

African elephant social structure:
Visual, tactile, and acoustic communication that underlies social behaviour.

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Social Structure:

There are few species in the animal kingdom that live together in permanent social groups. The development of close and enduring social relationships between members is seen in many non-human primates, some marine mammals, social carnivores, and Asian and African elephants (Sukumar, 2003). Elephants are similar to other social species in that they form close social bonds preferentially with kin, however, they are different because the relationships they form are unusually fluid and rival chimpanzees and humans in their complexity (Archie et al, 2011). These social relationships are thought to have evolved through the benefits of protection afforded an individual, better attainment of resources, reduced parasite loads, mate selection, and rearing offspring (Stacey and Ligon, 1991). There are also costs to social living such as intensified competition. To balance these costs and benefits, elephants have developed a “fission-fusion” society that enables them to react to changing environmental conditions (such as drought). This “fission and fusion” of social relationships in elephants is seen in short-term grouping dynamics and long-term permanent associations (Moss and Lee, 2011). Female elephants live in matrilineal groups led by the oldest female or matriarch, which change in size and composition over time, with some family units joining temporarily and other families occasionally associating with males. Males have an equally large network of relationships as females within and beyond the population; however, males live an almost completely separate social life from females once independent after they leave the family between 8 and 16 years old (Poole, 1982; Lee and Moss, 1999).

The social context in which a female finds herself is dynamic from day to day and may also vary over the long-term with the splitting off of one family group or the fusing of two family groups into one (Moss and Lee, 2011). A female is often part of several tiers of social structure

with the most basic level her offspring followed by a matriarch-led family unit, bond group, clan, sub-population, and population (Moss, 1981; Wittemyer et al, 2005). The family unit is defined by Buss and Smith (1966) as “an adult female and its offspring, or two or more closely related females and their offspring. These units usually number 4 to 15 individuals, their activities are closely coordinated, and large bulls seen with them are generally attached loosely and temporarily”, and in 1972 the family unit was confirmed as the basic social unit of elephant society by Douglas-Hamilton (Figure 1).



Figure 1: Family unit drinking within A/B bond group in Pongola

Elephant families will often join other families for periods of time and if these families are frequently associated together and display affiliative behaviour (greeting and touching) between members they are called a bond group. Bond groups often form when a family breaks into two units so that these families spend more time together than other families in the population (Moss, 1981). Archie and others (2006) showed that members assigned to a bond group are usually related, particularly the two oldest females.

There are many factors that affect the fission and fusion of elephant society. Elephant families show a high degree of cohesion between related family units; however, females appear to have the choice of whether to associate with other members of her family or not (Moss and Lee, 2011). The only time a female is likely to be alone is when she is in estrous or sick and very old; these individuals tend to move on their own weeks or months before dying (Moss and Lee, 2011). Ecological stress has a greater influence on the gregariousness of families and only a slight effect on the cohesion of the family unit. Group size tends to be the highest during times of

high rainfall and abundant forage, but when the dry season comes, group size becomes smaller and families do not associate with other families to the same extent as during the wet season (Moss and Lee, 2011). Since elephant families are only slightly bigger than a particular individual female and her offspring, there is lower pressure for a family to split and family cohesiveness remains fairly stable. Cohesiveness may decrease in times of drought when females move and feed in smaller groups to avoid competition and energy costs of foraging (Mutinda et al, 2011); therefore, a female may forage with just her offspring, weighing the costs and benefits of grouping. When a female breaks away from the group with her young offspring she loses the benefits of grouping, the predation risk for her calf is increased, and younger females who split to reduce competition may also lose the knowledge provided by the matriarch. Matriarchs are repositories of knowledge that know migration routes, where to find food and water during drought, and how to avoid predators (McComb et al, 2001); older and more dominant matriarchs will tend to attract other elephants in temporary or permanent fusion due to the influence they have. Other benefits of group living include help in care of calves, contact with mates and mate choice (Poole and Moss, 1989; Rasmussen, 2005), the enhancement of socialization opportunities and opportunities to gain knowledge from familiar and unfamiliar individuals (Lee, 1986; McComb et al, 2003), and opportunities for learning and the transmission of information (Lee and Moss, 1999). These benefits of social grouping may explain the grouping behaviour of the Amboseli elephants where the influence of ecological factors was found to be less than other elephant populations (Moss and Lee, 2011). The seasonal shift of food types and habitats by female elephants in Amboseli was conducted more as social maximizers than energy maximizers; the largest possible group size was maintained for as long as possible even with some cost to energy intake (Lindsay, 1994), but once the costs passed some kind of threshold, the

elephants broke up into smaller family units. The benefits of family living are clear in how the Amboseli elephants prolong the larger elephant grouping, showing that the other combined benefits may outweigh the energy restrictions due to foraging in larger groups (Moss and Lee, 2011).

Elephant society is characterized by dominance hierarchies within females as well as males. In female groups, the matriarch is the most dominant female that makes decisions foraging decisions and decides when to leave a large group or when to join with another family (Mutinda et al, 2011). Douglas-Hamilton observed that female elephants have a strong age-related system of dominance based on kinship, age, and size with other females subordinate to the matriarch (Douglas-Hamilton, 1972). Evidence of this observation was found by Lee (1987) who showed 89% of older and larger females dominated young and smaller females in direct avoidance or direct contact interactions. There are very few overt competitive or aggressive interactions seen within the family but those that do occur are won by an older and larger female (Wittemyer and Getz, 2007). Nepotism was thought to have played a role in dominance interactions or the succession of a matriarch; however, Archie and others (2006) showed that this wasn't the case. In male elephants, dominance is related to age and size where older, larger males out-compete younger males for food, and older males threaten young and males and challenge large males (Poole, 1982). Aggression is high in mature males especially during musth (7.5 events/hour during musth and 3.5 events/hour not in musth, Poole, 1982). Musth is a time of heightened sexual and aggressive behaviour in male elephants that are approximately 25 years or older (Poole, 1987a). Males in musth interact aggressively with other large adult males (particularly those in musth), and spend much of their time searching for, attempting to gain access to and guarding oestrous females (Moss, 1983; Poole, 1987a). A large, dominant male in

musth often suppresses musth in smaller males. Musth has an interesting effect on dominance ranking in that a musth male is dominant over all other non-musth males regardless of size (Poole, 1989a).

In conclusion, female elephants live in a complex elephant society that is defined by multi-tiered relationships between individuals and families. The family unit of a female and her offspring are the core component of elephant society, with bond groups occurring between families that may have a closer degree of kinship than other families. Group living has many benefits can sometimes outweigh the energy restrictions due to foraging in larger groups. However, at some point ecological stress will cause large elephant groups to break into smaller families and even then some females will split from the family with their own offspring. This shows that female elephants are flexible their choices of group size and who they associate with. Dominance exists in both males and females, but dominance interactions are rare within family units. Dominance in both males and females is related to size and age, however, musth in males can skew this generalization so that a small musth male is dominant over a larger and older non-musth male.

Visual and Tactile Communication:

African elephants have complex ways of communicating with each other that involve olfactory, visual, tactile and auditory signals. Extensive work has been done on auditory communication and elephant calls in the range of infrasound which is lower than the range of human hearing. Work has also been done on olfactory communication, but mostly with captive elephants (mainly Asian elephants). The majority of tactile and visual communication has been described when the behaviour explains other social or sexual behaviours such as musth, oestrous

or female selection; however, Kahl and Armstrong have tried to compile a complete ethogram of African elephant behaviour with 83 ritual visual and tactile movements named in 2000 (Kahl and Armstrong, 2000). The book that extensively describes these behaviours by analyzing hours of video footage, *Ethology of the elephant in Zimbabwe*, by Kahl and Armstrong is currently in press. Meanwhile, Poole and Granli wrote descriptions for the 83 behaviours using input from Kahl and Armstrong, thousands of photographs, long-term observations, and descriptions from the literature; as a result of their work the database, www.ElephantVoices.org, was created (Poole and Granli, 2009). Poole and Granli used the information from their database to further describe elephant tactile and visual signals in the book *The Amboseli Elephants: A Long-Term Perspective on a Long-Lived Mammal*. Here they categorized tactile and visual behaviours into Aggressive, Ambivalent, Socially Integrative, Mother-Offspring, Group Defense, Sexual, Play and Generally Attentive. The behaviours in each of these categories are described in context of the Pongola elephants where the behavioural ethogram is not as extensive as that described by Poole and Granli (2011).

Aggressive Behaviour

Threat

The behaviour that falls into the aggressive category is often that which is related to dominance and is directed at a single individual. Elephants are capable of threatening an antagonist (elephant, human, or other) by simply turning to face the other head on with head high and ears lifted (Kahl and Armstrong, 2000). An elephant may also purposefully walk towards an individual and sometimes only one step is enough to elicit a reaction (Poole 1987a, 1989a). This may also be considered a non-physical displacement if the receiving elephant moves away from



Figure 2: Matriarch of orphan herd shows alert behaviour and ear folding

the acting elephant. In addition to standing tall or advancing forward, an elephant may also spread its ears and fold back the bottom so that a prominent ridge appears (Figure 2) (Moss, 1988). It should be noted that Poole and Granli (2011) report that ear folding may be an affiliative behaviour if it is

accompanied with head-raising, ear raising or rapid ear flapping. Head-shaking expresses an elephant's irritation at an individual or circumstance and causes the ears to flap sharply and the dust to fly (Figure 3) (Langbauer, 2000). A sharp sound can also accompany the ear flap which contributes to the display (Payne and Langbauer, 1992). To frighten potential predators such as lions or human, or a rival elephant, elephants may swing the trunk while stepping or lunging forward while blowing air through the trunk (Poole, 1987a). The trunk swing can be escalated to throwing debris such as large shrubs and small trees in the general direction of an opponent; an elephant's aim can be quite accurate even from a distance away (Poole, 1987a; Kahl and Armstrong, 2000).



Figure 3: Head shake by musth bull, Shayisa

Escalation

Aggressive behaviour such as that described under threat, can escalate into lunging, rushing at, chasing after and physical contact (Poole and Granli, 2011). An elephant may pursue an adversary by running or chasing after them (Poole, 1987a; Lee, 1986), which can take the form of a mock charge or real charge. A mock charge involves the elephant rushing towards an

opponent or predator with its head high and ears spread, stopping short of its target (Douglas-Hamilton, 1976). After stopping, an elephant may kick dirt in the direction of the adversary or swing their trunk (Poole and Granli, 2009). A mock charge is often associated with a shrill trumpet blast (Douglas-Hamilton, 1972). A mock charge was seen by a young bull elephant,



Figure 4: Mock charge by young bull, Kohlewe

Kohlewe, on Pongola Game Reserve (PGR) (Figure 4). The individual was alone purposefully walking in the northern part of the reserve without any clear direction (changed direction multiple times as if searching). We followed this elephant trying to get a sighting in order to do a focal observation. Finally he was along the side of the road in an open area so we could start a focal. During the focal, he started to head towards the road so we passed him to get ahead. After this move, he entered the road and started a pursuit after us with ears spread. We quickly drove away and he stopped, kicked dirt in our direction, and trumpeted shrilly. He clearly signaled that we were a nuisance and we left him alone without any further attempt at observation.

A contact charge or real charge is when an elephant rushes at another with the intent of following through. The head may be held high or low and the ears are spread out during the charge with the trunk held under so the tusks make contact first; a real charge is also usually silent (Kahl and Armstrong, 2000). Buga, the late matriarch of the A/B herd at PGR, was accused of contact charging game vehicles and rolling them over. She would pretend to feed and silently charge the vehicle with no threat behaviour as warning. This happened twice and there was finally an order to destroy the elephant to prevent injuries to guests and staff of PGR. It is more common in females to lower their head while charging and bow their neck so that the tusks are

horizontal, bringing her head and tusks to the level of the victim (Kahl and Armstrong, 2009). Elephants may work together to threaten or pursue an adversary through coalition or a group charge. In coalition, an older female or matriarch may assist a younger family member; standing parallel to each other they may advance towards, run after, or bow neck charge the adversary (Poole and Granli, 2011). A group charge is where an entire family charges towards an antagonist in a highly coordinated manner en masse (Ben-Shahar, 1999). This display is often associated with anti-predator behaviour. Male elephants take aggressive behavioural displays to a new level especially during musth, rushing towards each other in the attempt to gore the other male with his tusks. Males face towards each other, interlocking tusks, pushing against one another in an attempt to maneuver the other individual into a position where he can be gored (Figure 5); this behaviour is referred to as dueling (Poole and Granli, 2011). In some instances elephants will displace their aggression, threatening or attacking a nearby elephant or human that was not involved in the initial disturbance (Ben-Shahar, 1999). Researchers and elephant monitors must be aware of elephant threat behaviour to recognize when to back off and give elephants more space, especially if it is likely that a disturbance will be displaced onto the observing person.



Figure 5: Dueling behaviour between two young males

Submission

Elephants have social hierarchies that are developed through submissive and dominant behavioural displays. Submissive behaviour is displayed by one elephant towards another

elephant that is higher ranking. A submissive elephant will keep its head low (below the shoulder blades) to appear smaller. This may also be an appeasement display that suppresses aggression in a more dominant individual (Poole and Granli, 2011). This type of behaviour is often seen in younger males in the presence of a musth male. Lower ranking elephants also show submission by turning their rear end towards the dominant elephant or backing towards them (Kahl and Armstrong, 2000; Langbauer, 2000). To avoid conflict an elephant can retreat away from the aggressor by backing away (Kuhme, 1961), or turning and walking away with a wary look back (Poole, 1987a). If an elephant is being pursued during escalated aggression, the reaction is to run away from the aggressor (Poole, 1982).

Ambivalent Behaviour

Ambivalent behaviour involves displays where the elephant is unsure of what action to take or behaviour that seems inappropriate or irrelevant to the situation in which it occurs (Poole and Granli, 2011). In some



Figure 6: Dust bathing by bull elephant, Lucky

conflict situations elephants may throw grass or dirt on themselves, or pluck at vegetation as if eating but may not ingest any of it or may only do so distractedly (Sukumar, 1994). This behaviour is different from dust bathing or grooming behaviour where an elephant throws dirt on themselves to cool down (Figure 6). One of the young bull elephants, Asiphephe, displayed this displaced feeding behaviour when dominance interactions occurred between him and two other young bulls, Kohlewe and Khumbula. Asiphephe picked up grass, taking a few mouthfuls and then threw the rest of it in the direction of the other two bulls. Apprehensive behaviour occurs when elephants are unsure of a situation and how to react. An elephant may stand in one place

and twist the tip of its trunk back and forth (Poole, 1999a), or an individual may stand and swing



Figure 7: Trunk to face contact by Kohlewe

one of its forelegs intermittently (Moss, 1988). A distinct sign of uneasiness in elephants is when they display trunk to face contact (Figure 7). This is where an individual touches their face, mouth, ear, trunk, tusk, or temporal gland for reassurance (Kahl and Armstrong, 2000). Another distinct sign of apprehension or uneasiness is *Temporin* secretion from the temporal gland between the eye and ear. If an

elephant is highly excited or disturbed it may raise its tail and (Poole, 1999a). This was seen when Khumbula was frightened by guards patrolling by bicycle. He stared at them intently with ears spread and then turned and retreated at a run with raised tail, quickly looking behind him (Figure 8). The gait that he exhibited is referred to as a panic run and if elephants are in a group when frightened, they bunch together (Moss, 1988).



Figure 8a: Khumbula sees patrollers on bicycles



Figure 8b: Khumbula turns and runs from bikers.

Social Integrative

Affiliative

Elephants are highly social animals and engage in behaviours that help to maintain and strengthen the social bonds between family units and bond group members. One family member may initiate body contact by rubbing their head or side against the other individual (Lee, 1987). Elephants greet each other with the display of trunk in mouth where the one individual puts their trunk toward or in the mouth of another (Moss, 1981). This greeting is

used between non-relatives, especially males (Figure 9). This behaviour is used to reassure calves but also used as a part of social learning where calves place their trunk in the mouths of older individuals to test food (Lee and Moss, 1999). Rapid ear flapping can also accompany a



Figure 9 : Greeting between two adult females

greeting and may occur during other excited social interactions. As excitement increases during greetings or bonding interactions, elephants vocalize with rumbles, roars, or screams. In social events such as greetings,

births, calf rescues and matings, more exuberant displays occur including gathering, spinning, trunk grasping, and tusk clicking. In situations of high social arousal, family or bond members may gather into a close cluster, pressing their bodies against one another. While in the cluster they may turn toward and away from each other in a display called spinning, vocalizing loudly the duration of the display (Moss, 1988). Male-male greetings take on a different character to that between family members. Male greetings are not as vocal as the female family groups with just a few rumbles instead of the excited vocalization (Poole and Granli, 2011). The trunk in mouth greeting of males is also slower and may lead to the sniffing of one another's temporal glands and genitals, apparently to gather information on the other's sexual state and identity (Rasmussen, 1988). Body contact can also serve to maintain space around an individual or ensure proximity of other elephants. When moving in a group, a push can encourage the herd to keep moving together and a forceful tail swat may be used as warning for an elephant behind it to back off (Kahl and Armstrong, 2000). A gentler tail swat may be used to give a female the reassurance that her calf is still there and sometimes a kick backwards with her hind feet is used to push a calf (or individual) out of the way (Lee, 1987).

Mother-Offspring

The mother is a very important aspect of survival for elephant calves. She is a source of nourishment, protection and reassurance. In order to suckle at its mother, a calf will walk parallel to her and push at her legs or touch the trunk onto or near her breast (Figure 10). This begging behaviour is often accompanied with a small rumble or other begging calls (Langbauer, 2000). A mother can refuse or terminate suckling by a calf through walking away or blocking her breast with her leg. The mother can also force the suckling calf away by bumping it with her elbow, slapping, or pushing it away (Lee, 1986). This rejection of the calf is accompanied by protest cries or loud roars (Poole, 2011). If the female does not reject the calf, she stands very still with her ears lifted in an attentive posture with her eyes opening and closing (Poole and Granli, 2011). A common behaviour in elephants is to express comfort, protection or reassurance by touching the



Figure 10: Begging behaviour by young calf

calf with the trunk in the form of a caress. This gesture is not limited to calves but can be directed toward juvenile elephants and adults (Poole and Granli, 2011). A caress comes in different forms: the trunk may be wrapped over the back and around the belly of the calf or over the calf's shoulder and under its neck, touching its mouth. Adults and juveniles reach out to

touch genitals, temporal glands, face, legs, mouth, or trunk of another individual (Lee, 1987).

Adult females also have gestures that help guide a calf or to retrieve young infants when they are lying down. In immobilization experiments, Douglas-Hamilton observed that adult females would attempt to lift the immobilized calf using their front or hind legs to lift the calf and the trunk and tusks to pull or push the calf to its feet (Douglas-Hamilton, 1972).

Group Defense

When a threat is perceived to the family unit the members respond by freezing and standing still with ears spread to determine the direction of the threat (Langbauer et al, 1989). The elephants will then bunch into a tight group facing outwards with the younger individuals towards the center, decreasing the diameter of the herd size (McComb et al, 2000). Bunching behaviour is a response to other elephants, predators, humans, or strange sounds, smells or events which can precede a full retreat, panic running or a group charge (Poole and Granli, 2011). If the group goes into full retreat, a large adult female usually places herself at the back of the group as a rear guard, carrying her head high while looking over one shoulder and then the other. Although the elephants are in retreat in an alarmed state, a wrong move by predator or human observer can cause an attack (Douglas-Hamilton, 1972). The Orphan herd of PGR exhibited bunching when



Figure 11: Bunching behaviour exhibited by members of the orphan herd. In this case they appear relatively relaxed.

we were observing the herd from an old railway line (raised above the herd).

Throughout the day the matriarch Constant had exhibited alert and apprehensive

behaviour, carefully keeping an eye on us.

Later in the day, there were several individuals

feeding in a small clearing and one of the females, Charisma, came walking out of the thicket with a new calf in tow. Possibly seeing us as a threat, a few of the adult females bunched facing outwards with the young infant between Charisma's legs and other calves and juveniles near the center (Figure 11).

Sexual

Advertisement/ Attraction

The displays used by males during musth act as both advertisement for breeding purposes but also in male-male competition, especially where a more dominant male in musth suppresses and shortens musth in younger males. A male is considered to be in musth if he exhibits a musth

walk, temporal gland secretions, urine dribbling, and individual ear wave. A musth walk is exclusive to males, characterized by high head, tense ears, chin tucked in and a rolling swaggering gait (Poole and Moss, 1981; Payne, 2003). One of the most distinctive signs of musth and one that is easily identified by a distant observer is temporal gland secretions (TGS) (Figure 12). The temporal gland is



Figure 12: Oldest male at Pongola, Ingani, with TGS

midway between the eye and ear and is secreted in a thin to heavy stream, creating a dark streak down the face (Poole and Granli, 2011). Musth TGS is distinguished from *Temporin* secretion by its congealed appearance and strong odour (Poole and Moss, 1981; Poole, 1987a). Urine dribbling occurs from a retracted and sheathed penis, giving the inner hind legs a shiny black appearance and may turn the sheath a green colour (Hall-Martin, 1987). Both urine dribbling and TGS are primarily olfactory signals, especially since urine has a very pungent odour (Poole and

moss, 1981); however, they also serve as visual displays as well. The ear wave in musth males is different to other individuals because the ears are often waved individually, or the upper portion of the ear is swung vigorously forward, causing the bottom pinnae to flap upward which creates a wave appearance across the ear (Poole, 1982; Kahl and Armstrong, 2000). It is likely that ear waving helps to spread the scent of the TGS toward other elephants (Poole, 1987a).

Sexual Monitoring

The monitoring of sexual state in elephants involves several different behaviours performed between male-female, female-female, and male-male. Elephants may assess the reproductive state by using the trunk to sniff the genitals of another elephant (Rasmussen and Wittemyer, 2002). Females show the most interest in musth males and estrous females prominently exhibit this before immediately following a mating (Eisenberg et al, 1971). Elephants may touch the tip of the trunk on, in or near urine or a urine spot to test for oestrous, musth or individual identification (Rasmussen and Wittemyer, 2002; Rasmussen and Krishnamurthy, 2000). In testing the urine (and other liquids), an elephant will touch the tip of their trunk in the liquid and bring it to touch paired orifices on the roof of their mouth that leads to the vomeronasal organ in a Flehmen response (Rasmussen et al, 1982). The vomeronasal organ plays an important role in processing chemicals relevant to reproduction (Rasmussen et al, 1993; Rasmussen, 1998). Physiological and sexual state in males is also possibly monitored through the smelling of temporal glands between male-male greetings (Poole, 1982; Rasmussen and Wittemyer, 2002).

Courtship

Several distinctive behaviours characterize oestrous in female elephants, which have been described by Moss (1983) and Poole (1989b). A female is wary in the presence of males and she is intolerant to the approach of any males. She holds her head high and her eyes open wide, directing her gaze at other elephants and avoids males by walking in an arc around her family members with her head high and turned to one side in a characteristically long gait called an oestrous walk (Moss, 1983). A male will pursue an oestrous female at a fast walk or shuffling run (Poole, 1982, 1989b), and once he catches up with the female he will attempt to stop her forward motion by reaching his trunk across her back (Kuhme, 1961; Eisenberg et al, 1971). The trunk over body display is also seen in male-male interactions where one male exhibits dominance over another. Once a male has stopped an oestrous female, the male will attempt to mount the female by placing his forelegs on the female's back. Mounting may be successful (intromission and ejaculation occur) if the female stands for the male or she may move away, causing the mating to be unsuccessful (Moss, 1983; Poole, 1982). Guarding behaviour is exhibited by males when they protect an oestrous female by remaining 5 to 15 m from her and threatening any approaching males (Poole, 1982, 1989b). A consorting pair of elephants occurs when the guarding male and oestrous female are responsible for remaining close to each other (Kahl and Armstrong, 2002). In consorting pairs, chasing and reach over behaviour is not exhibited by the male; however, he may rest his head on her back or drive the female (sometimes roughly) with his forehead (Eisenberg et al, 1971). The female attempts to stand her ground, pushing back against the male by locking her legs (Jainudeen et al, 1971). After a successful mating, a female rapidly flaps her ears, has streaming temporal glands, and calls with a powerful series of rumbles with her mouth open (Poole and Granli, 2011). The female may turn toward and away from the

male, repeating several powerful calls, holding her head high and ears out to ensure long-distance advertisement (Poole, 1989c; Poole and Granli, 2011). The relatives of the mated female rush to her side and join in exuberant calling, displaying, defecating, and urinating in what Poole and Granli (2011) describe as mating pandemonium.

Play

Solicit Play

Many of the aggressive and affiliative behaviours that have been described are seen in play. These displays are different in play because they are out of context and out of sequence, and exaggerated in their nature and expression (Poole and Granli, 2011). Individuals may signal their intent to play by raising their trunk above their head, curling the tip towards the other individual (Kuhme, 1961, 1963). Elephants may also stretch out their head out and down to look over the tusks at an individual to encourage play or waggle their head back and forth (Poole, 1996). If an elephant is smaller than an individual soliciting play, the individual may get down on their knees to appear smaller or even lie down, which encourages smaller calves to climb on (Poole and Granli, 2011). If a smaller male shows intimidation towards an older male who wants to playfully spar, the larger male may lower himself down onto his knees to encourage the other elephant's participation (Moss, 1988; Poole, 1996).

Lone and Object Play

Lone-locomotor and object play are most highly engaged in by young elephants. An elephant may sit down and flap its trunk around its head repeatedly. One of the young bulls, Khumbula, exhibited this while playing and swimming in the Jozini Lake. Some elephants will suck up

water and spray it out while swinging their trunk, apparently in a form of amusement (Poole and Granli, 2011). Tusking the ground occurs in excited play where lifting the vegetation may also occur. Running around through long grass and throwing objects accompanied by trumpeting is also a display of exuberant play (Poole and Granli, 2011). Elephants will also play with a man-made (cloth, bag, or glove) or natural object (palm frond or stick) by throwing it in the air, kicking or rolling it, biting it, swing it around, place it on head or back, tusk it, and throw it away only to stare at the object deliberately and finally retrieve it (Poole and Granli, 2011). Object play can fully engross an elephant for ten minutes or longer, especially if the object is novel. Similar behaviour is seen when elephants come across another elephant's bones; however, the behaviour is usually conducted in a quieter manner (Douglas-Hamilton, 1972; Payne, 2003).

Social Play

The most distinctive form of social play is sparring exhibited primarily between males. Sparring is distinct from fighting males because the ears are relaxed. Sparring may involve gentle pushing and trunk interlocking in greeting or more unruly shoving, to boisterous and aggressive tusking (Langbauer, 2000). Young males may also test each other's strength by pushing an opponent's head down and back with their trunk. Sparring can be initiated by trunk interlocking where two



Figure 13: Two young elephants exhibiting play behaviour

elephants twist their trunks in a spiral (Lee, 1987), which may be interrupted when one individual runs after another with head, ears, and tail raised. The elephant being chased and doing the chasing often changes during play, and young calves may mount another irrespective of sex (Figure 13) after bouts of play or giving chase during play

(Lee, 1986). During play, young elephants often clamber onto others which can lead to a pile of wriggling, squirming elephants (Moss, 1988; Poole, 1996). Chasing play behaviour is not limited to elephant-elephant interactions, but may be interspecific. A young male OJVM3 exhibited this chase play behaviour to a herd of cattle on the shores of the Jozini Dam (Figure 14).



Figure 14: Young male, OJVM3, chasing cattle

Generally Attentive

There are several gestures and displays that aid elephants in gaining sensory information about their environment. There are several postures that an elephant may utilize while trying to gather olfactory input. An elephant may hold its trunk relatively straight and turn the tip in the direction of interest, raise the trunk straight up to sample scents carried on the wind (Figure 15), or suspend the trunk over a particular scent on the ground (Rasmussen and Schulte, 1998). In situations where elephants want to appear uninterested (such as a young bull in the presence of a musth male and oestrous female), the trunk is furtive and curved slightly back (Poole and Granli,



Figure 15: Bull elephant, Shayisa, smelling the wind

2011) The trunk is extended out horizontally when an elephant is curious about an object but will not approach any closer (Kahl and Armstrong, 2000).

Tracking elephants purposefully walk while moving the trunk back and forth along a scent trail when in prolonged pursuit of an elephant or while tracking a

human (Poole, 1999a). Elephants have long distance auditory recognition and are able to decipher individual calls over 2 km away (McComb et al, 2003). To gather information on social

sounds or potential danger, an elephant ceases movement and stands listening with its ears raised and slightly extended, possibly turning side to side to locate the direction of the sound; this is different to resting where the elephant relaxes both head and ears (Poole et al, 1988). Freezing behaviour is very similar where an individual or group of elephants stands stock still listening for sounds or feeling for vibrations (Moss, 1988; Langbauer et al, 1989).

Death

When an elephant is sick, injured, dying or dead the remaining elephants respond accordingly. Family members may try to raise or even carry the afflicted or dead elephant using their tusks, trunk and feet (Douglas-Hamilton, 1972). They have also been observed trying to feed individuals who can no longer use their trunks as well as feed elephants who have died (Poole and Granli, 2011). Males may attempt to rouse a dead elephant by mounting it. Elephants are also known to cover the dead (elephant or human) with leaves, branches and dirt (Moss, 1992; Poole, 1996), and if responsible for the death, vigorously trample the ground around the body; similar behaviour is observed after a birth (Poole, 1996). Elephants may also guard the body of a dead elephant or person, protecting it from other elephants, predators, or other individuals that appear threatening (Douglas-Hamilton, 1972; Poole, 1996; Payne, 2003). Investigation of elephant remains occurs using the trunk and feet to explore and move the bones, considering them in what Poole and Granli (2011) describe as quiet reflection (McComb et al, 2006).

Acoustic Communication:

Elephants are highly social animals that have a complex fission and fusion society that is based on the relationships between individuals, family units, bond groups and clans. The associations, partnerships, consorting pairs, and enduring relationships of elephants are maintained and established based on the ability to receive, distinguish, and transmit auditory signals. The survival of an elephant and her offspring is dependent on the cohesion and coordination of the family group and the ability to compete with other families for scarce resources (McComb et al, 2001). To ensure a family is cohesive, family members call to each other to reinforce social bonds between relatives and associates, care for calves, reconcile differences between “friends”, defend close associates, form coalitions against aggressors or predators, coordinate movements, and to keep in contact with each other over long distances (Poole et al, 1988; Poole, 1994a). Males lead more independent lives than females but they still depend on acoustic communication to advertise sexual state, identity and rank (Poole, 1999a).

The anatomy of elephants plays a large role in the sounds they produce and those they can hear. Elephant vocalization is unique and unusual due to their large body size and the inclusion of a trunk in their vocal tract (Soltis, 2009). Sounds are produced in elephants by air passing over the larynx, which is a structure reportedly 7.5 cm long, suspended on the hyoid apparatus (Sikes, 1971). An elephant’s trunk provides a long, flexible resonator that is unusual because the majority of it (1.8 m) lies outside the cranium. The vocal tract itself is estimated to be 2.5 m, including the trunk, nasal passages in the skull, and the lips to larynx (Soltis, 2009). Another unique feature of the elephant is that the hyoid apparatus is made of only five bones instead of nine and these are attached to the skull by tendons, muscles and ligaments and not bones as in other animals, providing greater movement and flexibility of the larynx (Shoshani,

1998). This loose arrangement also houses a pharyngeal pouch at the base of the tongue that functions as an emergency source of water but also appears to aid the production of low frequency calls (Shoshani, 1998). Elephants produce low frequency rumbling sounds below the level of human hearing or infrasound with some calls as low as 8 or 9 Hz (Poole, 2011). Heffner and Heffner (1980, 1982) showed that elephants have good low frequency hearing and very accurate localization skills. Elephants have a greater sensitivity to low frequency sounds because they have uniquely reverted to a reptilian-like cochlear structure (Fischer, 1990; O'Connell et al, 1998). Elephants are also able to detect seismic vibrations through bone conduction using massive ossicles in their ears (Reuter et al, 1998), and mechanoreceptors in the toes and feet (O'Connell et al, 1998).

African elephants have a large repertoire of sounds they produce from the stereotypical elephant trumpet to the imitation of humming or trucks. Elephants are capable of producing high frequency trumpets, cries, barks, roars, grunts, snorts, and low frequency rumbles. The very low frequency sounds by elephants are produced due to their large size and large vocal organs, and the majority of sounds made by an elephant are laryngeal in origin (Poole, 2011). Laryngeal call types include rumbles, roars, cries, barks and grunts. Rumbles are used in many social contexts and are the most frequent call type of all sex and age classes of African elephants, easily distinguished by their low frequencies and harmonic structure (Poole, 2011). Roars are variable bellowing, screaming or shrieking sounds that are mostly produced by elephants in some form of distress, usually calves and juveniles. Roars may also be used by adults when being tusked or chased, when attacking predators, when chased by males during oestrus, and during highly exciting social events (Poole, 2011). Essentially roars elicit the attention of other elephants to gain their support or attract males. When calves are in some sort of distress they will often use

short whimpering sounds called a cry. This may be used when calves are denied access to the breast or if they are stuck in a wallow. Barks are similar to roars in context and grunts are honking sounds made by infant elephants in the first days of life (Poole, 2011). Some sounds like trumpets and snorts are created by blowing air through the trunk and altering the position of the trunk, speed and duration of air moving through it (Soltis, 2009); these sounds are classified as trunk call types. Trumpets are produced by the forceful expulsion of air through the trunk and come in several forms (Berg, 1983; Poole and Granli, 2004). Elephants will trumpet when they are highly stimulated in situations where they are fearful, surprised, aggressive, playful, or socially excited (Poole, 2011). Where group participation is important, trumpets are often associated such as in highly stimulating social events such as births, matings, greeting ceremonies; in these settings, Poole postulates that rumbling defines the context of the event (greeting, mating etc) and trumpeting is a kind of “exclamation mark”, expressing the excitement and importance of an event (Poole, 2011). Snorts are short noisy sounds produced by blowing air purposefully through the trunk when an elephant is surprised by something or to alert other elephants to a change in a situation (Leong et al, 2003).

Vocal signals are unique to individual elephants and elephants can recognize the contact calls of members of their family and discriminate contact calls from non-family or bond group members. In playback experiments performed by McComb and others (2000), female elephants were shown to recognize family and bond group members from other individuals on the basis of their contact calls. When the contact call of a missing family or bond group member is played to a family unit, the subjects typically contact call themselves shortly after the playback. If a non-family or group member contact call is played, the family unit would either respond by listening to the call and resuming original behaviour after the playback, or become agitated and bunch

together into defensive formation. The reaction of the family to non-family/bond group calls depends on the level of association the family unit has with the caller. If the call is from a non-member that has a high frequency of association with the family, the reaction is more relaxed than if the caller is a non-member with a low association frequency (McComb et al, 2000). The playback experiments showed that females can recognize the contact calls of approximately 100 frequent associates (McComb et al, 2000). Not only can elephants distinguish family or bond group member contact calls but they also have a long-term memory of those calls (McComb et al, 2000). Different families show different abilities in discriminating calls, which has been linked to the age of the matriarch (McComb et al, 2001). Families with an old matriarch were significantly more reactive to an unfamiliar female with a low association index than a female with a higher association index; in comparison, bunching behaviour by families with a young matriarch increased marginally when the call came from an unfamiliar female than one with a high association index. Older matriarchs appear to have larger networks of vocal recognition that allow them to be more adept in discriminating correctly between the calls of familiar and unfamiliar females in the vicinity and responding appropriately (McComb et al, 2001).

Elephants are unusually long-lived and their social structure and communication is influenced by relationships in the distant or remote past. The ability to remember the calls of others can be beneficial to elephants in a fission-fusion society where individuals may often come into contact after long periods of separation (McComb et al, 2011). Elephants have a broad range of acoustic communication signals that are either laryngeal or trunk type calls. The sounds an elephant can produce are due to its unique anatomy of trunk and loose and flexible larynx. There are several variations of the common call types that are used in different social contexts.

These social contexts are described by Poole (2011) in a similar fashion to the categories of visual and tactile communication.

Conclusion:

Elephants are unique mammals that are not only remarkable for their longevity and large size but also for their high sociality and communication strategies that enable them to maintain relationships both spatially and temporally. Elephant society is a fission-fusion model where individuals aggregate and dissociate based on ecological pressures and other factors such as predator avoidance, calf care, and mate selection. The core unit of elephant social structure is the family unit which consists of an adult female and her offspring. Family units that are found to be highly associated are bond groups. To maintain cohesion and coordination of the family group and association with bond groups, numerous tactile and visual communication cues are used along with a complex system of auditory signals. The African elephant has been extensively studied over the past fifty years and for good reason, they are truly a fascinating species!

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