Chapter 1.

Mind and Movement: Meeting the Interests of Elephants

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The Elephantidae, once widespread across the continents of America, Europe, Asia and Africa, now occur as fragmented remnants in parts of Asia and sub-Saharan Africa (Meredith 2001). Three species, African savanna and forest elephants (*Loxodonta africana* and *Loxodonta cyclotis)* and Asian elephants (*Elephas maximus)* represent the impoverished remains of what was once a rich family tree. The elephants have evolved over 50 million years from small, aquatic and sedentary creatures (Shoshani & Tassy 1996) to increasingly large-bodied, long-lived animals dependent upon moving over vast distances in search of food, water, minerals and social and reproductive partners (e.g., ATE database; Lindeque & Lindeque 1991; Verlinden & Gavor 1998; Whyte 2001). Physically impressive and vigorous, an adult male African elephant may be four meters tall and weigh as much as 7,000 kg. No other terrestrial animal alive today weighs even half as much (Haynes 1991). With a maximum lifespan in the wild of 65 years (Moss 2001), the extant elephants are unusually long-lived mammals (Eisenberg 1981). Excluding mortality caused by humans, the life expectancy of a free-ranging female

elephant is 54 years (ATE database), an age not very different from our own species in the absence of medical care.

Elephants in zoos and circuses are plagued by a host of physical and psychological ailments (Clubb & Mason 2002; Schmidt 2002; Kane, Forthman & Hancocks, Chapter 17) that are not observed among their free-living counterparts. Regardless of the regular health care they receive, and despite the lack of human predation and the vagaries of drought and disease, captive elephants suffer from obesity, arthritis, foot problems and reproductive and psychological disorders—and die at a younger age (Clubb & Mason 2002; Lee & Moss, Chapter 2). Unlike free-living elephants, those kept in zoos show relatively low fertility and a high rate of stillbirths; they also encounter difficulties giving birth and raising their young (Clubb & Mason 2002). Furthermore, they may engage in a wide variety of abnormal behaviors such as stereotypic swaying, killing of infants and hyper-aggression toward other elephants. What are the underlying causes of these abnormal physical and psychological disorders? A look at some of the essential elements of the lives of free-ranging elephants provides some compelling answers.

In the wild, elephants are rarely still; some segment of their bodies, whether legs, ears, eyes, trunk or tail, is in motion. Despite their great size, elephants are vigorous animals, perpetually active in mind and body. Apart from the two to three hours of a 24-hour day when wild elephants may stand or lie down to sleep, they are searching over vast areas for food, water, companions and mates or they are actively engaged in preparing a food item for ingestion, interacting with a conspecific or another species or occupied in some frivolity. Their movements may be deceptively slow, allometrically

befitting of such an enormous animal, but even when their bodies are at rest, their minds are active.

Elephants are large-brained, intelligent and inquisitive animals (Rensch 1956; Rensch 1957; Shoshani & Eisenberg, 1992; Poole, 1998; Roth 1999; Cozzi, Spagnoli & Bruno 2001; Hart, Hart, McCoy & Sarath 2001; Hakeem, Hof, Sherwood, Switzer et al. 2005; Douglas-Hamilton, Bhalla, Wittemyer & Vollrath 2006; Plotnik, de Waal & Reiss 2006; Shoshani, Kupsky & Marchant 2006; Poole & Moss in press); we only need watch the tip of an elephant's trunk, the posture of its ears and the angle of its head to gain a window into its actively engaged mind. In the wild, everything elephants do is an intellectual challenge: locating and manipulating a wide variety of food items; remembering the location of water during a drought; searching for potential mates; deciding where to go, who to go with, who to join and who to avoid. Discriminating between the individual scents, voices and appearances of hundreds of familiar and unfamiliar individuals, including friends and foes, relatives and non-relatives, higher-ranking and lower-ranking competitors and friendly and unfriendly other species is a continually engaging activity. What happens to the psychological and physical well-being of such intelligent creatures when we remove the need to search for or manipulate widely dispersed and diverse food items? Or when we eliminate the multifaceted demands of being part of a vast social network in a complex and fluid society?

The stated aim of zoos is to meet the behavioral and biological needs of the species they hold captive. When it comes to elephants, however, zoos are woefully inadequate. Zoo proponents and welfare activists alike have tended to focus on the proximate causes of suffering in captive elephants (e.g., foot problems, arthritis,

reproductive health issues, obesity, hyper-aggression, stereotypic behavior). But unless we address the ultimate source of captive elephant suffering—the overall lack of biologically relevant mental stimulation and physical activity—we will never meet their behavioral and biological needs. We must ask ourselves whether meeting their requirements is an attainable goal, and, if so, within what constraints. The perspective that we take in this chapter is that an elephant-centric approach *is* possible, though certainly expensive and challenging. Nonetheless, we choose to believe that discerning future zoo visitors will demand to experience thriving elephants if they accept them in captivity at all.

On the Move

Free-living elephants are on the move at least 20 out of every 24 hours (Figure 1), actively engaged in foraging, exploring, socializing and searching for conspecifics. Activity patterns of wild elephants vary enormously depending upon the season, and the age, sex, reproductive state and population of an individual (ATE database). In Amboseli, elephants spend between 30 and 55 percent of daylight hours feeding (low end of the range: lone musth males; high end of the range: non-musth males), five to 15 percent walking while feeding (low: male elephants in bull groups; high: elephants in mixed groups), 15 to 55 percent walking (low: non-musth sexually inactive males; high: males in musth), three to 23 percent interacting (low: non-musth sexually inactive males; high: musth males), three to 15 percent resting (low: musth males; high: sexually inactive non-musth males), and approximately five percent collectively engaged in standing, comfort activities and drinking. While adults usually rest standing during the day, they frequently sleep lying down for a couple of hours at night.

Modern elephants exist across a broad range of habitat types from deserts to swamps, lowland rainforests, gallery and montane forests, upland moors, floodplains, open savannas and woodland. Ranging from sea level to as high as 4,875 meters (Grimshaw, Cordeiro & Foley 1995), elephants can survive extreme temperatures for short periods, yet they thrive between 15 and 35 degrees Celsius, typically seeking shade or water above 30 degrees Celsius. In rare cases, elephants have become adapted to desert conditions, for example in Bourma, Mali and Kaokoveld and Damaraland in Namibia (Leggett 2004).

Across these habitats the home ranges of individual male and family groups vary tremendously from 15 to approximately 11,000 km^2. Very few studies report home ranges of less than 100 km^2 and these probably represent incomplete datasets. In Kruger National Park, South Africa, for example, the ranges of adult females vary in size from 86 to 2,776 km^2, with a mean of 880 km^2 (Whyte 2001). In Northern Botswana home range size averages over one thousand square kilometers, varying from 447-3,309 km^2 with some groups traveling up to 200 km in search of dry-season water (Verlinden & Gavor 1998). In the semi-arid savanna of the Samburu-Laikipia region of Kenya, elephant ranges vary from 102-5,527km^2 (Thouless 1996), while in the more arid environments of Namibia, ranges may vary from 2,136-10,738 km^2, with a mean of 5,860 km^2 (Lindeque & Lindeque 1991). Asian elephants, a typically forest dwelling species, and African forest elephants generally have smaller home ranges than African savannah elephants. The home ranges of Asian elephants fluctuate between 34 and 800 km^2 for females and 200 and 235 km^2 for males, though some home ranges appear to cover thousands of square kilometers (Sukumar 2003). Elephants living in harsh desert

conditions characteristically have the largest home ranges. In the best-studied desert population in northwest Namibia, elephants survive seasonally scarce water and forage by moving over vast areas of up to 12,600 km^2 (Leggett 2005; Leggett, Fennessy & Schneider 2003; Lindeque & Lindeque, 1991; Viljoen, 1987; 1989; Viljoen & Bothma, 1990).

The variation in home range can, to a large extent, be explained by habitat type, though home range also varies considerably within populations, and individual preference, tradition, inter-family relationships, sex and season, all play a role in determining home range size (ATE database). Despite the fact that the elephant's energetic cost of walking is the lowest recorded for any living land animal (per gram of tissue one-fortieth the rate of a mouse; Langman, Roberts, Black, Maloiy et al.1995), elephants still behave in ways to conserve energy (Wall, Douglas-Hamilton & Vollrath 2006). Consequently, smaller home ranges generally reflect higher habitat quality and *vice versa*. Proponents of the modern zoo have used this fundamental energetic truth to argue that since elephants in captivity are provided with food and water they don't require large spaces. For instance, Bill Foster, past President of the American Zoo and Aquarium Association (AZA), was reported by the Deseret Morning News (2005) as saying that the reason animals move so much in the wild is to seek security or food, but in zoos with food, protected environments and veterinary care, elephants live enriched lives. "Yes, they can move miles," he said, "but only because they have to." Nothing could be further from the truth.

Over millions of years, as large-bodied animals, the elephants have evolved a range of specialized physical and behavioral adaptations to allow them to cover long

distances so as to meet their ecological, social and reproductive requirements. *In other words, elephants are adapted for "long-distance living," just as polar bears are adapted for arctic climates*. To survive long walks without access to water, elephants have developed a pharyngeal pouch for water storage. To defend themselves and their offspring from large carnivores and human hunters, elephants evolved a tight-knit, highly cooperative society, and elaborate parental care and defense behaviors. To adapt to a life where those close companions and potential mates may be separated by many kilometers, elephants have evolved a range of specialized traits allowing them to produce, receive and localize distant, very low-frequency acoustic and seismic signals (Heffner & Heffner 1982; Fischer 1990; Nummela 1995; O'Connell, Hart & Arnason 1998; Reuter, Nummela & Hemila 1998; Weissengruber, Egger, Hutchinson, Groenewald et al. 2006a).

Unique and morphologically peculiar, the relatively inflexible, pillar-like legs and cushioned feet of elephants have evolved to support their vast weight (Weissengruber & Forstenpointner 2004) and enable them to walk efficiently over long distances on rough surfaces. The skeletons of the mammoths, mastodonts and modern elephants are all similarly inflexible, characterized by columnar legs and a nearly horizontal spine, which offer support for their heavy bodies, and lacking flexed joints. Unlike those of other animals, the upper and lower portions of the legs are aligned almost vertically when the limbs are extended (Haynes 1991), and the maximum forward and rearward motion of the legs is limited so that the legs are almost always beneath the body.

The design of the muscular structures, too, matches the precise requirements of heavy weight-bearing, as well as of Proboscidean limb posture and locomotion patterns. For example, the musculoskeletal foot arch is designed in a manner that allows an

elephant to stand on an extensive cushion such that none of its toes touch the ground. Each toe has separate muscles, indicating that movements of the digits, such as spreading and contracting, are important. The toes of the elephant are then embedded within a common "skin-shoe." Both the musculoskeletal foot arch and its cushioning provide an important shock-absorbing function. The proper posture of the foot and its skeletal elements likely play a key role in supporting the elephant's enormous body weight and in distributing the mass over the entire sole (Csuti, Sargent & Bechert 2001); elasticity mechanisms aid in minimizing stress and energy consumption during both resting and locomotion (Weissengruber & Forstenpointner 2004).

Some of the features described above, which make elephants so well-designed for living in large spaces, become the very reasons for their unsuitability in the traditional zoo. For example, individuals so behaviorally and emotionally well-adapted to living in a close-knit society must often live in captivity without companions. A species so beautifully designed for the detection of meaningful (e.g., conspecifics, thunder) low-frequency sound (Heffner & Heffner 1982; Poole, Payne, Langbauer & Moss 1988) and seismic vibrations (O'Connell, Hart & Arnason 1998; Reuter, Nummela & Hemila 1998), is exposed in city environments to continuous low-frequency machine, vehicle and air traffic noise, which may interfere with inter-individual communication and likely influences negatively both their psychological and physiological health (Rylander 2004). Endowed with a high concentration of Vater-Pacinian corpuscles (sensitive to pressure and vibration) in the cushions of the feet and Meissner corpuscles (mechanoreceptors) in the adjacent skin, the elephant's foot is highly sensitive (Weissengruber et al. 2006a). The elephant's large body and rather inflexible limb joints, so well adapted for energy-

efficient locomotion, are particularly vulnerable to arthritis in a sedentary captive environment (Weissengruber Fuss, Egger, Stanek, Hittmair & Forstenpointner 2006b). The pads of an elephant's foot are designed for walking long distances on uneven and rough surfaces, not for standing on concrete. As a result of the predominantly stationary existence on smooth surfaces, the feet of captive elephants wear unevenly (Schmidt 2002) causing improper posture of the feet, and consequently of the legs and spine, leading to painful arthritis and other joint problems (Figure 2). G. Weissengruber (Pers. comm. March 31, 2006) found in zoo elephants that not only the joints of the extremities but also the joints of the vertebral column were affected by pathologic alterations. The uneven wear shows up regularly in zoos (Schmidt 2002). The adage "use it or lose it" applies aptly to captive elephants: *Elephants need to walk to stay well.*

Walking to stay well applies to more than just an elephant's physical health. Elephants in small spaces with little mental and physical stimulation also exhibit stereotypic behavior, rocking and swaying. In an elegant comparison across carnivores, Clubb and Mason (2003) showed that species that were naturally wide-ranging were more vulnerable to welfare problems in captivity, including psychological dysfunction and stress as exemplified by stereotypy.

Proponents of the modern zoo have claimed that data from the wild is not necessarily applicable to zoo elephants. For example, Hutchins (2006) claims that data from the wild show elephants to be extremely flexible animals. Though his observation is correct, no zoos come close to meeting the lower range of environmental or social parameters that exist in nature. If the general state of elephants in captivity were one of thriving, this might be acceptable, but it isn't (e.g., Clubb & Mason 2002). Other zoo

managers (e.g., Stephen Thompson, Director of Conservation at Lincoln Park Zoo, quoted in Kennedy 2005) go further, asserting that research from the wild is not applicable to zoo elephants because captive elephants have different requirements from free-ranging elephants. The argument may have its roots in the long-term tradition of keeping captive elephants and in a misunderstanding of the term "domesticated." In biological terms, domestication refers to changes in the genetic makeup of a population that affect the physical or behavioral character of individuals, a process which takes hundreds, if not thousands, of generations of *selective* breeding. Elephant capture and taming began in the Indus Valley around 4,000 years ago and Asian elephants have continued to be captured, trained and worked since that time. Asian elephants are often referred to as a domesticated species, but this is an erroneous use of the term. The vast majority of captive elephants in each generation have been wild-caught, and among the minority born in captivity, most are probably the progeny of wild fathers. In addition, there has been no selection to create domestic "breeds" among Asian elephants. The number of generations of captive-bred elephants is not sufficient for any physical or behavioral adaptations to occur and therefore it is incorrect to refer to or think of them, as a "domesticated species." So, while elephants may become habituated to, or tamed by, human beings, they are still wild animals with the same inherent physical, behavioral, social and emotional interests as wild elephants. The interests of captive elephants anywhere should clearly be based on conclusions from studies of elephants in their natural habitat.

Mental and Physical Challenges in the Daily Life of a Wild Elephant

The activities experienced by a free-ranging elephant motivate an active mind and keep fit a vigorous body. No matter what the arena—foraging, defending, socializing or reproducing—an elephant's daily life is distinguished by need, purpose, challenge, choice, will, autonomy and camaraderie. Social learning, too, is seen in many aspects of an elephant's daily life and is a vital component of mental activity. These elements, so fundamental to the lives of wild elephants, are currently all but absent in captivity.

Foraging

Elephants continue to grow throughout most of their lives due to delayed epiphyseal fusion of the long bones (Haynes 1991). Owing to their enormous size, indeterminate growth, long and energetically expensive reproductive lives and lack of a specialized digestive system, elephants must consume vast quantities of food, and foraging occupies the majority of an elephant's daily movements. Each day an adult eats 150 to 350 kg, or four to six percent of its body weight, and drinks 160 liters of water. To realize this input, elephants must spend up to three-quarters of a 24-hour day foraging (Wyatt & Eltringham 1974; Lindsay 1994).

Effective foraging is achieved through constant smaller and larger movements: the coordinated action of feet, tusks and dexterous trunk selects individual items of fruit, tugs up tufts of grass, opens heart of palm, flattens the hard thorns of an acacia branch or strips bark off trees; slow meandering carries an elephant from one food item to another, purposeful walking takes an elephant through a variety of habitats on a daily basis and migrations on a seasonal basis. The physical activity and mental stimulation involved in the search for food items (walking, reaching and smelling with the trunk), their

manipulation (digging, kicking, stabilizing with the feet; prying, levering and breaking with the tusks; pulling, ripping, breaking, defoliating, cleaning with the trunk), their ingestion (trunk and tongue) and mastication constitutes the very core of an elephant's interest and survival. Many of the techniques used by wild elephants to locate, select and extract food must be learned, either through experience or by watching others, and social learning plays a critical role in calves' acquisition of foraging knowledge and techniques of manipulating food items (Lee & Moss 1999; Figure 3).

The lack of space available in zoos and circuses does not permit elephants to search for, select from, learn about and manipulate a wide variety of food items, thus depriving elephants of much-needed physical activity and mental stimulation. A few zoos have introduced food "spreads" (Kinzley 2006) and while these are a breakthrough in elephant husbandry, it is a time-consuming and expensive process requiring dedicated staff.

A Complex Network of Relationships in Time and Space

Wild elephants live in a complex fission-fusion society that is remarkable for its fluidity on the one hand, and its close and enduring social relationships on the other. Elephant relationships radiate out from the mother-offspring bond through family, bond group, clan, sub-population, independent adult males and even beyond the population to strangers (Moss 1988; Payne 2003; Poole & Moss in press). Within this social arena, the lives of adult female and male elephants differ radically (Poole 1994). An intricate network of bonds among individuals and families typifies the lives of females and their offspring, while fluctuating sexual states distinguish the dynamic activities, associations and relationships of adult males (Moss & Poole 1983; See Box 1 and Box 2; Figure 4 and

5). The social relationships of elephants are particularly complex because individuals interact with many animals from different social units across a population, and cooperative social partners may not always be together in the same group. Members of the same family are frequently kilometers apart, and much of a family's daily activity may be focused on approaching close associates or circumventing individuals they wish to avoid. This pattern of attraction and evasion is clearly illustrated by the patterns of simultaneously radio-tracked individuals (Charif, Ramey, Langbauer, Payne et al. 2005; Douglas-Hamilton, Krink & Volrath 2006).

The combination of social qualities observed in elephants—close and lasting cooperative social relationships, and fission-fusion sociality—exists in only a small number of cooperatively hunting carnivores (e.g., hyenas, lions and sperm whales) and a few primates (e.g., chimpanzees and humans: Archie, Moss & Alberts 2006). The social complexity hypothesis posits that intelligence has evolved to allow individuals to cope with the changing and often difficult-to-predict behavior of partners with whom they must cooperate and compete. And, like other species that live in fission-fusion societies (e.g., human beings, chimpanzees, social carnivores, whales), elephants are recognized for their intelligence and reasoning abilities (Poole & Moss 2006).

Although the Amboseli elephant population is relatively small (numbering 1,500 at the end of 2006), compared to many elephant populations, it is, nevertheless, a big society. A female elephant in Amboseli may seek the company of and/or purposefully avoid literally hundreds of other individuals in the course of her daily range (Poole & Moss in press; see Lee & Moss, Figure 7, Chapter 2). Searching from group to group for receptive females, sexually active males may also interact with hundreds of different

individuals, both male and female, in the course of a 24-hour day (Poole & Moss 1989). The sheer number of elephants involved in an individual's social network, and the hierarchical character of the formation and dissolution of aggregations make elephants remarkable. The ability of elephants to distinguish genuine strangers from a wide range of more regular associates through recognition of voices (McComb, Moss, Durant, Sayialel & Baker 2000) and scents (Rasmussen & Krishnamurthy 2000) may be explained by the extremely large and convoluted temporal lobes of the elephant's brain (Shoshani 1998; Shoshani et al. 2006).

Learning from Others

Social learning and behavioral innovation are essential elements of individual development and of the very fabric of elephant society, tradition and culture (Lee & Moss 1999; Poole & Moss in press). For example, social learning via allomothering (care of calves by juvenile females) provides young females with an array of care taking experiences and skills that persist through the birth of their own first calf. This transfer of social knowledge is vital for successful mothering (Lee 1987; Lee & Moss 1999). Distinguishing between friends and foes, learning where to go to find water during droughts and where to find particular food items or minerals, is passed on from mother to daughter (e.g., McComb, Moss, Durant, Sayialel et al. 2001; Payne 2003).

The acquisition of appropriate estrus and consort behavior, too, requires a social context for learning (Poole & Moss in press). Both the acquisition of estrus behaviors and the choice of mates appear to be facilitated by the presence and behavior of the mothers of these young females (Poole & Moss in press). The birth of a female's first calf is another life event where the presence and behavior of experienced females aids

inexperienced mothers. Experienced family members assist young females to cope with the physical demands of birth, including helping a newborn to its feet, and with the immediate protection and socialization of the newborn calf (Moss 1988; Lee & Moss 1999). Interaction with other elephants and the transmission of social and ecological knowledge is key to an elephant's survival, and the stimulation such relations provide is, we believe, necessary for an elephant to thrive.

The traditional zoo does not offer the space necessary to allow elephants to live in natural family groups, nor does it present elephants with the option of choosing associates from among other families, clans or populations or provide the opportunity for learning survival skills through experience or from others. By depriving elephants of adequate space, zoos not only severely restrict an elephant's ability to obtain adequate and essential exercise, but they take away an enormous source of mental stimulation needed for the basic well-being of such a highly social and intelligent individual.

The Search for Mates

Reproductive behavior is an essential component of the daily life of any animal. In elephants, reproduction involves highly energetic physical and mental activities. Intricate chemical and acoustic signals and a finely honed memory are employed in the search over vast distances for both rivals and mates (Poole 1989a; Poole 1999; Poole & Moss 1989). Courtship, mating, male-male competition and female choice constitute intensely interactive behavior, alternatively highly subtle and immensely overstated. The confined spaces that zoos and circuses offer do not allow for the fluid intermingling of numerous males with females and thus have a major influence on the purpose, choice, autonomy and will of an elephant.

By age 30, most males have experienced their first heightened period of sexual and aggressive activity, or musth (Poole & Moss 1981; Hall-Martin & Van der Wilt 1984). Characterized by a distinct, rigid, head-high posture, swollen and secreting temporal glands, dribbling of strong-smelling urine (Poole & Moss 1981; Poole 1987) and distinctive vocalizations (Poole 1987, 1999; Poole et al. 1988), musth males experience impressive surges of circulating testosterone (Hall-Martin & Van der Walt 1984; Poole, Kasman, Ramsay & Lasley 1984). With the onset of musth, a male's behavior goes through a striking psychological transformation. A male in musth spends the majority of his time interacting aggressively with other large adult males or enthusiastically searching for receptive females, attempting to gain access to, or guard those in peak estrus (Moss 1983, Poole 1987, 1989a, b; Poole & Moss 1989). Highly active, a male in musth may pursue another male or search for a mate over many kilometers in the space of a few hours. Musth has a pivotal effect on the relative dominance ranks of males (Poole 1989a); with few exceptions, musth males, whether large or small, rank above non-musth males. The duration of musth is age-related and may also be influenced through suppression by proximity to higher-ranking males (Poole 1989a). In populations without older individuals (Slotow, van Dyke, Poole, Page et al. 2000), or in captive situations (Jainudeen, McKay & Eisenberg 1972), musth starts at a younger age and lasts longer.

Like young females, young male elephants also benefit from social learning and are often observed to follow older musth males, testing the identical urine spots and the same females as the older do (Poole & Moss in press). Musth males are extremely tolerant of these youngsters, allowing them to stand less than a meter from an estrous

female, while they ensure older males are kept at long distances (Poole 1982). Successful mounting and intromission require considerable skill and practice, which may, in part, be gained by watching the behavior of older, more experienced males. Experience from southern Africa also highlights the importance of social learning in the acquisition of appropriate male reproductive behavior (Slotow et al. 2000). Juvenile male elephants who witnessed their families killed in a culling operation and then were translocated to areas without adult males, exhibited abnormal reproductive behavior as young adults, including the mounting, tusking and killing of black rhinos. While trauma is likely to have been a causal factor in the development of this abnormal behavior (Bradshaw, Schore, Brown, Poole & Moss 2005), it is also likely that the absence of adult male role models contributed to the inappropriate sexual reaction of these young males. The behavior ceased after the later introduction of older males (Slotow et al. 2000).

Communication

The fluid nature of elephant society, in which closely bonded individuals may be many kilometers apart, requires that elephants possess a communication system combining multifaceted short- and long-distance signaling. A combination of trunk, ear, limb and body postures and movements signal a broad range of agonistic, defensive and affiliative gestures and complex emotional responses (Kahl & Armstrong 2000; Poole & Granli 2003; Poole & Granli 2004). Chemical signals including saliva, mucus secretions from the eyes, fluids from the ano-genital tracts, temporal glands, ears and interdigital glands, also play an essential role in elephant social and reproductive communication (Rasmussen, Hall-Martin & Hess 1996; Rasmussen & Schmidt 1998; Rasmussen & Krishnamurthy 2000; Rasmussen & Wittemyer 2002). Elephant acoustic communication

includes a broad variety of sounds with components ranging from five Hz to over 9,000 Hz; Poole in press). Calls include very low-frequency rumbles and higher-frequency trumpets, snorts, screams, barks, roars, cries, chirps, croaking and other idiosyncratic sounds (African: Berg 1983; Poole et al. 1988; Poole 1994; Langbauer 2000; Leong, Ortolani, Burks, Mellen et al. 2003; Soltis, Leong & Savage 2005a, b; Poole in press; Asian: McKay 1973). Elephants use these acoustic signals to communicate agonistic, defensive, affiliative, protective, reproductive, logistical and social messages (Poole in press). Elephants utilize powerful, very low-frequency sounds to coordinate their movements (Payne, Langbauer & Thomas 1986; Poole et al. 1988; Langbauer, Payne, Charif, Rapaport & Osborn 1991; Garstang, Larom, Raspet & Lindeque 1995; Larom, Garstang, Payne, Raspet & Lindeque 1997; McComb et al. 2000). Via such acoustic signals, elephants can recognize the individual voices of other elephants at distances of up to 1.5 kilometers (McComb, Reby, Baker, Moss et al. 2002) and may detect the location of conspecifics over an area of up to 300 km^2 depending upon atmospheric conditions (Larom et al. 1997). When an elephant vocalizes with a low-frequency rumble an exact replica of this signal propagates separately through the ground. Elephants respond appropriately to this signal component (O'Connell et al. 1998; O'Connell-Rodwell, Wood, Rodwell et al. 2006). Elephants are capable of vocal production learning (imitation), and this rare talent may have evolved to facilitate social bonding and cohesion in the elephants' highly dynamic fission-fusion society (Poole, Tyack, Stoeger-Horwath & Watwood 2005). Social learning, so fundamental to the development of elephants, plays a further role in acoustic acquisition (Wemmer & Mishra 1982; Wemmer, Mishra & Dinerstein 1985). The very rich communication system that we

observe in the extant elephants is likely to have coevolved with increasing sociality and brain size (e.g., Shoshani et al. 2006). The versatile and intricate, short- and long-distance communication of elephants is yet one more indicator of their adaptation to a rich social environment and for complex use of space.

Conclusion

Elephants are intelligent and vigorous creatures that have evolved in expansive and complex physical and social environments. Adapted to large space, the continual search for food, water, companions and mates involve constant large- and small-scale movements that are essential for the well-being of elephants. Based on decades of research, it is our considered opinion that today's zoos and circuses do not come close to meeting the interests of either male or female elephants. Nor do we believe that the slightly expanded exhibits that many zoos are currently contemplating, at vast expense, will make a significant difference.

It is our opinion that the interests of elephants in captivity can only be met within environments that:

- Enable the development of normal social relationships, the formation of families (with calves), the possibility for at least small-scale fission-fusion sociality, cooperative behavior, social learning and play;
- Enable choice of association and interactions among numerous social partners and mates;
- Enable natural foraging behavior and activity patterns;
- Necessitate roaming in search of varied food, social partners and mates;
- Inspire physical and mental activity in all aspects of daily life.

Throughout this essay we have emphasized that space is crucial to the well-being of elephants; to meet each of the above criteria space is a necessity. And, by attaining these criteria, zoos will also meet a final requirement:

- Ensure freedom from chronic illnesses and mental and physical suffering due to lack of physical movement and mental stimulation.

However, defining the minimum space needed to meet the interests of elephants is exceedingly difficult. Our belief is that two to three family groups (or 20-30 individuals) are necessary to enable the development of fission-fusion characteristics. In addition to this number, the "population" must include adult males. To reduce the problems of prolonged musth, a natural hierarchy must be permitted to establish, and males must have a mechanism for safe retreat. We estimate that a minimum of four to five adult males ranging in age from young adult (15-20 years) to fully mature adult (40-50+ years) should be included. To accommodate a population of 25-35 or more individuals and allow natural foraging and socializing behavior we believe 50-70 km^2 (~two km^2/individual) of varied terrain and habitat is an indication of the space required.

Assuming such a scenario is acceptable, a few of these large elephant zoos could be located in the warmer climatic zones of the United States and Europe. The elephant "populations" in these zoos would be composed from existing zoo or circus elephants, as the capture and import of elephants from range states are unacceptable. Once a population is established, the transfer of females and calves to other facilities would be highly undesirable due to the potential trauma inflicted by the disruption of close social bonds.

Rooted in our knowledge of elephant social behavior is our firm belief that it is not possible to meet fully the well-being of female elephants without the presence of calves. Yet we have strong misgivings concerning ethical issues surrounding the captive breeding of elephants and its longer-term consequences. Any such large facility holding a naturally functioning elephant population, complete with natural breeding and mortality, is likely to experience increasing numbers and, due to the confined nature of the exhibit, would have to intervene to maintain an appropriate population size. The culling of elephants has generally been extremely controversial (e.g., Owen-Smith, Kerley, Page, Slotow & van Aarde 2006). Culling elephants in the United States or Europe would be ethically unacceptable, as would the transfer of individuals (particularly females and calves) from one facility to another. Fertility regulation, though possible, would likely lead to extremely low birth rates, since mortality in these facilities is expected to be low.

The issue of captive breeding is so problematic that most elephant welfare proponents argue for no breeding whatsoever. Clearly a no-breeding policy would translate into the eventual extinction of captive elephants outside their native range. Whether this is a good or a bad thing depends upon whom you listen to, and is not within the scope of this essay to consider. We conclude merely by posing the following questions: Do we have the right to preside over the suffering of intelligent animals for our own entertainment and pleasure, whether or not they represent ambassadors for their free-living cousins? How much mental and physical suffering by individual elephants is tolerable in exchange for a measure of conservation support generated? And, is the keeping of several hundred elephants in shamefully confined spaces the best way to

educate the public and prevent the extinction of free-ranging elephants? We don't think so.

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Box 1. Families and Bond Groups

The close and lasting social relationships formed by female elephants are remarkable in the context of their fluid social system (Archie et al. 2006). Elephant families are composed of a discrete, predictable composition of (mostly) related individuals, but over the course of hours or days, these groups may temporarily separate and reunite, or they may mingle with other social groups to form larger social units or aggregations. Such groupings may be predicted on close social and genetic bonds, home range and season (Douglas-Hamilton 1972; Moss & Poole 1983; Sukumar 2003; Wittemyer, Douglas-Hamilton & Getz 2005; Archie et al. 2006; Moss & Lee in press). Habitat type, season, relatedness, personality traits, tradition, deaths of influential members, and the strength of a matriarch's leadership all play a role in the cohesiveness of families (Moss and Lee in press). In general, elephant families are smaller in forest habitats and larger in mixed savanna habitats (Sukumar 2003). Over years, families may split to form bond groups (Douglas-Hamilton 1972; Moss and Poole 1983; Wittemyer, Douglas-Hamilton & Getz 2005) or, sometimes, fuse to form new families (Moss & Lee in press; ATE database). Close acquaintances may be distinguished by association patterns, greeting behavior, coordinated movement and decision-making, and strong affiliative, cooperative and defensive behavior (Douglas-Hamilton 1972; Dublin 1983; Moss & Poole 1983; Lee 1987; Moss 1988; Poole 1998; Payne 2003). Individuals who have no close relatives within their family still benefit from the same cooperative behavior (Archie et al. 2006).

Box 2. Male Society

The social life of a wild male elephant is mentally and physically challenging. Developing in the tightly bonded society of females, young males maintain close relationships with their relatives and participate in social events affecting their family, albeit at lower intensities than their female age-mates (Lee and Moss 1999; Lee, Poole & Moss in press). By age nine males begin to spend time away from their families, and by fourteen they have usually departed (Lee & Moss 1999). Newly independent males must acquire fresh skills to adapt to the society of males where body size and fluctuating sexual state determine interactions and relationships (Poole 1989a). During the transition, young males' social activities center on getting to know age-mates, and playing with novel partners from outside the natal family (Lee 1986; Lee et al. in press). In this way males gather information crucial to longevity and reproductive success (Poole 1989a, 1989b; Poole, Lee & Moss in press; Lee, Poole & Moss in press). Among sexually inactive adults, relationships are "courteous," while interactions between those who are sexually active, particularly between those in the heightened sexual period of musth, become combative and highly aggressive (Poole 1987, 1989a). Male reproductive success is strongly dependent upon longevity; older, larger males in musth are dominant and produce significantly more offspring (Poole 1989a & b; Hollister-Smith, Poole, Archie, Vance et al. in press). The peak breeding age is between 45-50 years old. To survive to an age when a male can breed successfully requires utilizing skills that he has learned and honed over decades. A male must learn to recognize a large number of individual males by their scent, appearance and voice; remember their strengths relative to his own; keep track of which individuals are in musth, where they are located and what condition they are in; and monitor the changing location of pre-estrous and estrous females.

Figure 1. Elephants follow a daily routine in Amboseli: walking from the bush lands across the open plains to the swamp. (Photo: Petter Granli)

Figure 2. Asian female, Toni crippled by arthritis; photographed at the National Zoo in 2005. (Photo: Petter Granli)

Figure 3. Elephant calves learn what to eat by sampling food items from the mouths of their relatives. (Photo: Petter Granli)

Figure 4. An intricate network of bonds between individuals and families typifies the lives of females and their offspring. (Photo: Petter Granli)

Figure 5. Two males in musth battle for supremacy; fluctuating sexual states distinguish the dynamic activities, associations and relationships of adult males. (Photo: Joyce Poole)

Figure 6. Wild elephants live in a complex fission-fusion society that is remarkable for its fluidity on the one hand, and its close and enduring social relationships on the other. (Photo: Petter Granli)