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REVIEW ARTICLE

Elephant Social Systems: What Do We Know and How Have Molecular Tools Helped?

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Abstract | We review studies of the social systems of the living elephants—the Asian elephant (*Elephas maximus*), African savannah elephant (*Loxodonta africana*), and African forest elephant (*Loxodonta cyclotis*). Social systems include social organisation, the way relationships are structured, and the mating system; we describe each of these in turn, drawing from long-term observational studies and studies based on indirect methods in more inaccessible populations. Male and female elephants exhibit different adult lifestyles: females live in fission–fusion societies, whereas males disperse from their natal groups and subsequently associate with other males and females only temporarily. Associations and dominance relationships among females and among males may be complex and structured by factors such as genetic relatedness and relative ages. Elephants are polygynous and males compete amongst themselves for access to females. The outcome of such competition may be shaped by musth (a rut-like phenomenon) and age. Molecular markers have been used to understand aspects of social structure and mating system in some populations; we point to these studies and discuss further avenues of research. We also comment on how anthropogenic activities affect social systems, and the relevance of studying social systems in the context of conservation.

1 Introduction

Group-living may confer benefits such as cooperative defence against predators, enhanced success in locating and defending resource patches, increased mating opportunities, reduced risk of infanticide, and increased inclusive fitness[140, 173], while also incurring costs in terms of competition for resources[71, 140, 174] and increased risk of disease transmission[4]. Different social systems are thought to have evolved based on the specifics of these benefits and costs, apart from other ecological and phylogenetic factors (for example, see[27, 72, 74, 134, 151]). In this paper, we describe the social systems of elephants, especially drawing on the multiple studies carried out since a previous review[161]. In describing these social systems, we mention how molecular markers have been used to throw light on some aspects of sociality. We also touch upon the relevance of social organisation to conservation.

Elephants are long-lived social species that occupy ecologically diverse habitats that may offer varied challenges. Moreover, being megaherbivores with poor digestion and, consequently, having to spend large parts of the day feeding (60–80% of a 24-h period[9, 110]) to maintain their body mass, elephants have high food requirements and are likely to face considerable feeding competition in groups. Therefore, although detailed data on social organisation, genetic relatedness, and dominance relationships are available only from a small number of populations so far (see sections below), elephants offer a good system to study the effects of different ecological factors on sociality. Additionally, although the Order Proboscidea is not phylogenetically diverse

Group: a set of individuals, who are seen together in close proximity with each other in the field and may exhibit coordinated movement and/or affiliative behaviours.

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in terms of living species, multiple extinct species are known, and it is possible that more insights into the social systems of extinct species may be obtained in the future based on fossil evidence and molecular techniques.

Here, we focus on the extant species of elephants: the Asian elephant (*Elephas maximus*), African savannah elephant (*Loxodonta africana*), and African forest elephant (*Loxodonta cyclotis*)[128, 129]. The Asian and African elephants are estimated to have diverged 4.2–9 million years ago (Mya) based on genomic DNA and 6.6–8.8 Mya based on mitochondrial DNA, and the African forest and savannah elephants are estimated to have diverged 2.6–5.6 Mya[129–131]. Within the Asian elephant, elephants from Sumatra and Borneo have been found to be genetically differentiated from the other populations[39, 42, 162], and the Sumatran elephant is currently recognised as a separate subspecies[54]. The Asian elephant is currently listed by the IUCN as Endangered[164] and the African elephant (assessed as a single species) as Vulnerable[14].

Social systems include social organisation, social structure, and mating system[74]. Following Kappeler and van Schaik's[74] definitions, social organisation refers to the sexual composition, size, and cohesiveness of a society, whereas social structure refers to the social interactions amongst members of the society and the ensuing social relationships. We describe each of these in turn.

2 Social Organisation and Structure

In a categorisation of the social organisation of species into solitary, pair-living, or group-living, elephants would be described as group-living. However, adult females and males live in very different kinds of societies: females and dependent young of both sexes live in groups whereas adult males may spend significant proportions of their time alone (see below).

Fission–fusion society: a society in which group sizes and compositions change over short time periods (many times within an individual's lifespan), due to the splitting of groups into subgroups and rejoining of the subgroups into larger groups; this may occur in response to spatiotemporal changes in resource availability.

2.1 Female Elephant Social Organisation

Elephants live in matriarchal societies, comprising adult females and their dependent and subadult offspring, while pubertal males disperse from their natal groups/*clans (see below)*[19, 30, 95, 99, 148, 29, 155]. However, female societies differ in complexity across the three species. Africana savannah elephant females exhibit a multitiered (hierarchically nested, multileveled) social organisation, the basic unit of which is a *family group* that comprises one or more mother–offspring units[30, 99, 165]. Associations of family groups (also called *core groups*) have been identified as *bond groups* or *kinship groups*[30, 99]. Although bond groups that shared the same dry season home range were initially termed a *clan* ([99] in the Amboseli population), subsequent cluster analysis of female associations has identified clans as social, rather than spatial, entities[167]. Thus, the clan is the most inclusive level of social organisation (or the most inclusive socially meaningful community). Clan sizes ranged from 50 to 250 individuals in the Amboseli population[98] and the inter-quartile ranges (IQR) of clan size were 28.8–80.3 and 23.5–38 individuals during two time periods in the Samburu population[49].

Clan: the most inclusive social unit of female elephant social organisation.

Female elephants show *fission–fusion dynamics*, in which group sizes and compositions are not fixed, but change over short periods of time[30, 95]. Fission–fusion dynamics are thought to have evolved in response to spatiotemporally changing resources (for example,[21, 32, 81, 167]), with fission resulting in smaller group sizes when resources are more dispersed, and fusion resulting in larger groups when resources are more abundant and clumped locally[81]. A *group* or *herd* seen in the field is identified as a set of individuals that show close proximity, coordinated movement, and/or affiliative behaviour, and may comprise a portion of the clan or the entire clan[105]. Groups may consist of a single family, or a bond group with all its constituent families, or the entire clan with all its constituent bond groups. This kind of fission–fusion pattern would be classified as a *strictly nested multilevel society*, one of the three modal types of fission–fusion societies (see[56], Fig. 1). It is also possible that a group consists of a few of the families of a bond group rather than necessarily the entire bond group, or some of the bond groups of a clan, thus affording more flexibility in grouping. This would be seen in a *flexibly nested multilevel society*. It is also possible in a fission–fusion society that individual females associate with any other female as long as they are part of the same clan. Therefore, unlike the previous two modal societies, females do not necessarily have to associate with all their family group members all the time, or there is no distinct family structure. Such a society is called an *individual-based fission–fusion society* (Fig. 1).

Despite the long history of co-habitation with elephants in Asia, little was known about the details of Asian elephant social organisation until recent studies in Uda Walawe, Sri Lanka, and Nagarahole-Bandipur (henceforth, Kabini), southern India. Alternatively thought to have a social organisation similar

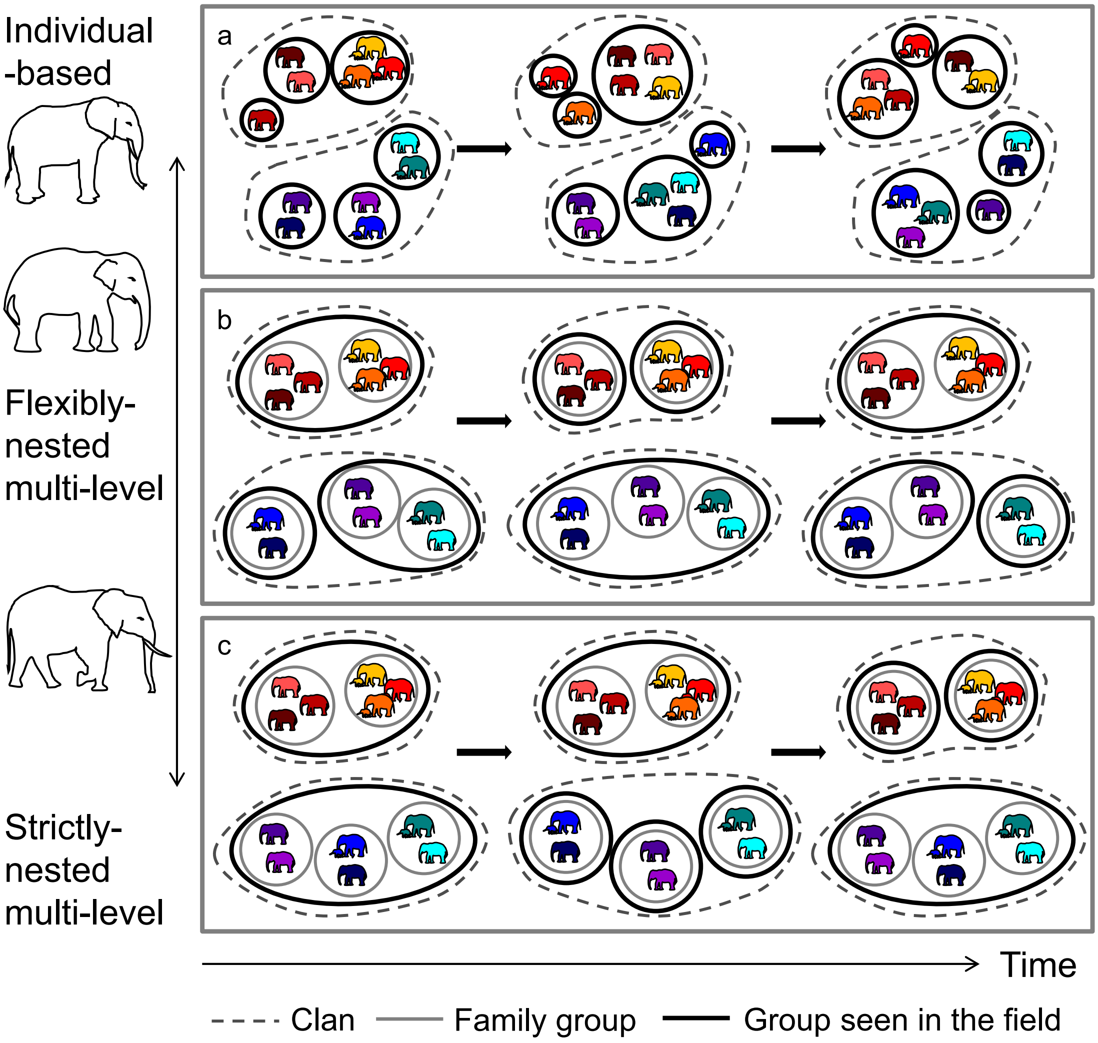

Figure 1: Temporal changes in female associations in different kinds of fission-fusion societies. Individual female elephants (and their dependent offspring if present) are colour-coded to identify them across time. How these individuals change their associations across time and become part of different groups (thick black lines) under different kinds of fission–fusion scenarios are shown. The three modal types of fission–fusion societies form the three panels. Individuals from different social levels (clan, family group) form different groupings with time: **a** individual-based society, in which any female can associate with any other female from the same clan, **b** flexibly nested multilevel society, in which some or all of the family groups of a clan may form a group, **c** strictly nested multilevel society, in which all the family groups of a clan are seen together if they associate at all. Two clans are shown within each panel and it can be seen that individuals do not switch between clans. Elephant species (top to bottom: African forest elephant, Asian elephant, African savannah elephant) are arranged vertically along the continuum of the different types of fission–fusion societies. Only two levels of social organisation are shown in this figure for the sake of simplicity, whereas b and c can have more levels. African savannah elephants have bond groups, which are not shown here, between the family and the clan (see Fig. 2c). Figure based on Nandini et al.[105].

to that of the African savannah elephant[148] and to have a social organisation limited to family groups[37], Asian elephant females are now known to show multilevel social organisation, with long-term associations amongst clan-mates[104, 141] (the IQR of clan size in the Kabini population was 17–39.5 individuals). However, Asian elephant females within clans are not as strongly connected to one another as are African savannah elephant females[105, 144]. Thus, while female social organisation of the African savannah elephant probably lies between the strictly nested and flexibly nested multilevel societies, that of the Asian elephant

Haplotype: a set of gene variants that are inherited together from a single parent; since animal mitochondrial DNA is inherited only from the mother, a particular mitochondrial DNA sequence would correspond to one haplotype, while a mutation in the sequence would create a new haplotype.

lies between the flexibly nested multilevel and individual-based fission–fusion societies[105] (Fig. 1). This difference has been attributed to the, possibly ecologically imposed, constraint on group sizes, with smaller average group sizes seen in Asian elephants, which prevents all the females of a social level from associating with one another, and reduces the overall cohesion in the society[105]. The average (SD) group size (number of adult females) was 5.03 (4.61) in the Samburu African savannah elephant population, 3.07 (2.34) in the Uda Walawe Asian elephant population, 2.35 (1.84) in the Kabini Asian elephant population (but 3.16 (3.14) when calculated using the same group definitions as in the previous two populations), and 1.48 (0.80) in the Lopé African forest elephant population[105, 137, 144].

African forest elephant females are found in small groups that appear to be nuclear families, with an adult female and her dependent offspring[154, 155]. The average (SD) female group size including dependents was 2.7 (1.3) in the Dzanga Bai forest elephant population[155]. However, they maintain larger networks of associations from their encounters with other individuals at forest clearings[52, 136, 154, 155], even maximising social opportunities during their visits to such clearings[41]. Since their average group sizes are smaller and social networks more disconnected than those in Asian and African savannah elephants[105, 136, 154, 155], African forest elephant females possibly show an individual-based fission–fusion society. This is yet to be examined.

2.2 Female Elephant Social Structure

2.2.1 Associations and Genetic Relatedness Between Females

Since elephants are matriarchal, females of a clan are expected to be related to one another. Genetic relatedness may then affect social relationships. However, given the long lifespan of elephants, of over 60 years, and the possibility of multiple males mating with the same females, it would be difficult to identify all the relationships between clan members based on observational data alone, even if carried out over a long period. The use of molecular markers, along with non-invasive sampling, has helped in this regard. The earliest such field study in elephants examined mitochondrial DNA, which is maternally inherited, in Asian elephant females in southeastern Sri Lanka by collecting their dung samples and extracting DNA from dung[37]. The study found that all the individuals sampled within a social group (thought to represent family groups in that study) shared the same mitochondrial DNA haplotype, whereas individuals from neighbouring social groups with adjacent or overlapping home ranges had different mitochondrial DNA haplotypes, establishing the matrilineal nature of the society and the absence of female transfer between social groups[37]. However, since populations may lack mitochondrial DNA diversity (see[157, 158]), the presence of a single mitochondrial DNA haplotype within a clan would not be sufficient to establish close genetic relatedness between individuals. Nuclear microsatellite DNA, which is faster mutating and, consequently, more diverse than mitochondrial DNA, is, therefore, more suitable for estimating genetic relatedness. Vidya and Sukumar[160] found that adult females in southern India that were part of small groups sighted in the field (which could be similar to family groups) were highly related to one another (mean ± 95% CI = 0.37 ± 0.159, $N = 13$ groups), possibly as a combination of mother–daughters, full-sisters, and half-sisters. The genetic relatedness between adult females within clans and within *first-level communities* (similar to a family group but detected based on social network analysis) within clans has been examined in some detail more recently. Females within first-level communities had high pairwise relatedness (mean ± 1.96 SE = 0.215 ± 0.082, $N = 20$ first-level communities from 10 clans[103]) in keeping with previous findings[160]. The average genetic relatedness at the level of the entire clan was lower than that within first-level communities, but was greater than zero, indicating that clans comprise related females[103]. However, the average relatedness between adult females in some clans was not significantly different from zero, suggesting that there might be some unrelated or distantly related clan members also[103], as in the case of the African savannah elephant (see below). A study that molecular-sexed and genotyped individuals by sampling dung from dung surveys in the Nakai Plateau, Lao PDR, found that females sampled from the same area at the same time were significantly related to one another (mean relatedness = 0.061, relatedness of individuals of the same mitochondrial DNA haplotype: 0.072–0.200;[1]), although the extent of relatedness was lower than those in the studies mentioned above.

Core groups (family groups) in African savannah elephants have also been found to comprise related females. Almost all females sampled within core groups in the Amboseli population shared the same mitochondrial DNA, and were significantly related to each other based on pairwise comparisons using nuclear microsatellite DNA (mean ± SE = 0.150 ± 0.016, $N = 221$ females from 34 core groups[7]). However, 5% of the core groups contained an immigrant female, who probably joined a different core group after the death of her relatives[7]. Members of the same bond group tended to have the same mitochondrial DNA haplotype, and the matriarchs (oldest female of the core group) of the core groups from the same bond group were more closely related to each other than expected by chance (mean relatedness = 0.085, $N = 10$ matriarch pairs from 6 bond groups[7]). Females within family groups in the Samburu population were closely related to one another, as second-order relatives, based on microsatellite DNA (mean ± SE = 0.234 ± 0.023, $N = 87$ pairs) and tended to share the same mitochondrial DNA haplotype, although there were more immigrants there than in Amboseli[170]. Members of the same bond groups were more related than expected by chance (mean ± SE = 0.067 ± 0.012, $N = 155$ pairs), but most of the matriarchs from the same bond groups were not more related to each other than expected at random[170]. Some of the differences across the two populations probably result from the Samburu population experiencing more poaching of elephants, thus disturbing the genetic basis of social grouping.

It is difficult to observe the behaviours and associations of African forest elephants due to the dense forests they inhabit; thus, most of their observations come from forest clearings. Associations between individuals in the forest are often inferred then by the spacing of dung piles. Closely spaced dung piles belonging to adult females (based on the size of the dung and molecular sexing) showed high genetic relatedness (mean ± SE = 0.22 ± 0.04, $N = 34$ pairs) in a disturbed study site with oil fields (Industrial Corridor) but not in Loango National Park, in southwest Gabon (mean ± SE = − 0.01 ± 0.03, $N = 27$ pairs[100]). Another study that sampled dung from Lopé National park, Gabon, found adult females that were spatially close to be significantly related to each other (mean = 0.236) and most, but not all, groups of adult females to have the same mitochondrial DNA haplotypes[136]. The only study based on observational data of female associations as well as assignment of dung to these females (with varying degrees of certainty) was carried out in Lopé, and the relatedness between adult females belonging to the same social network communities was found to be significantly higher than random (mean ± SD = 0.105 ± 0.078[136]).

Associations between adult females may be influenced by genetic relatedness. In the Amboseli population of African savannah elephants, the closest associates were first-order maternal relatives, who remained together during temporary group fissions. Female association strength and relatedness were positively correlated within core groups, and core groups that had the same mitochondrial DNA haplotypes had higher association strengths than those that did not share haplotypes[7]. Kinship has also been observed to play a role in cooperative behaviours: female siblings commonly provided allomaternal care in the same population[84]. In the Samburu population, there were positive but weak correlations between female association and genetic relatedness in the population overall and among matriarchs of family groups, but not between females within family groups[170]. The stability of family groups was not correlated with the group's relatedness value. However, female associations and genetic relatedness were significantly correlated within bond groups[170]. Due to the low relatedness between females that belong to the same clan, it is unlikely that inclusive fitness benefits lead to these more complex social levels.

In the Kabini Asian elephant population, the strength of association between adult females was positively but weakly correlated with genetic relatedness at the population level, and correlated within about half the number of clans examined at the clan level[103]. Adult females were significantly more closely related to their top associate (the individual with whom they associated the most) and second associate compared to the average associate[103]. A study of captive female Asian elephants also showed that females exhibited more affiliative interactions and fewer agonistic interactions in a group of related females compared to a group with unrelated females[58].

As mentioned above, it has been difficult to directly examine the relationship between associations and genetic relatedness in the African forest elephant, but the work so far suggests that there might be a positive relationship between association and genetic relatedness[136, 137]. African forest elephants associate with more individuals and with different individuals when they spend time at forest clearings as opposed to when they are ranging outside such clearings[41, 52]. Thus, the associations shown when spending time at the clearing formed a larger association network than the associations shown when just entering the clearing[52]. Both kinds of associations were stable, but the latter more so. Based on associations in forest clearings, younger females were more social (had higher strength of association) than older females in Dzanga Bai, Central African Republic[52], and young females tended to associate with older females in Odzala-Kokoua National Park, Republic of Congo[41]. Whether these associations were based on genetic relatedness is not known.

Elephants possess high cognitive abilities (for example,[18, 57, 65, 116, 126]). They can distinguish up to a hundred other individuals as familiar based on their calls[93] in the African savannah elephant, have an expectation of other individuals' spatial positions in the group[11] in the African savannah elephant, respond to others' distress or needs[10, 31, 84, 156] in the African savannah and Asian elephants, and can carry out cooperative tasks[115] in captive Asian elephants. Therefore, it would not be surprising to find relationships based on familiarity and individual recognition rather than on genetic relatedness alone, as in the case of immigrants into core groups mentioned above or relationships in disturbed areas (Sect. 4).

2.2.2 Dominance Relationships Between Females

Ecological model of female social relationships: a model that proposes that differences in female social organisation and structure arise from differences in resource-risk distributions: the distribution and abundance of food, and predation and other risks.

When individuals live in groups, competition and dominance amongst them are often inevitable. According to the ecological model of female social relationships which is part of *socioecological theory*, the distribution and abundance of food resources can shape different kinds of social relationships among females through feeding competition[67, 71, 80, 133, 147, 173]. *Scramble* competition is non-interference competition, in which the amount of resources available to individuals decreases as a function of the density of individuals in the area, while *contest* competition is interference competition, in which individuals can fight for access to a particular resource and the winner gets access to the resource whereas the loser does not[106]. When food resources are limiting and high-quality food resources are clumped in the form of large patches that can support entire groups, one would expect to find contest competition between but not within groups, leading to egalitarian relationships within groups (*resident-egalitarian* society[147]). On the other hand, if high-quality food resources are distributed in small patches such that individuals within a group can monopolise them, one would expect to find strong within-group contest competition. Individuals within groups may then form coalitions with relatives in order to defend those high-quality resource patches, thus giving rise to dominance hierarchies based on nepotistic relationships (*resident-nepotistic* society[147]). It is also conceivable that food resources are clumped in a manner that allows for both between-group and within-group contests, in which case, since large groups may be beneficial in between-group contests, dominant individuals may become more tolerant of subordinates within groups, giving rise to *resident-nepotistic-tolerant* societies[147].

Contest competition: interference competition that involves direct interaction between individuals over a monopolisable resources, such that there is a winner and a loser; the winner obtains the contested resource.

Dominance relationships within family/core groups in African savannah elephants were not found to be egalitarian or nepotistic and were based on age (age and body size are correlated) instead[6]. Transitive relationships resulted in a linear dominance hierarchy, with older females winning almost all the agonistic interactions over younger females. Competition within family groups could occur over rare or usurpable point resources such as *Acacia xanthophloea* tree bark or mineral resources that was monopolisable by individuals[6]. Contests over such point resources were seen between family groups also, but social contests were also observed in roughly equal proportion, in which resources were not contested[168]. Age affected dominance relationships between family groups also, with a linear dominance hierarchy observed between the matriarchs of the different family groups that was based on matriarch age[168]. The dominance strengths of non-matriarchal adult females within family groups were correlated with those of their bond-group's matriarchs[168]. There were benefits to being part of high-ranking family groups because such groups travelled less and used areas closer to perennial water sources and within protected areas during the dry season, compared to low-ranking groups[169]. Thus, matriarchs, especially older matriarchs, are important in female African savannah elephant social structure. Apart from their influence on dominance relationships and, thereby, spatial behaviour, matriarchs lead the family group and influence the group's responses to conspecifics and threats, being a repository of social and ecological information[92, 94, 102]. Dominance relationships have not yet been examined in the African forest elephant. However, the matriarch is not prominent socially and younger females are more central socially than older females, possibly because they range independently of their mothers earlier than those in the African savannah elephant and explore new associations in the forest clearings[52].

Asian elephants also show an effect of age on the outcomes of dominance interactions between females, but with more reversals than in the African savannah elephant[103, 142]. Unlike African savannah elephants, Asian elephants in Kabini, southern India, and Uda Walawe, Sri Lanka, did not show linear dominance hierarchies, the latter also did not show significant transitivity in dominance interactions[45, 103, 142]. The matriarch (oldest female) was not the most dominant female within Asian elephant clans[45, 103], but the age of the matriarch, along with the age of the initiator, and group size had an effect on winning between-clan interactions[103]. Agonistic interactions between clans and how they relate explicitly to the spatial distribution of resources have not been studied in the African savannah elephants. In the Asian elephant population in Kabini, agonistic interactions (a surrogate of contest competition) were more frequent and more intense between clans than within clans[46]. This is consistent with the ecological model of female social relationships since the Kabini reservoir forms a large, high-quality resource patch[46]. In Uda Walawe too, the majority of dominance interactions had occurred between social units; however, these different social units usually ignored or avoided each other[142].

In Kabini, the directional consistency (consistency in winning/losing over multiple interactions) of dominance was low despite the high frequency of agonistic interactions[45], as opposed to higher directional consistency and lower frequency of agonistic interactions in African savannah elephants (based on[6, 168]). Female African savannah elephant society has been thought of as a modified resident-nepotistic-tolerant society, with between-group contest reducing the expression of a true nepotistic hierarchy[168], and dominance being structured by age/size rather than nepotism in order to reduce the rate of conflict (due to less uncertainty in the outcomes), which could be deadly because of the presence of tusks as weapons[6]. Female Asian elephants lack tusks. However, the female Asian elephant society in Kabini is also possibly a resident-tolerant society but because of the resource distribution that results in higher between-clan than within-clan agonism.

The role of nepotism in dominance interactions between Asian elephant females is not yet known. Estimation of genetic relatedness between females based on molecular markers and the correlation with the agonistic interactions shown by them can be carried out in the future. The possible short- and long-term effects of dominance ranks on fitness also remain to be examined in some detail. Strongly expressed, linear dominance hierarchies are expected to offer a rank-based advantage in accessing food to the dominant individuals, while weakly expressed hierarchies are not expected to offer this advantage[71, 79]. In keeping with this, there was no correlation between dominance status and feeding success in the Kabini population, in which there is no strong linear dominance hierarchy[45]. Archie et al.[6] had suggested that dominance rank may not predict fitness of females in African savannah elephants because rank is not based on nepotism. However, core groups with older matriarchs had greater reproductive success than those with younger matriarchs[92], and the older matriarchs presumably had higher dominance ranks if the patterns found by Wittemyer and Getz[168] in Samburu held in Amboseli also.

Reproductive success: the number of offspring produced by an individual during a defined period.

2.3 Male Elephant Social Organisation

Elephants are precocial as calves but have a long period (at least 2 years) of nutritional dependence on the mother and also take many years to mature into adults. Although male and female calves interact closely with their mothers and other family or clan members initially[43, 127], differences in behaviour between the sexes emerge early in life[83]. Males are more explorative, show a greater tendency to interact with unfamiliar peers, and start spending more time away from their natal family groups/clans[29, 86]. Pubertal males, around ten years of age, show a gradual process of dispersal away from their natal clans[29, 30, 99]. Once dispersed, adult males may spend significant amounts of their time solitarily, and only temporarily associate with other males and with female groups[28, 29, 77, 95, 99, 118]. Adult male Asian and African savannah elephants exhibit a rut-like behaviour called musth[69, 118], which is characterised by high plasma testosterone levels, temporal gland secretion, urine dribbling sometimes, and increased aggression towards conspecifics[34, 69, 118], more details below). Non-musth male Asian elephants in Kabini were found to spend over half their time solitarily, only about 12% of their time in all-male groups with other adult males, and about 30% of their time with female groups (mixed-sex groups)[77]. On the other hand, studies of African savannah elephants in Amboseli found 63%[24] or 30.5%[87] of adult male (≥ 15 years old) sightings to comprise all-male groups. Only 12.5% of the male sightings were of solitary males[87]. A study of the African forest elephant in the forest clearing of Dzanga bai, Central African Republic, found that adult males entered the clearing alone most of the time, and rarely with other males (multi-male groups were found less than 0.3% of the time) or with female groups[155]. A constraint on the group sizes of all-male groups was observed in Kabini[77]; one wonders if this is also present in the African forest elephant.

Social dispersal: dispersal of an individual away from its natal social group but not away from its natal home range; such individuals may temporarily leave the natal home range to mate outside.

Locational dispersal: permanent dispersal of an individual away from its natal home range.

Dispersal of males can potentially be either social or locational[66]. Social dispersal involves males dispersing away from their natal clans but remaining in their natal home range and potentially making forays outside to breed. Locational dispersal involves males dispersing away from their natal clan and natal home ranges to different locations. While the first may afford greater familiarity with food resources, the second may afford greater breeding opportunities. Microsatellite-based genotyping of Asian elephants across different locations in southern India showed that, while adult females within locations were more related to each other than adult females across locations, adult males and adult females within locations were not related to each other, suggesting locational rather than social dispersal[160]. Locational dispersal was also inferred in a population in Laos since adult males and adult females within the population were not closely related to each other based on microsatellite genotyping and sexing of dung samples[1]. Mitochondrial DNA haplotypes in northeastern India also showed a pattern of male locational dispersal[157]. In southern India, males within locations were also found to be more significantly related to one another than to males across locations, suggesting biased locational dispersal, which is the phenomenon of related males dispersing, simultaneously or at different times, to the same location[160]. Adult and subadult males in Laos were not related to one another. However, the older adult males (based on dung size) were more related (more relationships with relatedness ≥ 0.25) to other adult or subadult males than to adult females; whereas, younger adult males were more related to adult females than to adult or subadult males[1]. Thus, biased locational dispersal cannot be ruled out.

There has been no systematic study of social versus locational dispersal in the African savannah elephant, although the presence of fathers and adult females who were natal family members and/or close kin (relatedness > 0.25) in the same population[5] suggests some social dispersal. In the African forest elephant, genotyping and sexing dung samples from the Industrial Corridor area and Loango National Park, SW Gabon, showed that adult males and adult females within these locations were not significantly related to one another[100], which would imply locational dispersal. Although adult males within areas were not significantly related to one another on average, there were some adult males that were first- or second-order relatives in Loango[100]. It must be noted that there were also a few highly related adult male–adult female pairs in both these areas. Schuttler et al.[136] found adult males within Lopé National Park to be unrelated to one another, and to be less related to each other than females were amongst themselves. All the studies above that have examined the relatedness between adult males are based on small sample sizes (partly because adult males are fewer in number than adult females). Since random dispersal of males can also result in some highly related pairs of adult males, more studies with larger sample sizes are required to clarify the issue of biased dispersal of males.

2.4 Male Elephant Social Structure

2.4.1 Associations and Genetic Relatedness Between Males

Interactions amongst adult male elephants are expected to be competitive because of receptive females being rare (see section on Mating system below) and because elephants are not known to form coalitions to obtain access to females. However, in other species, male groups have been found to provide opportunities to either assess one another's strengths in a more relaxed setting or to learn socially from older males (for example,[12, 15]). Since male elephants grow in bulk as they age, it would presumably be easy to assess their dominance ranks vis-à-vis much older or much younger males. However, spending time with age-peers might provide opportunities to test their strengths against them, to find out their relative positions in the dominance hierarchy and also hone their tactics and responses to future dominance interactions. In an environment with predictable spatiotemporal distribution of resources, older individuals are expected to be repositories of knowledge about these resources. In such cases, it might be beneficial for younger individuals to associate with older individuals to obtain ecological and social knowledge that might help in survival and/or reproduction.

Both testing strengths and learning from older males probably shape adult male associations in the African savannah elephant. Adult males have been found to preferentially associate with age-peers in the Amboseli and

Samburu populations[24, 51] in sexually inactive males. In Amboseli, old (≥ 30 years old) adult males significantly preferred age-peers, but associations amongst young males in all-male groups were random[24]. Sparring partners were closer in age than expected at random[24]. On the other hand, young (20–29 years old) adult males associated with old males more than expected by chance in Amboseli[24], and males of all age groups (from 10 to 15 years old onwards) preferred old (≥ 36 years old) males as their nearest physical neighbours in a study area in the Okavango Delta[35]. Older males spent more time with other males[87] or were significantly affiliated with a greater proportion of available dyads (of sexually inactive males)[51] compared to younger males. Older males were also more central in association networks constructed from all-male groups in Amboseli[24], but age was not correlated with centrality in sexually inactive males (and negatively correlated in sexually active males) in Samburu[51]. Older males seemed to affect behaviour through social learning, with the probability of raiding crops increasing when a male's second-closest associate was an older male crop raider[26]. Old (≥ 30 years old) non-musth males showed greater stability in association strength over time in a population in South Africa, although old and young (20–29 years old) males did not differ in (a) the likelihood of maintaining stable relationships over time, (b) their actual association strengths or eigenvector centrality, or (c) the stability of eigenvector centrality across time[101].Older males were also found to lead all-male group movements in a population in Botswana[3]. The greater sociality and centrality of older males from some of the studies above have suggested that old males may play an analogous role to the matriarchs of female groups by being a repository of knowledge[3, 35]. Adult male associations were also found to be based (albeit weakly) on genetic relatedness in the Amboseli African savannah elephant population[24]. These associations were different from those based on similar ages and did not serve as a means for safe sparring [24].

As mentioned in Sect. 2.3 above, adult male African forest elephants range solitarily most of the time. However, they form associations with other individuals in forest clearings. Males of all ages were found to be more likely to join other males than to join other group types in a forest clearing in Odzala-Kokoua National Park[41]. Males, irrespective of age, were also more likely to form mixed-sex groups than were females[41]. A study in Loango mentioned in the previous section has suggested that related adult male forest elephants may associate together[100]. However, detailed studies on forest elephant male associations are awaited.

What we know about the details of Asian elephant male association patterns comes from the Kabini population in southern India. Adult non-musth male associations in this population may be based on the opportunity for testing strengths rather than social learning from older males[77]. Old (> 30 years old) non-musth males preferred to associate with their age-peers while young (15–30 years old) males did not preferentially associate with or initiate associations with old males[77]. We are currently studying possible genetic relatedness-based preferences in associations.

The structuring of subadult male associations has not been extensively studied in any elephant species. Adolescent (10–15 years old) male African savannah elephants were seen to prefer larger groups and older males to associate with, which could have benefits in the form of social learning from older males or protection from older, related males[35]. In Asian elephants, subadult males (5–15 years old) associated with each other to a greater extent in the presence than in the absence of females[75]. They also associated to a greater extent than expected with their age-peers (5–10-year-olds or 10–15-year-olds) in the absence of females, and with old subadult males (10–15 years old) in the presence of females; thus, it was possible that associations between subadults were based on both testing strengths (in female absence) and social learning (in female presence)[75]. Whether the associations of subadult males amongst themselves or with adult males and females are based on genetic relatedness is not yet known.

2.4.2 Dominance Relationships Between Males

Male elephants are expected to compete intensely with one another for access to females as females are a limiting resource given their long inter-birth intervals[143, 166] and short periods of receptivity[34]. As mentioned in Sect. 2.3 above, adult male Asian and African savannah elephants can exhibit musth, during which there is high plasma testosterone levels and possibly increased aggression towards conspecifics[69, 118]. Male dominance interactions in the African savannah elephant have been found to be affected by age (and, hence, body size) and musth status, with musth overcoming the size advantage that non-musth males generally have[118, 121]. Dominance relationships

Scramble competition: non-interference competition that occurs when a resource is limiting but not monopolisable; therefore, the resource gain of all the individuals is reduced due to the faster depletion of the resource by the addition of more individuals (higher density).

may also be affected by ecological conditions. Male African savannah elephants in Etosha National Park, Namibia, displayed a linear dominance hierarchy in dry but not in wet years, and also showed more agonistic interactions during the latter[108]. Male dominance has not been examined in the African forest elephant.

In Asian elephants in Kaziranga National Park in northeastern India, musth status, followed by body size affected the outcome of male dominance interactions, while the presence and length of tusks (about half the males in this population are tuskless) were not as important[22]. Among non-musth adult males in the Kabini population, age/body size and body condition, but not tusk length, affected dominance outcomes[75]. Although significant linear dominance hierarchies were not observed, this was likely due to multiple individuals not encountering one another, and there was an orderliness in the dominance relationships[75]. Whether dominance relationships are influenced by genetic relatedness or whether males avoid aggressive interactions with relatives remains to be explored.

3 Mating System

Elephants are polygynous[149] and show sexual dimorphism: males grow in bulk as they age (Mumby et al. 2015) and full-grown adult males are considerably larger in size than adult females[85, 150]. Although males and females can potentially mate with multiple individuals of the opposite sex during a single year, since females give birth predominantly to single offspring and have long periods of gestation and lactation, the variance in reproductive success is expected to be higher in males than in females, with some males siring offspring from multiple females. There is no fixed breeding season in elephants; therefore, males and females can breed throughout the year. However, there may be peaks in breeding based on the influence of primary productivity on female fecundity[171]. The oestrous cycle is about 16 weeks[61], during which females are receptive only for a few days[34]. Females may advertise their oestrous through chemical (studied in the Asian elephant)[124] and/or behavioural (studied in the African savannah elephant)[97] signals. If a female becomes pregnant, she is not available for reproduction for the next 4–5 years because of the long periods of gestation (20–22 months) and lactation (2 years or more).

As females are a rare resource, males are expected to show intense contest competition with each other. However, since fertile females are few and presumably unpredictably distributed, there is also likely to be some scramble competition to find them. Musth may offer an advantage, in terms of roving over larger areas (studied in the Asian elephant)[40, 73, 76] , and/or in increasing dominance status (studied in the African savannah elephant)[119, 121], and, thereby, facilitate successful reproduction. Musth is considered an honest signal as it is expensive to maintain and can affect body condition[70, 121]. Male Asian elephants may first display musth when they are 10–15 years old, first sporadically and later more regularly[70, 76], and the probability of being sighted in musth increases with age[23, 76]. African savannah elephant males seem to enter musth at a later age (at least 24 years old in Amboseli[121], at least 26 years old in Tarangire[68]). However, high-ranking males are known to suppress musth in younger or low-ranking males[121]. Therefore, differences across populations in the age of first musth may depend on the presence of old males, apart from ecological and phylogenetic differences.

Although musth is expected to increase access to females, Keerthipriya et al.[76] found that this was age-class specific (applying to old males), with young (15–30-year-old) males associating with female groups to a smaller extent when they were in musth than when not in musth. Even old (> 30 years old) musth males in the Kabini Asian elephant population were found to spend considerably smaller proportions of their time (< 40%) associating with female groups compared to old (> 35 years old) musth males in the Amboseli African savannah elephant population (> 90% of their time[119]). However, intraspecific variation has been observed in the proportions of musth males[78], and studies of more populations of the two species are required to better understand this difference.

African savannah and Asian elephant females in oestrous may prefer musth to non-musth males[97, 135]. Females of both species may exercise some mate choice and have been found to respond more positively to mating attempts by large/musth males[23, 120]. In the Amboseli African savannah elephant population, old/musth males showed more mate guarding and obtained a higher number of matings than young/non-musth males[120]. Subsequent paternity analyses also showed that age and musth affected paternity success, with older males amongst those in musth usually being more successful in siring offspring[63]. However, paternity success was not restricted to musth males, and non-musth males of all age-classes over 25 years old showed low levels of paternity[63]. There is also some evidence for behavioural inbreeding avoidance of close kin (relatedness > 0.25) by males in this population[5]. Paternity analysis in the Samburu African savannah elephant population that had been subject to more poaching than Amboseli also found old musth males to have sired the greatest number of offspring[125]. However, 60% of adult males, including males over 20 years old that were not in musth, were estimated to have sired offspring, suggesting that male reproductive success was not highly skewed, and that young males might be following alternative reproductive tactics other than musth[125]. In the African savannah elephant, a distinction has been made between sexually inactive and sexually active states even when males are not in musth[44, 51], whereas, no such distinction has been observed in non-musth Asian elephants. African savannah elephant males range in separate bull areas (retirement areas), where they are either on their own or associate with other males, when they are sexually inactive. When sexually active, they leave their bull area and search for females[118]. In the Tarangire population that had also been poached, almost all the observed matings were by musth males and most of them were over 35 years old[68]. Although paternity analysis in this population showed that the oldest remaining males seemed to be siring most of the offspring, whether poaching had reduced or increased the variance in male reproductive success is not known[68]. Non-musth males are known to mate in the Asian elephant also. However paternity analyses and studies on inbreeding have not yet been carried out in Asian or African forest elephants.

4 Social Organisation and Structure, and Conservation of Elephants

Species with strongly knit social networks need special attention when conservation strategies are developed. Anthropogenic pressures have led to a drastic reduction in areas available for wildlife, forcing animals to move out of their habitat, and increasing contact and conflict with humans (for example,[152, 172]). To avoid or control conflict, one or combinations of multiple management strategies such as translocation, capturing, maintaining the population in situ, or culling are often considered, and it is important to have scientific data on population size and structure, habitat availability and connectivity, and the origin of small populations to make these decisions. Social organisation and structure are affected by anthropogenic change and can also affect the success of management interventions. We describe these below.

Drastic anthropogenic disturbance in the form of ivory poaching has altered social compositions in various populations of elephants. In Asian elephants, as only males carry tusks and not all males carry tusks, ivory poaching has led to heavily-skewed sex ratios and possibly lowered effective population sizes[8, 122]. Historical capture of tusked males for warfare and other purposes may possibly have also altered the relative proportions of tusked and tuskless males in different populations in Asia, which can, in turn, have different consequences depending on whether tusks are preferred by females[82]. Since ivory poaching targets the biggest tusks, often borne by the biggest males, it can also affect the demographic structure of the population and, thereby, affect social interactions. The absence of older males can also result in younger males, which are usually kept in check by the former, coming into musth early[123, 146], or harassing females that are usually mate-guarded by old males. Unchecked young males have also become aggressive and killed other species[145]. In terms of reproductive success, depending on whether there is a linear dominance hierarchy amongst males for access to females and depending on the extent to which males can monopolise females, it is possible that either more younger males are able to mate (thus decreasing the variance in reproductive success) or that the fewer remaining old males are able to monopolise matings (thus increasing the variance in reproductive success).

Effective population size: the size of an ideal population that has the same amount of genetic drift as that of the real population in consideration; real populations have a smaller effective population size than the census size because of factors such as unequal adult sex ratio, temporal variation in population size, and variation in reproductive success across individuals.

Both sexes possess tusks in African elephants, and, therefore, when older females or the matriarch of a family is removed, it disrupts female social structure[107]. To cope up with such stressful situations, different family groups were seen to join together to form unusually large groups, which in turn, might lead to habitat degradation[107]. In contrast, mean family group sizes were observed to be smaller (28% of family groups had only single adult females) in North Luangwa National Park, Zambia, but this was a population in which over 93% of the elephants had been poached[109]. This also resulted in female reproductive age dropping drastically. Studies on the long-term effects of poaching on African savannah elephant females in Mikumi National Park, Tanzania, using behavioural and molecular data, found that female groups without a matriarch or closely related individuals exhibited weaker social relationships, associations with unrelated individuals, higher stress hormones, and lower reproductive output[47, 48]. In some populations, daughters may occupy their poached mothers' social positions, thus ameliorating the social effects of poaching[49].

Apart from disturbance due to poaching, habitat loss and alteration can affect social organisation and relationships. Drastic habitat loss and the accompanying elephant deaths due to the war in Vietnam has resulted in altered social organisation, with a single social group of females harbouring multiple mitochondrial DNA haplotypes[163]. This suggests that remnant females from different social groups must have come together in the wake of the disturbance. Loss of habitat or access to crop plants that leads to crop-raiding by elephants can also impact elephants by altering (improving in some cases) their body condition or size, increasing the propensity to take risks, or increasing stress[2, 25, 64], but see[117]. Different populations across elephant species have incurred human–elephant conflict to varying degrees. Whereas the adverse effects of habitat loss are better known, it is also possible to create disturbances by artificially increasing rather than decreasing resources. The proliferation of artificial waterholes in southern Africa resulted in elephants reducing their seasonality in ranging, in turn affecting the regeneration of vegetation[88], and leading to increased elephant densities[20]. Large waterbodies such as artificial reservoirs that provide abundant grass during the dry season may also result in high competition between female clans for access to the clumped resources[46]. Since social organisation and behaviour are affected by anthropogenic factors, in addition to ecological and biological factors, such factors need to be considered when comparing the social organisations of different species and populations of elephants. For instance, as mentioned in a section above, the Samburu African savannah elephant population has undergone considerable poaching compared to the Amboseli population, both of which have been studied over the long term. The Uda Walawe and Kabini Asian elephant populations use habitats that have been partly modified by the construction of dams; however, these are undisturbed compared to many Asian elephant populations, which come into more contact, and often conflict, with humans. To tease apart the influence of anthropogenic factors and ecological factors on social organisation, many more long-term studies of elephant populations are required.

Because of the different ways in which social organisation and structure can be affected by human disturbances, social factors need to be kept in mind when planning management interventions such as translocations[50], captures, or culling. Operations to cull elephants in Kruger National Park, South Africa, resulted in decimated families, orphaned elephant calves, and what was equivalent to post-traumatic stress disorder in some survivors[17]. Such negative social effects can be long-lasting[138]. Culling operations to remove the entire group have taken advantage of the matriarchal nature of the society, shooting the large females first so that the others mill around and the entire group can be killed. Translocations would be expected to be more successful if the entire social group rather than single females were translocated. Translocated females in eastern Africa were found to benefit from associating with conspecifics in the new area even if the conspecifics were not genetically related, the initial associations were with other familiar, translocated females rather than the resident females in the new area[114]. Captive Asian elephant females that were reintroduced into the wild in Thailand formed groups around calves even if they were unrelated[153]. Since male elephants disperse and adult males spend large amounts of their time solitarily, translocation of males is not expected to be as stressful as in the case of females. Adolescent captive African savannah elephant males that were released into the wild in the Okavango Delta were found to successfully integrate into the wild population[36]. However, translocation of "problem" males (who are being translocated because they get into conflict with humans due to crop-raiding) from one area to another may result in the animals returning back or the problem being translocated[38], and other elephants may also learn to raid crops from existing crop-raiders[26]. Translocations may also result in higher mortality rates, but some proportion of male and female elephants have been found to be able to integrate into the population after translocation[113, 114].

Although long-term studies are ideal to uncover social organisation, studies based on molecular data can be used when the former are not available to make decisions about translocations. For instance, Chakraborty et al.[19] used microsatellite markers and molecular sexing to genotype and sex individuals from dung samples in a high-conflict area with little forest in southern India, and found that there were discrete small social groupings of females (that possibly independently colonised the area) rather than one large clan. The results led to the suggestion that the different social groups could be managed separately in terms of translocation or capture and did not have to be considered as a single unit. Translocations would also have to take into account, social structure and population genetic structure, apart from ecological factors such as habitat suitability, resource availability, and density. Translocated groups would be expected to find it more difficult to survive in a new area if the predominant competition regime in that population is between-group contest (for example, a resident-egalitarian society) rather than within-group contest (for example, a resident-nepotistic society).

Whether the new area has a similar genetic composition to the individuals to be introduced is also a factor to be taken into account. There are instances when individuals are deliberately introduced into an area to increase diversity and prevent inbreeding (for example, see[60]—Florida panther,[91]—adder,[62]—Rocky Mountain bighorn sheep), but, generally, attempts have been made to preserve historical patterns of gene flow as there could be adaptive gene complexes in different areas. Therefore, in Asian elephants, mitochondrial and nuclear microsatellite markers have been used to examine gene flow between different areas (for example, see[158, 162]) and delineate “Management Units”[96] across which movement of individuals is not recommended. Gene flow across locations also suggests that there has been historical connectivity and makes the case for preserving or establishing corridors across these locations (for example,[89]). More ancient patterns of genetic differentiation can also be discerned based on mitochondrial and nuclear markers, and such phylogeographic or phylogenetic patterns (for example,[8, 39, 129, 162]) can be used to inform conservation and management. Molecular markers have also been used to census elephants in forests in which it is difficult to observe animals directly so that the numbers or densities of animals can be obtained (for example[33, 55, 59]).

Knowledge of social organisation and structure may also allow for informed decisions to be made relating to disease-spread and the spread of specific behaviours. Since behavioural propensities such as that to raid crops may be linked to social association (for example[26]), when individual animals are found to engage in a specific behaviour, others who are often associated with them can be monitored if such associations are known. A similar approach may be taken in the case of certain diseases since social structuring can affect disease-spread (for example, see[132]). Intestinal nematodes are highly prevalent in elephants, but these parasite loads may be low and are not significantly affected by social factors, and these parasites are not a leading cause of death[90, 111, 159]. However, more acute viral and bacterial diseases that are not commonly prevalent may show a relationship with social structure.

5 Looking Forward

Some aspects of elephant social systems have been described above (see Figs. 2 and 3 for a summary), but others remain to be understood. This is especially true of the forest-dwelling Asian and African forest elephants. Long-term studies of identified individuals of many additional populations are desirable in these species, but molecular markers can also help uncover some aspects of sociality. The former are required to better understand the types of fission–fusion dynamics shown, and how they might relate to ecological factors. They are also required to study dominance relationships between individuals, and to test predictions of socioecological theory. On the other hand, although radio-collaring dispersing males might allow us to find out whether there is social or locational dispersal, genetic studies in multiple locations would be valuable and more feasible to address this question. As mentioned above, while biased locational dispersal of males has been suggested[160], whether this is a more general pattern remains to be seen. Analyses of genetic relatedness between individuals are also required to find out whether associations between adult males are based on genetic relatedness, whether there is a relationship between relatedness and dominance relationships in females, and whether there is a relationship between relatedness and dominance relationships in males. As mentioned above, the first two questions have been examined in only one population of African savannah elephants[6, 24], and the third, not at all.

How dispersing males associate with other males and with females during their extended period of dispersal and whether they seek out or avoid relatives also remain to be studied. Similarly, when adult males rove over large areas during musth in search of receptive females, whether they can recognise paternal sisters and relatives can be examined. If adult males could recognise whether they were related or not, and there were multiple related males in same area, related males might be able to stagger musth in order to avoid competition amongst themselves for mates. Whether females can recognise paternal relatives in other clans and avoid aggressive interactions with them is also not known. These lines of thought can be explored in future studies using behavioural and molecular data.

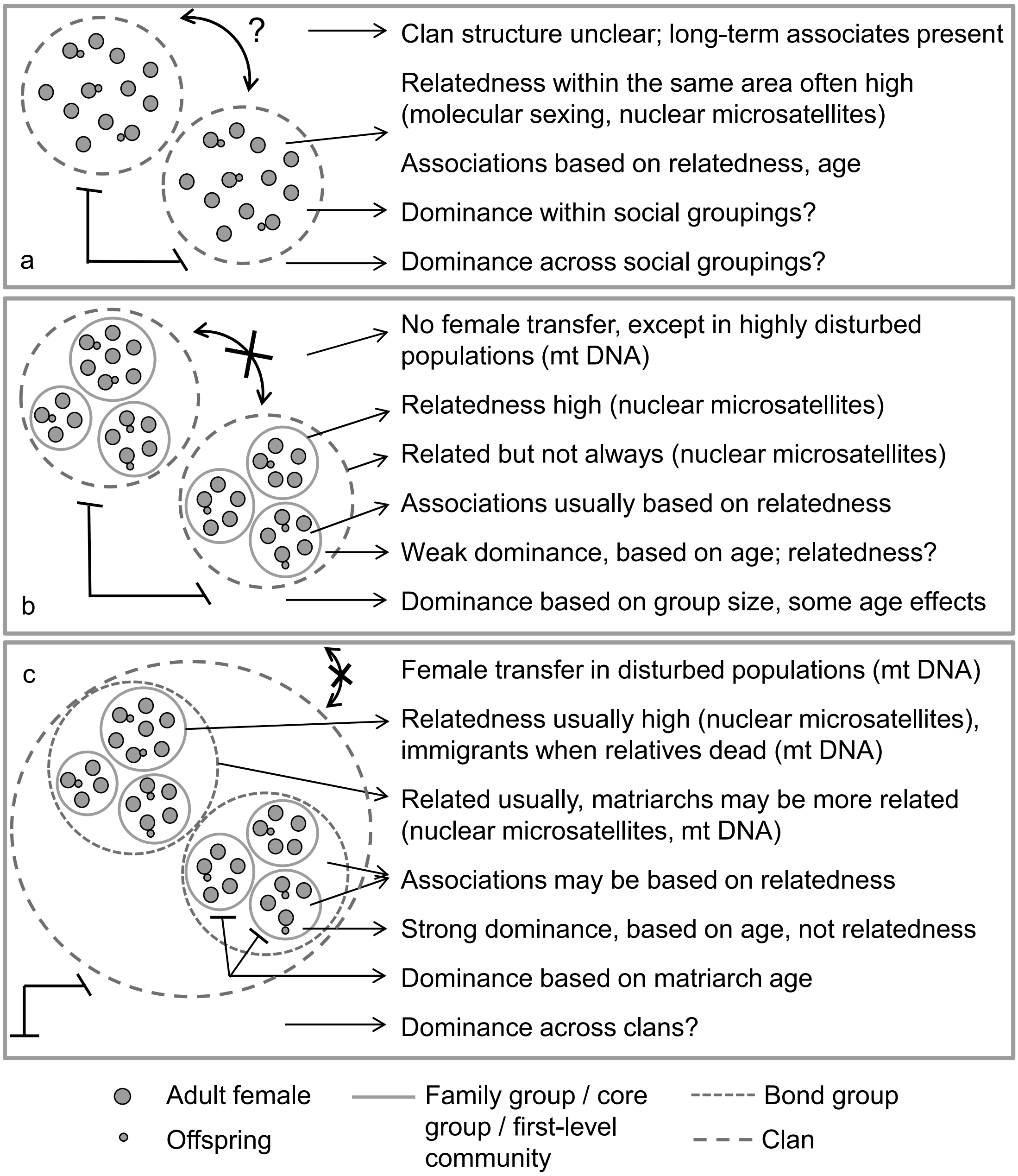

Figure 2: Summary of some salient features of female social structure in the **a** African forest elephant, **b** Asian elephant, and **c** African savannah elephant. Whether adult females within different social levels are related to one another, and upon what are associations and dominance relationships based at these levels are indicated. Groups seen in the field are not indicated here unlike in Fig. 1. A society corresponding to an individual-based fission–fusion society is shown in **a** but it is not known whether this is in fact the social organisation in African forest elephants. Only one clan is shown in (**c**) unlike in (**a**) and (**b**) because of space constraints. The question marks indicate that the answer is not yet known.

In terms of conservation, it is important to estimate the variance in reproductive success of males by carrying out paternity analyses and finding out what proportion of adult males sire offspring. This would be important in assessing the effective population size of a population. Estimating this in populations that are affected by varying degrees of ivory poaching, such as those in southern India, would be important to understand the extent to which the loss of males affects the number of breeding males. Although free-ranging elephants have been genotyped so far mostly by using microsatellite loci, advances

a	African forest elephant	- Locational dispersal? (nuclear microsatellites) - Related individuals within the same area sometimes (molecular sexing, nuclear microsatellites) - Associations based on relatedness? Age? - Dominance between males?
b	Asian elephant	- Locational dispersal (nuclear microsatellites, mtDNA), biased male dispersal? - Related individuals within the same area sometimes (nuclear microsatellites) - Associations with age-peers (older males not sought out); relatedness? - Dominance based on musth and age; relatedness?
c	African savannah elephant	- Some social dispersal; locational dispersal? - Some related individuals in the same area (nuclear microsatellites) - Associations based on age (age-peers, older males preferred), to a small extent on relatedness - Dominance based on musth and age; relatedness?

Figure 3: Summary of some salient features of male social organisation and structure in the **a** African forest elephant, **b** Asian elephant, and **c** African savannah elephant. Whether males show social or locations dispersal, whether males in the area are related to one another, and upon what are associations and dominance relationships based are indicated. Question marks indicate that the answer is not yet known or not known satisfactorily. Comments within parentheses indicate the molecular marker used so far or additional details of the results found so far.

in genomics have allowed for single-nucleotide polymorphisms (SNPs) to be identified and used from dung-extracted DNA[16, 53, 139]. SNPs may become more common for genotyping individuals and estimating the relatedness between them, and also for identifying previously genotyped animals that come into conflict (such as those raiding crops in crop fields) from their dung samples.

Finally, while we have focussed on the social systems of the living elephants, studies of genomic data, morphology, placement of fossil remains, and trackways have provided glimpses of the social organisation of extinct species. For example, genomic data and fossil numbers have suggested that the woolly mammoth had female social groups and dispersing males[112]. Analysis of trackways has suggested that an extinct Proboscidean, possibly *Stegotetrabelodon*, lived in social groups[13]. With newer molecular and other techniques, further insights into the social systems of extinct species may be obtained.

Explanations of terms used:

1. Socioecology theory: a framework to explain the evolution of different social systems across species/populations based on the differences in ecological conditions; this has largely been studied in primates.
2. Family group/core group/second-tier unit: the basic social unit of female African savan-

nah elephant social organisation, comprising one or more mother–offspring units who are likely to be related to each other.

3. First-level community: a social level comprising adult females that associate to a greater extent with each other; this is similar to a family group but is detected based on social network analysis (described in Asian elephant).
4. Bond group/kinship group/third-tier unit: a social tier found in female African savannah elephants comprising multiple family groups.
5. Agonism / agonistic interaction: an aggressive interaction that may take place between two individuals; there may or may not be a clear outcome (with a winner and a loser) of the agonistic interaction.
6. Dominance relationship/hierarchy: a relative ordering of individuals into higher and lower ranking ones based on the behaviours shown (aggressive or submissive) towards each other; more dominant individuals may be able to get priority of access to food or mates. A linear dominance hierarchy has transitive relationships while a society with weak dominance or an absence of a linear hierarchy is characterised by circular relationships within triads of individuals, and retaliation between individuals.

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Declarations

Conflict of interest

The authors declare that they have no conflict of interests.

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