

Social and reproductive behaviour in elephants

T. N. C. Vidya and R. Sukumar*

Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560 012, India

We present a review of studies on elephant social and reproductive behaviour. While the social organization of the African savannah elephant (*Loxodonta africana africana*) has been intensively studied, that of the African forest elephant (*Loxodonta africana cyclotis*) and the Asian elephant (*Elephas maximus*) are poorly understood. Noninvasive molecular methods are useful in combination with behavioural data in understanding social organization and dispersal strategies. The ecological determinants of social organization, and the importance of matriarchal leadership to social groups, and relative importance of different forms of communication under various ecological conditions remain interesting topics that await investigation. Reproductive behaviour also has been examined in detail only in the African savannah elephant, although rigorous chemical analyses continue to be carried out using captive elephants of both species. Improved laboratory techniques may enable future work on reproductive signalling in free-ranging elephants, allowing for comprehensive studies of male-male interactions and mate choice by females.

Keywords: Acoustic communication, dispersal, *Elephas maximus*, *Loxodonta africana*, musth, social organization.

ELEPHANT behaviour has fascinated humans for centuries; written accounts of their behaviour in ancient Indian poetry and literature include the *Gajasastra* (attributed to Palkapya in the 6th–5th century B.C.E.), the *Matangalila* (by Nilakantha), and several references in Tamil Sangam literature^{1–4}. Their size, strength, fierce protectiveness of young, gentleness, intelligence, and nonchalance, make elephants one of the most inspiring subjects for a study of animal behaviour. In addition, along with primates and cetaceans, elephants constitute one of the most socially advanced groups of vertebrates⁵. However, despite the charm associated with studying elephant behaviour, detailed work has been largely lacking, with the exception of the Amboseli population in Kenya in eastern Africa, perhaps due to the denser forests elephants inhabit elsewhere and the protracted studies that would be required to understand various behaviours of this long-lived animal with a lifespan of over 60 years. In this review, we describe several aspects of elephant behaviour that have been studied, their possible relevance to management, and questions that still wait to be explored. We categorize elephant behaviours as those

associated with either social integration or reproduction, although these are not necessarily mutually exclusive.

Social behaviour

Social organization

The family group in both Asian and African elephants is one that is stable and a rich source of social interactions. A complex, fluid, fission–fusion society is known in the African savannah elephant (*Loxodonta africana africana*), the basic unit of which is the mother–offspring unit, two to three such units comprising a family group headed by a matriarch⁶. The matriarch is generally the oldest adult female in a family and often a repository of critical ecological information^{7,8}, the matriarch's experience influencing and guiding the movement patterns and habitat utilization by the family group^{6,9–12}. While the matriarch is generally dominant in competitive and cooperative situations, the degree of leadership exhibited by the matriarch may vary from one family to another (unpublished long-term records of the Amboseli Elephant Research Project, <http://www.elephant-voices.org/>). The importance of the matriarch to its family groups became evident during elephant culls in the Luangwa Valley population in Zambia, during which family members became disoriented if the matriarch was shot first¹³. On the other hand, in Ruhuna National Park (Yala) in southeastern Sri Lanka, no evidence for strong matriarchal leadership has been found¹⁴, though this does not preclude the importance of the matriarch during periods of environmental or social stress. Much obviously remains to be learnt about the role of the matriarch as this has not been examined in other populations, and the effect of ecological conditions on the importance of matriarchal leadership and the dominance and reproductive fitness of matriarchs in comparison to other adult females may be topics to begin with.

In the African savannah elephant, members of a family group spend a significant (over 80% in the Amboseli population) percentage of time together, interact and behave in a coordinated manner¹², and exhibit cooperation in group defense, acquisition of resources, and care of offspring^{11,15}. A few related families may show significant social association amongst themselves and constitute 'kinship groups'⁶ or 'bond groups'¹⁶, usually formed due to the fission of a large family in the past. Families or bond groups that share a dry season (when resources are scarce) home range constitute a clan¹⁶, the most inclusive unit in this hierarchical social

*For correspondence. (e-mail: rsuku@ces.iisc.ernet.in)

structure. A clan may consist of up to several hundred elephants and clans may interact with one another during the wet season when resources are not limiting¹⁷. This social structure is thought to be quite stable, although there have been observations over the long term, of individuals changing families, bond groups, and clans (unpublished long term records of the Amboseli Elephant Research Project, <http://www.elephantvoices.org/>). A long-term study of social organization in the African forest elephant (*L. a. cyclotis*) in the Central African Republic indicates that social organization in this taxon is much simpler, usually comprising of only groups of single adult females and their offspring¹⁸.

Studies of the Asian elephant (*Elephas maximus*) have also confirmed the existence of basic units comprising mother and dependent offspring^{19–21}. Associations of two or more mother–offspring units have been variously described as ‘family groups’²² in southeastern Sri Lanka and as ‘joint family groups’ in southern India²³. Higher levels of organization including ‘bond groups’ and ‘clans’ have also been discerned in southern India^{21,24}. However, in the absence of any comprehensive behavioural study of Asian elephants, the social organization of this species remains poorly understood. The use of molecular techniques has begun to unravel pieces of the story, but a lot remains to be learnt. A study of mitochondrial DNA haplotypes (which are maternally inherited) of Asian elephants in Sri Lanka showed that all the individuals of a social group had the same haplotype, indicative of shared maternal ancestry²². More recently, in a study of genetic relatedness using nuclear microsatellite DNA, Vidya and Sukumar²⁵ have shown that the adult females of ‘family groups’ in southern India are indeed closely related, probably as a combination of mother–daughter, full sisters, and half sisters, indicating that the basic Asian elephant social group does represent a family group as in the African savannah elephant. No evidence for inter-group transfer of females has been found in the Asian elephant^{22,25} based on genetic analyses of family groups. However, a detailed behavioural and genetic study involving associations of family groups and the relatedness between them in the Asian elephant is much awaited in order to understand the additional hierarchical levels of social organization that may exist. It appears that Asian elephants in rain forests exhibit social organization that is limited to the family or bond group, somewhat similar to the situation in the African forest elephant²⁶. The simpler social organization may simply be a result of the availability of forage, or due to different social requirements or as a response to threats, and additional studies spanning different habitats are required to understand the ecological determinants of social organization.

These ecological factors would also influence the home ranges of social groups. Elephant social groups are known to show a high degree of fidelity to their home ranges^{24,27}. Home ranges vary by orders of magnitude in the African

elephant, from 14 to 52 km² in Lake Manyara National Park, Tanzania⁶ to over 5000 km² in Laikipia-Samburu, Kenya²⁸ and over 10,000 km² in Etosha National Park, Namibia²⁹. In the Asian elephant home ranges are small (~ 60 km²) in southeastern Sri Lanka²², while larger home ranges of ~ 650 km² and ~ 600 km² are found in the Nilgiris in southern India²⁴ and in Buxa Tiger Reserve in northeastern India³⁰, respectively.

As in many other sexually dimorphic mammals, adult male and female elephants live in very different societies. Pubertal African savannah elephant males, 9–18 years of age, leave their natal family group through a gradual process that may take up to four years³¹. The proximate factors leading up to the dispersal have not been well-studied. Adult males are largely solitary, but may associate with female groups or form loose associations with other males³² depending on their age and sexual state³³. Pubertal Asian elephant males also disperse from their natal groups^{21,34} when they are about 10–15 years old⁴, but it had not been clear whether they move away from their natal range³⁴ (locational dispersal) or whether they remain in their natal range and move long distances only to mate (social dispersal). Although not well-studied, there are indications that both types of dispersal may exist in the African savannah elephant³⁵. There is now some evidence for locational dispersal of males in the Asian elephant, as demonstrated by the presence of adult males of a different mitochondrial haplotype in areas with adult females of a common haplotype in central and northeastern India³⁶ and the absence of significant genetic relatedness between adult females and sub-adult and adult males within locations in the Nilgiris in southern India²⁵. Locational dispersal may increase accessibility to mates³⁷, although making it more difficult to forage in an unfamiliar area and make this form of dispersal a ‘high-cost–high-gain’ strategy. Although behavioural studies on bonding between Asian elephant bulls are entirely lacking, with the exception of possible bonding or cooperation while raiding cultivated crops^{21,23}, there is preliminary genetic evidence that points towards non-random dispersal of related bulls in southern India²⁵. We conjectured that non-random migration may be advantageous under the scenario of locational dispersal in situations of male–male conflict with new males that are encountered. This aspect has yet to be investigated in detail in both elephant species.

Communication within the social group and bonding

Communication is central to social, long-lived, intelligent, animals that can transmit information across generations. Interactions within and among elephant social groups are mediated by scent, sound, touch, and sight¹⁹, olfactory and acoustic communication appearing more critical than tactile and visual communication overall, though acoustic and tactile communication may be more important within the social group.

Visual communication: Elephants possess relatively poor vision, although they are sensitive to movement. Nevertheless, elephants of both species do exhibit an impressive array of visual displays comprising of different combinations of head, ear, eye, trunk, tail, body, feet, and postures^{9,19,35,38}. In the social context, these are used during play behaviour, aggression (charge and retreat behaviour), and possibly during greeting.

Tactile communication: Elephants are very tactile animals, using tactile communication in social groups to exhibit reassurance, affection and affiliation, exploration, aggression, and play. The elephant's trunk is extremely sensitive, being endowed with densely packed Pacinian corpuscles that can pick up minute vibrations³⁹. The trunk tip is placed in another elephant's mouth during reassurance, and on the ears, mouth, eyes, tail, and body, while greeting family members that were separated for a while⁴⁰. Elephants also rub bodies against one another in greeting, while socializing, and during play. Play behaviour is extremely tactile, with juveniles/calves scrambling onto one another, play mounting, trunk wrestling, and pushing and shoving, and allows for young animals to assess their relative strengths and prepare for future roles. Gender differences are observed during play, males tending to play more than females, playing with peers of similar age rather than with much younger individuals as females do, and playing with less familiar peers from other families unlike females⁴¹. Tactile communication also seems to be important in mother-calf interactions⁴², probably as a means of obtaining information on the state of well-being of the calf⁴³.

Olfactory communication: Elephants have a highly sensitive and sophisticated chemosensory system, olfactory signals probably being important in individual recognition^{44,45} and maintaining social cohesiveness^{46,47}. These signals are carried as chemicals in urine, faeces, temporal gland secretion, saliva, and interdigital Meibomian glands, and detected by olfactory sniffing behaviour and flehmen behaviour, in which the substance is collected on the trunk tip and lifted up into the mouth, to the opening of the vomeronasal ducts⁴⁶. Unlike Asian elephants, in which temporal gland secretion is exhibited only by males in *musth* (a period of high serum testosterone levels, see below) and occasionally faintly by females in late pregnancy or just after calving, all adult individuals and sometimes juveniles in the African savannah elephant are observed to secrete from the temporal gland. This secretion by females is associated with conditions of social excitement, stress, or fright^{12,48}. Family greetings include touching each other's temporal glands and rubbing faces, and touching the anus and genitalia of other animals^{40,48}. Temporal gland secretion, urination and defaecation are also observed during other socially exciting events such as calving, mating and group defense in the African savannah elephant³⁵.

Acoustic communication: The variety of sounds elephants can produce ranges in frequency from 10 to 14 Hz to 9000 Hz and as loud as 103 decibels at 5 m from the source^{49,50}. Repertoires of various sounds and their contexts have been compiled by McKay¹⁹ for the Asian elephant and by Poole *et al.*⁵⁰ and Poole⁵¹ for the African savannah elephant. Acoustic signals are used in short and long distance contact, conflict, threat display, nervousness, and in greeting family or bond group members. A significant proportion of acoustic communication of both Asian^{38,49} and African⁵⁰ elephants occurs through the use of low frequency sound (infrasound), some of which can be transmitted seismically through the ground. Infrasonic signals may be used to communicate with members of the family group or to maintain contact with families of the same bond group or clan and synchronize ranging patterns^{50,52}. Infrasound suffers lesser attenuation through reflection, refraction, and absorption, than high frequency sound, and is possibly more useful to forest-dwelling elephants than savannah elephants²³ as recent research seems to show (Payne and Gulick, unpublished data).

As mentioned previously, African savannah elephant family groups exhibit a fluid fission-fusion society in which they range widely, coalesce with other family groups and then split up as they feed and move from one place to another¹⁶. Therefore, when acoustic communication is used, receivers, other than those for whom the signal was intended, may also perceive the signal and learn the vocalizations of animals of various family groups in the population. In the Amboseli population, in which ranging and social associations of different family groups have been well documented since the late 1970s, McComb *et al.*⁷ used playback experiments of infrasonic contact calls to assess the extent of vocal recognition by adult females. Family groups thus tested were able to discriminate between calls of family or bond group members and those of other family units in the population with lower association indices, suggesting that adult females are familiar with the calls of a large network of about 100 adult females. In addition, older matriarchs showed less defensive behaviour and alarm in response to playback calls, probably indicating greater social confidence and/or a larger network of recognition⁸, and were also more discriminating and reactive to groups with low association indices, which could potentially be competitors. It is remarkable that families with older matriarchs also showed a higher measure of reproductive success, indicating the role that memory can play in a long-lived vertebrate by accumulating social knowledge with age, influencing the knowledge that is available to other individuals of the family group, and enhancing long-term reproductive fitness⁸. This enhanced ecological knowledge of the older matriarchs is of relevance to conservation, as older African elephant females, which usually have bigger tusks, are often the targets of ivory poachers. When such females are removed from the population, the resulting family groups

are deprived of the enhanced knowledge of the matriarch and are therefore seriously disadvantaged. Entire populations can be affected by the removal of a few matriarchs⁸. Asian elephant females do not carry tusks, but similar situations may arise if the matriarch is killed during instances of human–elephant conflict, or captured from the wild in areas where work-elephants are used.

Reproductive behaviour

Elephants are polygynous mammals and show a high degree of sexual dimorphism, with full-grown males being much larger than females. The age at sexual maturity varies between 9 and 22 years (more typically 11–14 years) in females⁴ and at least 15 (in the Asian elephant) or 24 (in the African savannah elephant) years in males. We describe the studies on oestrus and musth behaviours below.

Oestrus behaviour

The oestrus cycle of elephants is about 12–18 weeks long⁵³, comprising, as in other mammals, a follicular phase, ovulation, luteal phase, and degeneration of the corpus luteum if the egg is not fertilized. In the elephant, two successive waves of follicular development have been observed, the follicles formed in the first waves regressing to form the corpora lutea and the follicular development in the second wave resulting in a Graafian follicle that releases an egg⁵⁴. The follicular phase with low serum progestins and two sharp peaks of luteinizing hormone⁵⁵ lasts 4–6 weeks, and the luteal phase with high serum progestins lasts 8–14 weeks^{53,56}, with only a 2–10 day period of oestrus^{57,58} when the cow can conceive. Since the period of sexual receptivity is very short, it becomes important for females to attract and secure matings with high-ranking males, and for males to locate oestrus females. Females may signal their oestrus condition through auditory, chemical, and visual signals.

The ‘oestrus walk’⁵⁸ is a visual indicator of oestrus, in which the female walks away briskly from her group, with her head held high and turned to one side, and traces an arc before returning back. If pursued, the female may break out into a run and again trace an arc before returning. Females also show signs of wariness towards approaching bulls during oestrus⁵⁸. Tail-flicking behaviour, in which pre-ovulatory females slap the tip of the tail against the urogenital region and then hold it up for a few moments³⁸, may be a visual signal in addition to being olfactory (see below).

The role of olfactory signals during oestrus in elephants has been the subject of fairly intensive study^{57,59–62}. Adult males usually inspect each female of a herd with their trunks^{17,57,63} and exhibit a flehmen response if the female is in oestrus⁵⁹. A sexual pheromone (*Z*)-7-dodecen-1-yl acetate, also used by Lepidoptera⁶⁴, was identified as the compound present in the pre-ovulatory urine of female

Asian elephants that elicited non-habituating multiple flehmen responses and pre-mating behaviours from male Asian (but not African) elephants^{45,46,65}. It has also been hypothesized that the compound may prime males for sexual behaviour or stimulate musth⁶² as prolonged contact with oestrus females is thought to be important in stimulating musth in younger males⁵⁷. In addition, it has been found that females are able to detect the oestrus state of other females from chemicals in urine⁶². The tail-flicking behaviour also seems to serve as an olfactory signal to females in the group about impending oestrus since the tail hairs carry urine and mucus^{66,67}. Such female–female signals may be used to either synchronize receptivity or suppress the reproductive activity of subdominant females during lean times⁶⁸. Age, size, maternal rank, and the individual’s character may be important in determining a female’s status in the breeding hierarchy⁶⁸ and it has been seen that young subdominant females give birth during sub-optimal periods when infant mortality may be higher¹¹. This may result from the inability to acquire sufficient nutrition or due to social mechanisms. The latter may include delaying, inhibiting, or inducing infertile ovulations, chemically or by agonistic behaviour, or limiting access to mates by entering oestrus earlier or allowing copulation even while infertile in order to monopolize males¹¹. However, little attention has been paid to the subject of competition between females within elephant social groups, and these remain only hypotheses at present.

Vocalizations are often observed during or after copulation, probably to attract additional males and set up a competition between males so that high-ranking males are accessible^{62,69}.

Musth behaviour

Musth is a period of increased plasma testosterone levels, observed in adult male Asian and African elephants. It is analogous to the rutting period of several mammals but asynchronous across individuals. Although well described for Asian elephant in ancient elephant-lore and more recent studies^{63,70–72}, musth in the African elephant was discovered much later due to the confusing interpretation of temporal gland secretions from both sexes³³. Musth is characterized by the enlargement of and copious secretions from the temporal gland, persistent dribbling urine, increase in aggression towards other elephants and non-elephant objects, increased association with female herds, and increased sexual activity^{33,69}. The mean age of first musth was 29 years in Amboseli and the duration of musth was correlated with age of the elephant. Higher ranking, older males came into musth more regularly and for several months at a time, particularly when most females were in oestrus, while lower ranking males came into musth more sporadically and for short periods^{69,73}.

The following behaviours have been observed to be associated with musth: 1) ear wave during agonistic interac-

tions between males and during musth rumbling, 2) lifting the head and reaching up with the trunk to rub the temporal gland, 3) marking trees with the temporal gland area, 4) urinating with the penis inside the sheath, 5) musth walk, in which the head is held high, ears spread out stiff, and the head is swung from side to side in a controlled manner, 6) head oscillation in younger males, 7) tusking the ground, lifting up and hurling vegetation and mud, and 8) musth rumble^{69,74}. The musth rumble is a set of low-frequency context-specific calls ending with an ear wave or ear fold, given during contests with other males, during marking behaviour, in response to other low frequency sounds, and before copulation⁶⁹. Musth males rumble more often when they are alone than when with an oestrus female, and the rumble appears to elicit a vocal response from females⁶⁹. During musth, adult males visit family groups seeking out receptive females^{17,69} and, if the female is receptive, may exhibit mate guarding for a period of 2–3 days⁷⁵.

During musth, males advertise their physical and sexual state not only by giving off rumbles but also by a host of chemical signals carried in urine, temporal gland secretions, and even breath^{45,71,72,76,77}, that attract the attention of and evoke responses from females and other males^{63,76,78}. Several studies have been directed towards identifying and characterizing the specific compounds involved in musth, chemical signalling during musth^{72,76,77}, and the mechanism of reception, behavioural functionality, and relevance of the signals⁷⁹. Both Asian and African elephants in musth have significantly higher levels of testosterone and other androgens than males not in musth^{45,70,80,81}. Temporal gland secretions of Asian and African elephants have a variety of ketones that are similar across the two species^{45,72}. Studies of urinary chemicals have also been carried out; cyclohexanone, a trace chemical in the urine of Asian elephant musth males was found to elicit a response from females⁷⁹, but is also influenced by circulating testosterone concentrations in the male and the oestrus state of the female⁸². A detailed study of urinary chemicals during musth in the African elephant revealed compounds (several of which are bioactive) similar to those observed in Asian elephants, with greater numbers of ketones, alcohols, and substituted cyclohexenones than in non-musth males, whose urine contained more acids and esters⁸³. It was also discovered that young, socially immature, Asian elephant males release honey-like odours, their temporal gland secretions containing 3-hexen-1-ol, 2-heptanone and acetophenone, and several acetates, while older males release malodorous secretions, the concentrations of 3-hexen-1-ol and acetates being reduced and acetophenone being replaced by 2-nonanone, acyclic ketones, and substituted cyclohexanones that are foul smelling⁸⁴. These younger males in 'moda musth' seem to avoid conflict as older males ignore the mellifluous odours and do not consider them a threat⁸⁴.

From an evolutionary point of view, Poole⁸⁵ found that musth did not seem to be a reliable signal of fighting abi-

lity, but rather a physiological condition that the resource value is correlated with. Males in musth signal aggressive intent and these signals enable other individuals to make assessments about their roles, whether to fight for a resource or retreat⁸⁵, depending on the asymmetry in fighting ability and the asymmetry in the value of the resource⁸⁶. Since reproductive success of males increases with age and unnecessary fights may result in injury, depending on the costs and benefits from winning compared to benefits at a later possible stage, males may decide whether to exhibit musth or not⁸⁵. They may also avoid escalated contests by either utilizing different areas during musth if they are of the same fighting ability, or by dropping out of musth if they are younger or sub-dominant, or by avoiding all musth males if they are themselves not in musth⁸⁵. Therefore, musth may be opportunistic in the younger males especially, depending on the presence of dominant males in musth already and the presence of unguarded receptive females⁸⁵. In addition, musth is a physiologically stressful state⁸⁷ and therefore seems to be an honest indicator of the male's quality⁸⁵. Whether Asian elephant males also advertise their locations in order to avoid unnecessary conflicts with other males has not been studied. It would be interesting to examine male–male interactions in areas with different densities and age-distributions of adult males and adult males of different genetic relatedness.

Female mate choice

In a polygynous species like the elephant, the male can enhance its reproductive fitness by mating with as many females as possible, and the female is expected to be choosy about mating with the fittest males, in order to ensure healthy offspring. There is some evidence for female choice in both species of elephant^{75,78}. It has been observed in Amboseli that females in oestrus solicit guarding from musth males rather than non-musth males, and from older males preferentially^{58,73}. Older males are larger as elephant males continue to grow in size almost throughout their life and therefore better at mate-guarding. Thus large, dominant males, especially in musth, are able to garner most of the matings^{20,58,69}. Schulte and Rasmussen⁸² showed that females can distinguish between musth and nonmusth urine, and also between two familiar males. The response to musth or non-musth urine, however, also depends on the oestrus state of the female⁸². Females may also be able to test for approximate age and rank of the male⁸³. The extent to which a female is aware of the pool of available males and whether females show distinct preferences for particular males is however not known. The flexibility of females in choosing mates and whether they mate with young males in the absence of older males, for example, in populations subjected to past poaching also needs to be studied as this would have a bearing on the management of populations.

Discussion

As both species of elephants continue to face unrelenting threats to their survival from habitat loss and fragmentation, poaching for ivory, and human–elephant conflict, there is a need for innovative techniques for conservation and management. This is especially so given the elephants' intelligence and behavioural complexity. Knowledge of behaviour and communication in the living elephants will enable a better understanding of the species and more informed decisions on their management. For example, following the recognition of the role of the matriarch in African savannah elephant family groups, translocations of elephants in Kenya and South Africa involve entire family groups, and family groups are given sufficient time for the matriarch to organize them (<http://www.elephantvoices.org/>). Understanding the various signals associated with reproductive behaviour is important in increasing our knowledge about the elephants' mating system and improving the monitoring of reproductive activity⁶². Following standardization protocols, urine and possibly dung samples may be used from free-ranging populations and various aspects of reproduction can be examined non-invasively. The use of dung samples to study hormonal levels would take us several steps forward in addressing questions about male–male avoidance/competition, mate searching by males, female choice, and strategies used by females to synchronize or stagger ovulation. Advances in understanding reproductive behaviour would also help in captive breeding programmes and in modelling population dynamics more accurately. Work on contraceptives is also ongoing and immunocontraceptives have been designed and put to use⁸⁸ in South Africa and Kenya as an alternative to culling large numbers of elephants in over-populated parks.

Knowledge of the mechanism of olfaction and olfactory communication has been used to prevent crop raiding by elephants in Zimbabwe by using capsicum oleo-resin spray⁸⁹ that acts on the elephant's trigeminal system⁴⁶. It has been suggested that natural elephant compounds be used to tackle crop-raiding, for example by using chemical signals from a high-ranking musth male in Africa, where most of the crop-raiding males are non-musth males (<http://www.elephantvoices.org/>), or using other chemical signals for crop-raiding musth males in India⁸⁴. However, we do not advise using biologically meaningful signals in this fashion as they are likely to disrupt social structure and also affect responses to such signals in the long term. Understanding and characterizing the vocalizations of elephants has the potential of being used as tools for censuses in forests. Automated recordings from recorders set up in trees in dense forest (as is being carried out in central Africa) may yield important data on the number of individuals present and the frequency of usage of the area. They can also be used to influence the movement of elephants⁵², but again this would be invasive and perhaps suffer from the same drawbacks as with using olfactory signals.

The influence of human disturbance on elephant behaviour is also an area that requires study. With increasing human interference, qualitative data seem to suggest that elephants may be changing their behaviour, some populations becoming warier and more nocturnal and others more aggressive. The elephant is also an extremely intelligent mammal and our understanding of the higher cognitive abilities of elephants is still anecdotal. This would be a potential area for further research that would be quite challenging but at the same time very rewarding.

1. Edgerton, F., *The Elephant-love of the Hindus: The elephant Sport (Matanga-lila) of Nilakantha*, 1931, reprinted by Motilal Banarsidass, New Delhi, 1985.
2. Varadarajaiyer, E. S., *The Elephant in the Tamil Land*, Annamalai University, Annamalinagar, 1945.
3. Lahiri-Choudhury, D. K., Musth in Indian elephant lore. In *Elephants: Majestic Creatures of the Wild* (ed. Shoshani, J.), Rodale Press, Emmaus, 1992, pp. 82–84.
4. Sukumar, R., *The Living Elephants. Evolutionary Ecology, Behavior, and Conservation*, Oxford University Press, New York, 2003.
5. Wilson, E. O., *Sociobiology: The New Synthesis*, Harvard University Press, Cambridge, 1975.
6. Douglas-Hamilton, I., On the ecology and behaviour of the African elephant: the elephants of Lake Manyara. D Phil thesis, University of Oxford, Oxford, 1972.
7. McComb, K., Moss, C., Sayialel, S. and Baker, L., Unusually extensive networks of vocal recognition in African elephants. *Anim. Behav.*, 2000, **59**, 1103–1109.
8. McComb, K., Moss, C., Durant, S., Sayialel, S. and Baker, L., Matriarchs as repositories of social knowledge. *Science*, 2001, **292**, 491–494.
9. Douglas-Hamilton, I. and Douglas-Hamilton, O., *Among the elephants*, Viking Press, New York, 1975.
10. Leuthold, W., Spatial organization and strategy of habitat utilization of elephants in Tsavo National Park, Kenya. *Z. Säugetierkd.*, 1977, **42**, 358–379.
11. Dublin, H. T., Cooperation and reproductive competition among female African elephants. In *Social Behavior of Female Vertebrates* (ed Wasser, S.), Academic Press, New York, 1983, pp. 291–313.
12. Moss, C., *Elephant Memories*, William Morrow and Company, New York, 1988.
13. Hanks, J., *A Struggle for Survival – The Elephant Problem*, Country Life Books, Feltham, 1979.
14. Gunawardene, M. D., Jayasinghe, L. K. A., Fernando, P., Weerakoon, D. K. and Wikramanayake, E., Elephant social organization in southern Sri Lanka. Abstract in The Proceedings of the Symposium on Human–Elephant Relationships and Conflicts, Colombo, International Elephant Foundation, and Biodiversity and Elephant Conservation Trust, Sri Lanka, 2003.
15. Lee, P. C., Allomothering among African elephants. *Anim. Behav.*, 1987, **35**, 278–291.
16. Moss, C. and Poole, J., Relationships and social structure of African elephants. In *Primate Social Relationships* (ed Hinde, R.), Blackwell Science, Boston, 1983, pp 315–325.
17. Poole, J. H. and Moss, C. J., Elephant mate searching: Group dynamics and vocal and olfactory communication. In *The Biology of Large African Mammals in their Environment* (eds Jewell, P. A., and Maloiy, G. M. O.), Symposia of the Zoological Society of London, Clarendon Press, Oxford, 1989, vol 61, pp. 111–125.
18. Turkalo, A. and Fay, J. M., Studying forest elephants by direct observation: preliminary results from the Dzanga clearing, Central African Republic. *Pachyderm*, 1995, **20**, 45–54.

19. Mc Kay, G. M., The ecology and behavior of the Asiatic elephant in southeastern Ceylon. *Smithsonian Contrib. Zool.*, 1973, **125**, 1–113.
20. Kurt, F., Remarks on the social structure and ecology of the Ceylon elephant in the Yala National Park. In *The Behaviour of Ungulates and its Relation to Management* (eds Geist, V. and Walther, F), International Union for Conservation of Nature and Natural Resources, Morges, 1974, vol. 2, pp. 618–634.
21. Sukumar, R., *The Asian Elephant: Ecology and Management*, Cambridge University Press, Cambridge, 1989.
22. Fernando, P. and Lande, R., Molecular genetic and behavioural analysis of social organization in the Asian elephant (*Elephas maximus*). *Behav. Ecol. Sociobiol.*, 2000, **48**, 84–91.
23. Sukumar, R., *Elephant Days and Nights: Ten Years with the Indian Elephant*, Oxford University Press, New Delhi, 1994.
24. Baskaran, N., Balasubramanian, S., Swaminathan, S. and Desai, A. A., Home range of elephants in the Nilgiri Biosphere Reserve, south India. In *A Week with Elephants* (eds Daniel, J. C. and Datye, H. S.), Bombay Natural History Society, Oxford University Press, Bombay, 1995, pp. 296–313.
25. Vidya, T. N. C. and Sukumar, R., Social organization of the Asian elephant (*Elephas maximus*) in southern India inferred from microsatellite DNA. *J. Ethol.*, 2005, **23**, 205–210.
26. Khan, M., *The Malayan Elephant: A Species Plan for its Conservation*, Department of National Parks, Kuala Lumpur, 1992.
27. Desai, A. A., The home range of elephants and its implications for the management of the Mudumalai Wildlife Sanctuary, Tamil Nadu. *J. Bombay Nat. Hist. Soc.*, 1991, **88**, 145–156.
28. Thouless, C. R., Home ranges and social organization of female elephants in northern Kenya. *Afr. J. Ecol.*, 1996, **34**, 284–297.
29. Lindeque, M. and Lindeque, P. M., Satellite tracking of elephants in northwestern Namibia. *Afr. J. Ecol.*, 1991, **29**, 196–206.
30. Sukumar, R. *et al.*, Study of the elephants in Buxa Tiger Reserve and adjoining areas of northern West Bengal and preparation of conservation action plan. Final Report submitted to the West Bengal Forest Department, Centre for Ecological Sciences, Indian Institute of Science, Bangalore, 2003.
31. Lee, P. C. and Moss, C. J., The social context for learning and behavioural development among wild African elephants. In *Mammalian Social Learning: Comparative and Ecological Perspectives* (eds Box, H. O. and Gibson, K. R.), Cambridge University Press, Cambridge, 1999, pp. 102–125.
32. Croze, H., A modified photogrammetric technique for assessing age-structures of elephant populations and its use in Kidepo National Park. *E. Afr. Wild. J.*, 1972, **10**, 91–115.
33. Poole, J. H. and Moss, C. J., Musth in the African elephant, *Loxodonta africana*. *Nature*, 1981, **292**, 830–831.
34. Desai, A. and Johnsingh, A. J. T., Social organization and reproductive strategy of the male Asian elephant (*Elephas maximus*). *Abstract in A Week with Elephants* (eds Daniel, J. C. and Datye, H. S.), Bombay Natural History Society and Oxford University Press, Bombay, 1995, pp. 532.
35. Poole, J. H., *Coming of Age with Elephants*, Hyperion Press, New York, 1996.
36. Vidya, T. N. C., Fernando, P., Melnick, D. J. and Sukumar, R., Molecular genetic structure and conservation of Asian elephant (*Elephas maximus*) populations across India. *Anim. Conser.*, 2005, in press.
37. Greenwood, P. J., Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.*, 1980, **28**, 1140–1162.
38. Krishnan, M., An ecological survey of the larger mammals of peninsular India: the Indian elephant. *J. Bombay Nat. Hist. Soc.*, 1972, **69**, 297–321.
39. Rasmussen, L. E. L. and Munger, B., The sensorimotor specializations of the trunk tip of the Asian elephant, *Elephas maximus*. *Anat. Rec.*, 1996, **246**, 127–134.
40. Moss, C. J., *Portraits in the Wild*. University of Chicago Press, Chicago, 1982, 2nd edn.
41. Lee, P. C., Early social development among African elephant calves. *Natl. Geogr. Res.*, 1986, **2**, 388–401.
42. Nair, P. V., Studies on the development of behaviour in the Asiatic elephant. Ph D thesis, Indian Institute of Science, Bangalore, 1983.
43. Gadgil, M., Hegde, M., Joshi, N. V. and Gadgil, S., On the communication of well-being. *Proc. Indian Acad. Sci. (Anim. Sci.)*, 1985, **94**, 575–586.
44. Buss, I. O., Rasmussen, L. E. and Smuts, G. L., The role of stress and individual recognition in the function of the African elephant's temporal gland. *Mammalia*, 1976, **40**, 437–451.
45. Rasmussen, L. E. L., Hall-Martin, A. and Hess, D. L., Chemical profiles of African bull elephants (*Loxodonta africana*): physiological and ecological implications. *J. Mammal.*, 1996, **77**, 422–439.
46. Rasmussen, L. E. L., Chemical communication: An integral part of functional Asian elephant (*Elephas maximus*) society. *Ecoscience*, 1998, **5**, 410–426.
47. Rasmussen, L. E. L. and Krishnamurthy, V., How chemical signals integrate Asian elephant society: the known and the unknown. *Zoo Biol.*, 2000, **19**, 405–423.
48. Brown, R. E., The primitive ungulates: orders Tubulidentata, Proboscidea, and Hyracoidea. In *Social Odours in Mammals* (eds Brown, R. E. and McDonald, D. W.), Clarendon Press, Oxford, 1985, vol. 1.
49. Payne, K. B., Langbauer Jr., W. R. and Thomas, E. M., Infrasonic calls of the Asian elephant (*Elephas maximus*). *Behav. Ecol. Sociobiol.*, 1986, **102**, 283–316.
50. Poole, J. H., Payne, K. B., Langbauer Jr., W. R. and Moss, C. J., The social contexts of some very low frequency calls of African elephants. *Behav. Ecol. Sociobiol.*, 1988, **22**, 385–392.
51. Poole, J. H., Signals and assessment in African elephants: Evidence from playback experiments. *Anim. Behav.*, 1999, **58**, 185–193.
52. Langbauer Jr., W. R., Payne, K. B., Charif, R. A., Rapaport, L. and Osborn, F., African elephants respond to distant playbacks of low-frequency conspecific calls. *J. Exp. Biol.*, 1991, **157**, 35–46.
53. Hess, D. L., Schmidt, A. M. and Schmidt, M. J., Reproductive cycle of the Asian elephant (*Elephas maximus*) in captivity. *Biol. Reprod.*, 1983, **28**, 767–773.
54. Brown, J. L., Reproductive endocrine monitoring of elephants: an essential tool for assisting captive management. *Zoo Biol.*, 2000, **19**, 347–367.
55. Kapustin, N., Critser, J. K., Olson, D. and Malven, P. V., Nonluteal estrous cycles of 3-week duration are initiated by anovulatory luteinizing hormone peaks in African elephants. *Biol. Reprod.*, 1996, **55**, 1147–1154.
56. Plotka, E. D., Seal, U. S., Zaremka, F. R., Simmons, L. G., Teare, A., Phillips, L. G., Hinshaw, K. C. and Wood, D. G., Ovarian function in the elephant: luteinizing hormone and progesterone cycles in African and Asian elephants. *Biol. Reprod.*, 1988, **38**, 309–314.
57. Jainudeen, M. R., Eisenberg, J. F. and Tilakeratne, N., Oestrous cycle of the Asiatic elephant, *Elephas maximus*, in captivity. *J. Reprod. Fertil.*, 1971, **27**, 321–328.
58. Moss, C., Oestrous behaviour and female choice in the African elephant. *Behaviour*, 1983, **86**, 167–196.
59. Rasmussen, L. E. L., Schmidt, M. J., Henneous, R., Groves, D. and Daves, G. D., Asian bull elephants: flehmen-like responses to extractable components in female elephant oestrus urine. *Science*, 1982, **217**, 159–162.
60. Rasmussen, L. E. L., Schmidt, M. J. and Daves, G. D., Chemical communication among Asian elephants. In *Chemical Signals in Vertebrates: Evolutionary, Ecological, and Comparative Aspects* (eds Duvall, D., Silverstein, M., Muller-Schwarze, D.), Plenum Press, New York, 1986, pp. 627–645.
61. Rasmussen, L. E. L., Lee, T. D., Daves, G. D. and Schmidt, M. J., Female–male pheromones of low volatility in the Asian elephant, *Elephas maximus*. *J. Chem. Ecol.*, 1993, **19**, 2115–2128.

62. Rasmussen, L. E. L. and Schulte, B. A., Chemical signals in the reproduction of Asian (*Elephas maximus*) and African (*Loxodonta africana*) elephants. *Anim. Reprod. Sci.*, 1998, **53**, 19–34.
63. Eisenberg, J. F., McKay, G. M. and Jainudeen, M. R., Reproductive behaviour of the Asiatic elephant (*Elephas maximus* L.). *Behaviour*, 1971, **38**, 193–225.
64. Rasmussen, L. E. L., Lee, T. D., Roelofs, W. L., Zhang, A. and Daves, G. D. Jr., Insect pheromone in elephants. *Nature*, 1996, **379**, 684.
65. Rasmussen, L. E. L., Lee, T. D., Zhang, A., Roelofs, W. L. and Daves, G. D. Jr., Purification, identification, concentration and bioactivity of (Z)-7-dodecen-1-yl acetate: sex pheromone of the female Asian elephant, *Elephas maximus*. *Chem. Senses*, 1997, **22**, 417–438.
66. Rasmussen, L. E. L., Evolution of chemical signals in the Asian elephant, *Elephas maximus*: behavioural and ecological influences. *J. Biosci.*, 1999, **24**, 241–251.
67. Rasmussen, L. E. L., Lazar, J. and Greenwood, D. R., Olfactory adventures of elephantine pheromones. *Biochem. Soc. Trans.*, 2003, **31**, 137–141.
68. Sikes, S., *The Natural History of the African Elephant*, Weidenfeld and Nicolson, London, 1971.
69. Poole, J. H., Rutting behavior in African elephants: the phenomenon of musth. *Behaviour*, 1987, **102**, 283–316.
70. Jainudeen, M. R., Katongole, C. B. and Short, R. V., Plasma testosterone levels in relation to musth and sexual activity in the male Asiatic elephant, *Elephas maximus*. *J. Reprod. Fertil.*, 1972, **29**, 99–103.
71. Rasmussen, L. E. L., Buss, I. O., Hess, D. L. and Schmidt, M. J., Testosterone and dihydrotestosterone concentrations in elephant serum and temporal gland secretions. *Biol. Reprod.*, 1984, **30**, 352–362.
72. Rasmussen, L. E. L., Haight, J. and Hess, D. L., Chemical analysis of temporal gland secretions collected from an Asian bull elephant during a four-month musth episode. *J. Chem. Ecol.*, 1990, **16**, 2167–2181.
73. Poole, J. H., Sex differences in the behavior of African elephants. In *The Differences between the Sexes* (eds Short, R. and Balaban, E.), Cambridge University Press, Cambridge, 1994, pp. 331–346.
74. Kahl, M. P. and Armstrong, B. D., Visual displays of wild African elephants during musth. *Mammalia*, 2002, **66**, 159–171.
75. Poole, J. H., Mate guarding, reproductive success and female choice in African elephants. *Anim. Behav.*, 1989, **37**, 842–849.
76. Rasmussen, L. E. L., Chemosensory responses in two species of elephants to constituents of temporal gland secretion and musth urine. *J. Chem. Ecol.*, 1988, **16**, 687–711.
77. Rasmussen, L. E. L., Gunawardena, R. A. and Rasmussen, R. A., Do Asian elephants, especially males in musth, chemically signal via volatiles in breath? *Chem. Senses*, 1997, **22**, 775.
78. Eisenberg, J. F. and Lockhart, M., An ecological reconnaissance of Wildpattu National Park. *Smithsonian Contrib. Zool.*, 1972, **101**, 1–117.
79. Perrin, T. E. and Rasmussen, L. E. L., Chemosensory responses of female Asian elephants (*Elephas maximus*) to cyclohexanone. *J. Chem. Ecol.*, 1994, **20**, 2577–2586.
80. Poole, J. H., Kasman, L. H., Ramsey, E. C. and Lasley, B. L., Musth and urinary testosterone concentrations in the African elephant (*Loxodonta africana*). *J. Reprod. Fertil.*, 1984, **70**, 225–260.
81. Niemuller, C. and Liptrap, R. M., Altered androstenedione to testosterone ratios and LH concentrations during musth in the captive male Asian elephant (*Elephas maximus*). *J. Reprod. Fertil.*, 1991, **99**, 617–625.
82. Schulte, B. A. and Rasmussen, L. E. L., Signal-receiver interplay in the communication of male condition by Asian elephants. *Anim. Behav.*, 1999, **57**, 1265–1274.
83. Rasmussen, L. E. L. and Wittemyer, G., Chemosignaling of musth by individual wild African elephants (*Loxodonta africana*): implications for conservation and management. *Proc. R. Soc. London, B, Biol. Sci.*, 2002, **269**, 853–860.
84. Rasmussen, L. E. L., Riddle, H. S. and Krishnamurthy, V., Mellifluous matures to malodorous in musth. *Nature*, 2002, **415**, 975–976.
85. Poole, J. H., Announcing intent: the aggressive state of musth in African elephants. *Anim. Behav.*, 1989, **37**, 140–152.
86. Parker, G. A. and Rubenstein, D. I., Role assessment reserve strategy, and acquisition of information in asymmetric animal contests. *Anim. Behav.*, 1981, **29**, 221–240.
87. Chandrasekharan, K., Radhakrishnan, K., Cheeran, J. V., Muralidharan, K. N. and Prabhakaran, T., Some observations on musth in captive elephants in Kerala (India). In *The Asian Elephant: Ecology, Biology, Diseases, Conservation and Management* (eds Silas, E. G., Nair, M. K. and Nirmalan, G.), Kerala Agricultural University Press, Vellanikkara, 1992, pp. 71–75.
88. Fayrer-Hosken, R. A., Grobler, D., Van Altena, J. J., Bertschinger, H. J. and Kirkpatrick, J. F., Immunocontraception of African elephants: a humane method to control elephant population without behavioural side effects. *Nature*, 2000, **407**, 149.
89. Osborn, F. V. and Rasmussen, L. E. L., Evidence for the effectiveness of an oleo-resin capsicum aerosol as a repellent against wild elephants in Zimbabwe. *Pachyderm*, 1995, **20**, 55–64.