long-Term Impacts of Poaching on Relatedness, Stress Physiology , and Reproductive Output of Adult', Conservation Biology, 22(6), pp. 1590–1599. doi: 10.1111/j.1523-1739.2008.01035.x.

Gobush, K. S. and Wasser, S. K. (2009) 'Behavioural correlates of low relatedness in African elephant core groups of a poached population', Animal Behaviour. Elsevier Ltd, 78(5), pp. 1079–1086. doi: 10.1016/j.anbehav.2009.06.034.

Gobush, K.S., Edwards, C.T.T, Balfour, D., Wittemyer, G., Maisels, F. & Taylor, R.D. (2022).Loxodonta africana. The IUCN Red List of Threatened Species 2021: e.T181008073A181022663 doi: 10.2305/IUCN.UK.2021-1.RLTS.T181008073A181022663.en

Gobush, K.S., Edwards, C.T.T, Maisels, F., Wittemyer, G., Balfour, D. & Taylor, R.D. (2021). Loxodonta cyclotis. The IUCN Red List of Threatened Species 2021: e.T181007989A204404464. https://dx.doi.org/10.2305/IUCN.UK.2021-1.RLTS.T181007989A204404464.en.

Goldenberg, S. Z. Douglas-Hamilton, I. and Wittemyer, G. (2016) 'Vertical Transmission of Social Roles Drives Resilience to Poaching in Elephant Networks', Current Biology. Elsevier Ltd, 26(1), pp. 75–79. doi: 10.1016/j.cub.2015.11.005.

Goldenberg, Shifra Z. and Wittemyer, G. (2017) Orphaned female elephant social bonds reflect lack of access to mature adults, Scientific Reports, 7(1), pp. 1–7. doi: 10.1038/s41598-017-14712-2.

Goldenberg, S. Z. and Wittemyer, G. (2018) 'Orphaning and natal group dispersal are associated with social costs in female elephants', Animal Behaviour. Elsevier Ltd, 143, pp. 1–8. doi: 10.1016/j.anbehav.2018.07.002.

Goldenberg, S.Z., Owen, M.A., Brown, J.L., Wittemyer, G., Oo, Z.M., Leimgruber, P., (2019) Increasing conservation translocation success by building social functionality in released populations, Global Ecology and Conservation, doi: 10.1016/j.gecco.2019.e00604.

Goldenberg, S. Z., Turkalo, A. K., Wrege, P. H., Hedwig, D., & Wittemyer, G. (2021). Entry and aggregation at a Central African bai reveal social patterns in the elusive forest elephant Loxodonta cyclotis. Animal Behaviour, 171, 77-85. doi: 10.1016/j.anbehav.2020.11.008

Goldenberg, S. Z., Chege, S. M., Mwangi, N., Craig, I., Daballen, D., Douglas-Hamilton, I., ... & Owen, M. A. (2022). Social integration of translocated wildlife: a case study of rehabilitated and released elephant calves in northern Kenya. Mammalian Biology, 1-16. doi: 10.1007/s42991-022-00285-9

Greco, B. J., Brown, T. K., Andrews, J. R., Swaisgood, R. R., & Caine, N. G. (2013). Social learning in captive African elephants (Loxodonta africana africana). Animal cognition, 16, 459-469. doi: 10.1007/s10071-012-0586-7

Guldemond, R. A., Purdon, A., & Van Aarde, R. J. (2017). A systematic review of elephant impact across Africa. PloS one, 12(6), e0178935. doi: 10.1371/journal.pone.0178935

Lahdenperä, M., Mar, K. U., & Lummaa, V. (2016). Nearby grandmother enhances calf survival and reproduction in Asian elephants. Scientific reports, 6(1), 27213. doi: 10.1038/srep27213

Li, L. L., Plotnik, J. M., Xia, S. W., Meaux, E., & Quan, R. C. (2021). Cooperating elephants mitigate competition until the stakes get too high. PLoS Biology, 19(9), e3001391. doi: 10.1371/journal.pbio.3001391

Lee, P. C. (1986) 'Early Social Development amoung African Elephant Calves', National Geographic Research, pp. 388–400.

Lee, P. (1987) 'Allomothering among African elephants', Animal Behaviour, 35(1), pp. 278–291. doi: 10.1016/S0003-3472(87)80234-8.

Lee, P. C., Poole, J. H., Njiraini, N., Sayialel, C. N., & Moss, C. J. (2011). 17. Male Social Dynamics: Independence and Beyond. In The Amboseli elephants (pp. 260-271). University of Chicago Press.

Lee, P. C. et al. (2016) 'The reproductive advantages of a long life: longevity and senescence in wild female African elephants', Behavioral Ecology and Sociobiology, 70(3), pp. 337–345. doi: 10.1007/s00265-015-2051-5.

Lee, P. C. and Moss, C. J. (1986) 'Early maternal investment in male and female African elephant calves', Behavioral Ecology and Sociobiology, 18(5), pp. 353–361. doi: 10.1007/BF00299666.

Lindsay, K., Chase, M., Landen, K., & Nowak, K. (2017). The shared nature of Africa's elephants. Biological Conservation, 215, 260-267. doi: 10.1016/j.biocon.2017.08.021.

McComb, K., Moss, C., Sayialel, S., & Baker, L. (2000). Unusually extensive networks of vocal recognition in African elephants. *Animal behaviour*, *59*(6), 1103-1109. doi: 10.1006/anbe.2000.1406.

McComb, K., Moss, C., Durant, S. M., Baker, L., & Sayialel, S. (2001). Matriarchs as repositories of social knowledge in African elephants. Science, 292(5516), 491-494. doi: 10.1126/science.1057895.

McComb, K., Shannon, G., Durant, S. M., Sayialel, K., Slotow, R., Poole, J., & Moss, C. (2011). Leadership in elephants: the adaptive value of age. Proceedings of the Royal Society B: Biological Sciences, 278(1722), 3270-3276. doi: 10.1098/rspb.2011.0168.

McComb, K., Shannon, G., Sayialel, K. N., & Moss, C. (2014). Elephants can determine ethnicity, gender, and age from acoustic cues in human voices. *Proceedings of the National Academy of Sciences*, *111*(14), 5433-5438. doi: 10.1073/pnas.1321543111

Moss, C. J. (1983). Oestrous behaviour and female choice in the African elephant. Behaviour, 86(3-4), 167-195. doi: 10.1163/156853983X00354

Moss, C. J. and Lee, P. C. (2011) 'Female Social Dynamics: Fidelity and Flexibility', in Moss, C. J. Croze, H. and Lee, P. C. (eds) The Amboseli Elephants. Chicago: Chicago University Press, pp. 205–223.

Moss, C. J. and Poole, J. H. (1983) 'Relationships and social structure of African elephants', in Hinde, R. (ed.) Primate social relationships: An integrated approach. Oxford: Blackwells, pp. 314–25.

Mumby, H. S., & Plotnik, J. M. (2018). Taking the elephants' perspective: Remembering elephant behavior, cognition and ecology in human-elephant conflict mitigation. Frontiers in Ecology and Evolution, 6, 122. doi: 10.3389/fevo.2018.00122

Murphy, D., Mumby, H. S., & Henley, M. D. (2020). Age differences in the temporal stability of a male African elephant (Loxodonta africana) social network. Behavioral Ecology, 31(1), 21-31. doi: 10.1093/beheco/arz152.

Nandini, S., Keerthipriya, P., & Vidya, T. N. C. (2018). Group size differences may mask underlying similarities in social structure: a comparison of female elephant societies. Behavioral Ecology, 29(1), 145-159. doi: 10.1093/beheco/arx135

Nayarana, M.H. (2015) A study on elephant and human interactions in Kodagu, South India, PhD thesis, University of Stirling, UK.

O'Connell-Rodwell, C. E., Wood, J. D., Kinzley, C., Rodwell, T. C., Alarcon, C., Wasser, S. K., & Sapolsky, R. (2011). Male African elephants (Loxodonta africana) queue when the stakes are high. Ethology Ecology & Evolution, 23(4), 388-397. doi: 10.1080/03949370.2011.598569.

Parker, J. M., Webb, C. T., Daballen, D., Goldenberg, S. Z., Lepirei, J., Letitiya, D., ... & Wittemyer, G. (2021). Poaching of African elephants indirectly decreases population growth through lowered orphan survival. Current Biology, 31(18), 4156-4162. doi: 10.1016/j.cub.2021.06.091.

Pinter-Wollman, N., Isbell, L. A., & Hart, L. A. (2009). Assessing translocation outcome: comparing behavioral and physiological aspects of translocated and resident African elephants (Loxodonta africana). Biological Conservation, 142(5), 1116-1124. doi: 10.1016/j.biocon.2009.01.027

Plotnik, J. M., Lair, R., Suphachoksahakun, W., & De Waal, F. B. (2011). Elephants know when they need a helping trunk in a cooperative task. Proceedings of the National Academy of Sciences, 108(12), 5116-5121. doi: 10.1073/pnas.1101765108

Plotnik, J. M., & De Waal, F. B. (2014). Asian elephants (Elephas maximus) reassure others in distress. PeerJ, 2, e278. doi: 10.7717/peerj.278.

Plotnik, J. M. de Waal, F. B. M. and Reiss, D. (2006) 'Self-recognition in an Asian elephant', Proceedings of the National Academy of Sciences of the United States of America, 103(45), pp. 17053–17057. doi: 10.1073/pnas.0608062103.

Plotnik, J. M., & Jacobson, S. L. (2022). A "thinking animal" in conflict: studying wild elephant cognition in the shadow of anthropogenic change. Current Opinion in Behavioral Sciences, 46, 101148. doi: 10.1016/j.cobeha.2022.101148

Poole, J. H. (1987) 'Rutting behaviour in African elephants: The phenomenon of musth', Behaviour, 102, pp. 283–316. doi: 10.1163/156853986X00171

Poole, J. H. (1989a) 'Announcing intent: The aggressive state of musth in African elephants', Animal Behaviour, 37, pp. 140–52. doi: 10.1016/0003-3472(89)90014-6

Poole, J. H. (1989b) 'Mate guarding, reproductive success and female choice in African elephants', Animal Behaviour, 37(PART 5), pp. 842–849. doi: 10.1016/0003-3472(89)90068-7.

Poole, J. H. and Granli, P. (2011) 'Signals, Gestures, and Behavior of African elephants', in Moss, C. J. Croze, H. and Lee, P. C. (eds) The Amboseli Elephants. Chicago: Chicago University Press, pp. 125–161.

Poole, J. H., Tyack, P. L., Stoeger-Horwath, A. S., & Watwood, S. (2005). Elephants are capable of vocal learning. Nature, 434(7032), 455-456. doi: 10.1038/434455a

Poole, J. H. and Moss, C. J. (1981) 'Musth in the African elephant Loxodonta africana', Nature, pp. 830–831. doi: 10.1038/292830A0

Schuppli, C., & Van Schaik, C. P. (2019). Animal cultures: how we've only seen the tip of the iceberg. Evolutionary Human Sciences, 1, e2. doi: 10.1017/ehs.2019.1

Shannon, G., Slotow, R., Durant, S. M., Sayialel, K. N., Poole, J., Moss, C., & McComb, K. (2013). Effects of social disruption in elephants persist decades after culling. Frontiers in zoology, 10(1), 1-11. doi: 10.1186/1742-9994-10-62.

Shannon, G., Cordes, L. S., Slotow, R., Moss, C., & McComb, K. (2022). Social Disruption Impairs Predatory Threat Assessment in African Elephants. Animals, 12(4), 495. doi: 10.3390/ani12040495

Slotow, R., Van Dyk, G., Poole, J., Page, B., & Klocke, A. (2000). Older bull elephants control young males. Nature, 408(6811), 425-426. doi: 10.1038/35044191.

Slotow, R., & van Dyk, G. (2001). Role of delinquent young" orphan" male elephants in high mortality of white rhinoceros in Pilanesberg National Park, South Africa. Koedoe, 44(1), 85-94. doi: 10.4102/koedoe.v44i1.188

Smet, A. F., & Byrne, R. W. (2013). African elephants can use human pointing cues to find hidden food. *Current Biology*, *23*(20), 2033-2037. doi: 10.1016/j.cub.2013.08.037

Stoeger, A. S., Mietchen, D., Oh, S., de Silva, S., Herbst, C. T., Kwon, S., & Fitch, W. T. (2012). An Asian elephant imitates human speech. Current Biology, 22(22), 2144-2148. doi: 10.1016/j.cub.2012.09.022

Taylor, L. A., Vollrath, F., Lambert, B., Lunn, D., Douglas-Hamilton, I., & Wittemyer, G. (2020). Movement reveals reproductive tactics in male elephants. Journal of Animal Ecology, 89(1), 57-67. doi: 10.1111/1365-2656.13035.

Tiller, L. N., King, L. E., Okita-Ouma, B., Lala, F., Pope, F., Douglas-Hamilton, I., & Thouless, C. R. (2022). The behaviour and fate of translocated bull African savanna elephants (Loxodonta africana) into a novel environment. African Journal of Ecology, 60(4), 866-881. doi: 10.1111/aje.13038

Turkalo, A. K., Wrege, P. H., & Wittemyer, G. (2018). Demography of a forest elephant population. PloS one, 13(2), e0192777. doi: 10.1371/journal.pone.0192777

Viljoen, J. J., Ganswindt, A., Du Toit, J. T., & Langbauer Jr, W. R. (2008). Translocation stress and faecal glucocorticoid metabolite levels in free-ranging African savanna elephants. South African Journal of Wildlife Research-24-month delayed open access, 38(2), 146-152.

Viljoen, J. J., Ganswindt, A., Reynecke, C., Stoeger, A. S., & Langbauer Jr, W. R. (2015). Vocal stress associated with a translocation of a family herd of African elephants (Loxodonta africana) in the Kruger National Park, South Africa. Bioacoustics, 24(1), 1-12. doi: 10.1080/09524622.2014.906320

Wall, J., Wittemyer, G., Klinkenberg, B., LeMay, V., Blake, S., Strindberg, S., ... & Douglas-Hamilton, I. (2021). Human footprint and protected areas shape elephant range across Africa. *Current Biology*, *31*(11), 2437-2445. doi: 10:1016/j.cub.2021.03.042

Williams, C., Tiwari, S.K., Goswami, V.R., de Silva, S., Kumar, A., Baskaran, N., Yoganand, K. & Menon, V. (2020). Elephas maximus. The IUCN Red List of Threatened Species 2020: e.T7140A45818198. https://dx.doi.org/10.2305/IUCN.UK.2020-3.RLTS.T7140A45818198.en

Wittemyer, G., Okello, J. B., Rasmussen, H. B., Arctander, P., Nyakaana, S., Douglas-Hamilton, I., & Siegismund, H. R. (2009). Where sociality and relatedness diverge: the genetic basis for hierarchical social organization in African elephants. Proceedings of the Royal Society B: Biological Sciences, 276(1672), 3513-3521. doi: 10.1098/rspb.2009.0941.

Wittemyer, G. Douglas-Hamilton, I. and Getz, W. M. (2005) 'The socioecology of elephants: Analysis of the processes creating multitiered social structures', Animal Behaviour, 69(6), pp. 1357–1371. doi: 10.1016/j.anbehav.2004.08.018.