2 ELEPHANTS IN TIME AND SPACE
EVOLUTION AND ECOLOGY
RAMAN SUKUMAR

The Asian elephant (*Elephas maximus*), and the African savanna and forest elephants (*Loxodonta africana* and *L. cyclotis*), are the only living representatives of the elephants, or proboscideans, a group whose evolutionary history goes back about 60 million years, to the Paleocene epoch (Gheerbrant, Sundre, and Cappetta 1996; Shoshani and Tassy 1996). During this period, changes in the earth's geology, climate, and vegetation brought about a spectacular radiation of the proboscideans, which occupied all continents except Australia and Antarctica (Sukumar 2003). They used a diverse range of habitats from swamps to desert, tundra to tropical forest, and riverine lowlands to alpine mountains. Whereas large body size was one of the distinct characteristics of elephant evolution, aberrant dwarf forms occurred on islands. During the Pleistocene epoch (1.8 million to 10,000 years ago), several elephant groups, including the woolly mammoth (*Mammuthus primigenius*) and the American mastodon (*Mammut americanum*) disappeared rather suddenly (Martin 1984; Martin and Klein 1984). These extinctions probably resulted from climate change or overkill by humans and may provide important insights for elephant conservation today.

The amazing evolutionary history of elephants, as well as many characteristics of their biology and ecology, has made this group a favorite in the perceptions and imaginations of people. Elephant ancestors, such as the mammoth and the mastodon, feature prominently in comics, books, and animated movies. Their bones and skeletons are a mainstay in many natural history museums across the world. Their sheer body size, large ears, and characteristic trunk and tusks are among the animal features most often eliciting curiosity and best remembered after a zoo visit, for children and adults alike. In this essay, I briefly review elephant evolution and explain the function and importance of some of the most characteristic elephant features. Although this essay does not directly illuminate ethical issues about the management and treatment of elephants, it provides crucial background information and some insights about why people care about elephants

Origin and Evolution
Northern Africa was the cradle of the proboscideans, where the early evolution of true elephants was nurtured. The warm and shallow waters of the

ancient Tethys Sea provided the setting for the aquatic origin of the family nearly 60 million years ago, a period when the earth was much warmer than today. For almost a century after its fossil remains were first discovered in Eocene epoch (54.8 to 33.7 mya) deposits of Egypt's Fayum Basin, it was believed that *Moeritherium,* a pig-sized and hippo-like creature, was the ancestral elephant. More recently, however, several fossils older than *Moeritherium* have been discovered, also in northern Africa. Among them, *Numidotherium,* with a tapir-like proboscis and teeth specialized for stripping leaves from branches at head height (Mahboubi et al. 1984), and the closely related *Phosphatherium,* pushed the ancestry of the proboscideans a few million years farther back, into the Paleocene epoch (65 to 54.8 mya) (Gheerbrant, Sundre, and Cappetta 1996). The anthracobunids (represented by five genera) from Eocene rocks of the Indian subcontinent (West 1980) were also contenders for being considered the ancestral proboscideans, but the northern African fossils suggest this to be unlikely.

The habitats of these Paleocene and Eocene proboscideans were shallow, muddy waters along fluctuating shorelines. The dentition of these primitive forms exhibits varying degrees of specialization, from a full complement of teeth to loss of canines, enlargement of incisors, and increased lophs, or ridges, in the molars. An increase in body size can also be seen, with one late Eocene proboscidean, *Barytherium,* having attained 4–5 tons, the size of a modern African elephant. The cooling and consequent decrease in precipitation after the mid-Eocene can perhaps explain the need for an herbivore to adapt, through increased body size, to consuming larger quantities of lower-quality vegetation than had its ancestors. The larger body size effectively increases the surface-to-volume ratio, reducing loss of heat. The cooling and drying trend continued into the Oligocene epoch (33.7 to 23.8 mya) when two types of more advanced proboscideans, known as palaeomastodontids, flourished. These were *Palaeomastodon* and *Phiomia,* each with tusks in both the upper and lower jaws and a distinct gap between the tusks and the molars. However, in strong contrast to their Eocene forebears, the palaeomastodontids were land dwellers.

The Oligocene seems to have been a period of relative evolutionary quiescence for elephant species, but the Miocene epoch (23.8 to 5.3 mya) witnessed possibly their greatest diversification. A new warming trend set in, but this time it was accompanied by a drier climate. Several elephant groups appeared in the Miocene, among them the enigmatic *Deinotherium,* one of the largest of all proboscideans, with tusks curving inward from the lower jaw. Another well-known and successful group of elephants, the mammoths, or mammutids (family Mammutidae), also made its stage debut in the Miocene. The best-known mammoth may be the American mastodon, which survived until the end of the Pleistocene. However, the deinotheres

and the mammutids, doomed to extinction, were only sideshows in the great proboscidean drama.

For a long time the gomphotheres—the stem group for true elephants—were a poorly defined group into which paleontologists dumped all proboscideans of uncertain affinity. Now we know, from cladistics (phylogenetic systematics) analysis, that the gomphotheres are distinct from the mammutids in being "long-jawed proboscideans" (Shoshani 1996). Two gomphothere genera that have attracted much attention are the "shovel-tuskers," *Platybelodon* from Eurasia and *Amebelodon* from North America. Both had long, flattened lower tusks, perhaps used to dig up roots and vegetation. As large as a modern Asian elephant, the genus *Gomphotherium* was a conservative form, with a short but thick trunk, tusks in both the upper and lower jaws, and low-crowned molars with three cusps, thick enamel, and a sequence of vertical (erupting from below the existing molar) and horizontal (erupting from the rear of the jaw and gradually moving forward) tooth replacement. During the late Miocene, an advanced gomphothere is believed to have given rise to the ancestral elephant.

By the late Miocene (10 mya), the climate began cooling again, accompanied by further drying of continental interiors. By about 7 million years ago, the reduced atmospheric carbon dioxide—a "reverse greenhouse"—accentuated this cooling and dryness and, more important, allowed the expansion of highly productive grassland on a global scale (Cerling et al. 1997). Herbivores responded to these global changes by adapting to a grazing diet, taking advantage of the abundant grasses. Corresponding dental changes included their development of high-crowned teeth (hypsodonty) bearing complex surface patterns—ridges of enamel with clefts filled in by a special tissue, coronal cementum—providing excellent grinding surfaces. Such teeth allowed them to break apart tough plant tissues to extract whatever nutrients were available. The late Miocene proboscideans show such dental adaptations.

True elephants probably evolved in Africa from one of two genera, *Stegotetrabelodon* and *Stegodibelodon,* of the subfamily Stegotetrabelodontinae. These genera were probably true elephantids, or at least intermediate between gomphotheres and elephantids (Maglio 1973; Todd and Roth 1996). About 6 million years ago in Africa, still during the late Miocene, one of these forms gave rise to *Primelephas,* considered to be the progenitor of the genera *Mammuthus, Elephas,* and *Loxodonta* of the family Elephantidae.

When the Miocene came to a close around 5.3 million years ago, there were alive twenty-two of approximately thirty-eight presently recognized proboscidean genera and a very large number of proboscidean species, including the primitive deinotheres, the mammutids, the gomphotheres, the stegodontids, and the elephantids—an amazing diversity that coexisted around the globe, with the exception of Australia and Antarctica. The ra-

diation of the true elephants began during the late Miocene, proceeded through the Pliocene epoch (5.3 to 1.8 mya), and continued into the Pleistocene. During the Pliocene, the earth's climate continued to cool and remained dry, but Pleistocene climates alternated between twenty or more glacial and interglacial phases. Elephant evolution during these periods included many new adaptations, especially in skull architecture and dentition. The combined grinding-and-shearing design of the gomphotheres' teeth now changed into a design mainly good for shearing (Maglio 1973). Other adaptations in dentition included almost exclusively horizontal replacement of the molar teeth, increase in the number of plates (lamellae) per molar, and an increase in crown height accompanied by thinning of the enamel. These changes enabled the elephants to chew coarse plant material, including abrasive grasses and bark. While the rates of change in *Mammuthus*, *Elephas*, and *Loxodonta* did not differ greatly during the first 2 million years of their evolution, over the next 4 million years *Mammuthus* and *Elephas* evolved more rapidly in their dental characteristics, as compared with *Loxodonta* (Maglio 1973). The woolly mammoth (*M. primigenius*) had some of the most advanced dental adaptations.

Mammuthus showed not only the most rapid rate of evolution, but among the elephants it also migrated the farthest from its site of origin. The earliest form of mammoth known is *M. subplanifrons* from eastern and southern Africa, followed by *M. africanavus* from northern Africa. The latter is believed to have migrated during the late Pliocene across Gibraltar or the Middle East into Europe, where it evolved into *M. meridionalis*. Mid-Pleistocene cooling caused the mammoth's woodland habitat to retreat in Europe and Siberia, giving way to grasslands. The steppe mammoth *M. trogontherii* can be clearly recognized in Eurasia during the late Pleistocene, finally culminating in the woolly mammoth (*M. primigenius*) about 200,000 years ago. Earlier, at the outset of the Pleistocene, about 1.8 million years ago, one of these Eurasian mammoths migrated during a period of low sea levels across Beringia into North America and evolved into *M. columbi*. The woolly mammoth migrated into North America about 100,000 years ago.

Elephas ekorensis is the first recognizable species of the genus *Elephas*, coexisting with the earliest mammoth in eastern Africa. There, *E. ekorensis* gave rise to *E. recki*, the dominant species of elephant at this time and one that went through several clear stages of dental evolution. It was, however, *E. planifrons*, the Asian derivative of *E. ekorensis*, or a closely related form, that eventually gave rise to the modern Asian elephant (*E. maximus*) through *E. hysudricus*, whose fossils are found in early Pleistocene deposits of the Siwalik hills of the Indian subcontinent.

Loxodonta adaurora, the earliest recognizable species of the loxodont lineage, to which today's African elephant belongs, seems to have changed lit-

tle through the Pliocene. In fact, *E. recki* may have displaced it as the dominant elephant by the late Pliocene. It is only by the middle Pleistocene, when *Elephas* disappears from Africa, that *Loxodonta* reemerges, in the form of *L. atlantica*, as the common elephant of Africa. The modern African elephants *L. africana* and *L. cyclotis*, however, seem to be derived from an advanced form of *L. adaurora*.

One of the most interesting aspects of proboscidean evolution during the Pleistocene is the rapid dwarfing of certain elephant species on islands isolated by rising sea levels (Lister 1996). The phenomenon is not limited to elephants, but the reversal in body size of these proboscideans is usually explained as an adaptation to limited resource availability on these islands. The best known of the dwarf elephants comes from the islands of the Mediterranean. *Elephas falconeri* stood a mere 1 m tall as an adult. Another example is seen on the Channel Islands off the coast of California. There the Columbian mammoth, *M. columbi*, reduced in size to 1.2–1.8 m and became the dwarf species *M. exilis*. After its extinction in mainland Eurasia and North America by about 11,000 years ago, the woolly mammoth (*M. primigenius*) survived and dwarfed rapidly on Wrangel Island, off the northern coast of Siberia, during the early Holocene epoch (the past 10,000 years). It eventually died out by about 4,000 years ago (Vartanyan, Garutt, and Sher 1993).

During the late Pleistocene (40,000 to 10,000 years ago), a wave of extinctions swept through Australia, Eurasia, North America, and South America, with a devastating impact on larger mammals. The extinctions of the mammoths of Eurasia and North America, the American mastodon, and the gomphotheres of South America occurred toward the end of this period. The causes of this rapid extinction wave are still being debated. Two major classes of explanation have been suggested, one centered on climate change and the other on overkill, defined as "the human destruction of native fauna either by gradual attrition over many thousands of years, or suddenly in as little as a few hundred years or less" (Martin 1984).

The transition from the last Pleistocene ice age to the present climate was perhaps the most severe of any of the Pleistocene's many glacial-to-interglacial alternations. Not only did the globe warm considerably but the seasonal climate patterns changed. Resultant changes in flora and fauna may have led to the collapse of large-bodied mammal species through changes in available nutrition or disruption of reproductive cycles (Guthrie 1984; Kiltie 1984; Webb 1984). Opposing hypotheses invoke humans as the perpetrators of the late Pleistocene extinctions. The overkill idea first appeared when anthropologists proposed that Paleoindians, who had migrated across Beringia into North America about 12,000 years ago, went on a "Blitzkrieg" and hunted the mammoth and mastodon to extinction

within a few hundred years, using their characteristic "Clovis" spear points (Mosimann and Martin 1975; Martin 1984). Support for this theory comes from the coincident dates of human arrival and megafaunal extinctions on several continents, together with evidence at a few kill sites that demonstrates how Paleoindians may have killed these giants. Another human-caused extinction hypothesis postulates that humans carried a "hyperdisease" that infected a variety of mammalian species (MacPhee and Marx 1997).

Most likely a suite of factors contributed to the decline of so many proboscidean species. The more synthetic theories incorporate both climate change and human expansion in their reasoning (Haynes 1991). Whatever the true cause of the extinctions, they may hold lessons for the conservation of today's elephants. We may be witnessing the onset of another major phase of climate change, this time driven by human-induced increase of greenhouse gases in the atmosphere. At the same time, populations of both African and Asian elephants are being hunted extensively for ivory and other products, while their habitats are rapidly transforming into human-dominated landscapes. Conditions today may be ominously similar to those prevailing during the late Pleistocene.

By the end of the last ice age, the world had lost much of its megafauna. This period also marks the dawn of agriculture, the expansion of human societies, and, by the mid-Holocene, the rise of the early major civilizations in the Nile, Tigris-Euphrates, and Indus river basins. Concurrently, we find evidence that several human societies independently developed close relationships with elephants. The earliest evidence for elephant taming comes from the animal motifs on steatite seals, about 4,000 years old, of the Indus (or Harappan) civilization; though the elephant may well have been tamed earlier by people of the Indian subcontinent (Lahiri Choudhury 1991). In Asia this association deepened into a multifaceted relationship spanning the entire spectrum of the social, political, economic, and religious life of people. In Africa an early culture of capture of elephants in the north of the continent died out quickly.

Social Behavior

Elephants are among the most sexually dimorphic (different in form) of all mammals. Polygyny is a common mating system in dimorphic species. Polygynous males compete with one another to maximize their success in mating, but only a portion of the males succeed. As a result, variance in reproductive success is much greater in males than in females. The core of elephant society is the matriarchal family (Moss 1988), composed of an adult cow elephant and her immature offspring of both sexes. However, the number of elephants observed in a family or in larger social groups varies across the geographic ranges of African and Asian elephants. I have pro-

posed the term *joint family* be used if families consist of more than one adult cow and their offspring, as one can sometimes observe (Sukumar 1994). Higher levels of social organization such as bond/kin groups and clans have also been suggested for some African elephant populations in eastern Africa (Douglas-Hamilton and Douglas-Hamilton 1975; Laws, Parker, and Johnstone 1975; Moss 1988) and Asian elephant populations in southern India (Sukumar 1989; Baskaran et al. 1995). Indeed, Moss (1988) proposes that social organization in elephants radiates from the basic family unit through "a multi-tiered network of relationships" that eventually encompasses the entire population in a region. However, in central Africa (Turkalo and Fay 1995) and Sri Lanka (McKay 1973; Kurt 1974; Fernando and Lande 2000) observations indicate simpler levels of organization.

One of the primary functions of the elephant family group may be the protection of juveniles from large predators, such as lions in Africa and tigers in Asia (Douglas-Hamilton and Douglas-Hamilton 1975; Gadgil and Nair 1984). The largest elephant groups are indeed found in open habitats. Large carnivores are most abundant in savanna woodlands in Africa and deciduous forests and their associated grasslands in Asia. Elephant group sizes are probably determined by factors such as forage abundance, seasonality, animal density and numbers, human disturbance, natural predation pressure, and possibly even genetic relatedness. Among these factors, food and resource availability probably plays the most important role in determining family or group size. Open savanna or forest habitats tend to have a high abundance of elephant foods. Because these habitats also show much seasonal variation in food abundance, one would expect group sizes to vary likewise. However, larger elephant groups may be seen either during the wet season when resources are abundant (Western and Lindsay 1984; Poole and Moss 1989) or during the dry season when elephants congregate around scarce water sources and their chances of social contact and association increase (Sukumar 1985). In contrast, it is in the rain forests of central Africa where biologists have observed the simplest social groups and the smallest group sizes of any elephant population (Turkalo and Fay 1995). Forage plants are widely dispersed in these forests and large carnivores are absent. Several observers have also noted that elephants may come together in larger groups in regions where elephants are hunted or where there is a history of poaching elephants for ivory (Abe 1994). Here the predators are humans, and the response of elephants is similar to that shown to other natural predators.

In most regions, elephant social units, whether they are clans or family-bond groups, usually show rather fixed patterns of seasonal movement over the year. There is, however, enormous variation in home range size of elephant groups, both in Africa (Douglas-Hamilton 1972; Leuthold 1977; Lin-

deque and Lindeque 1991; Thouless 1996) and in Asia (Baskaran et al. 1995; Fernando and Lande 2000). Although the home range sizes of most elephant populations are between 500 and 2,000 km², they range from only 50–100 km² in Lake Manyara, Tanzania, and southeastern Sri Lanka, to as much as 10,000 km² in Namibia. In regions of low to medium rainfall, home range size is clearly inversely related to rainfall and productivity. However, in high rainfall areas such as rain forests, home range size seems to be larger because of the greater dispersion of food plants. Bull elephants show greater variation in their movement patterns and range sizes when compared with female elephants.

Social organization into family groups or clans requires well-developed communication among group members. Not surprisingly, different modes of communication seem well developed among elephants, and scientists have focused their research on this particularly interesting topic. Communication based on smell and sound is developed to a high degree of sophistication. Elephants can broadcast an array of chemical signals through urine, feces, breath, temporal glands, and sweat glands between the toes (Rasmussen 1998). The nose of an elephant, its trunk, is highly developed for receiving and assessing these signals. In this function, two specialized organs in the roof of the mouth, the vomeronasal organ and the palatal pits, play important roles.

Elephants also use infrasound, sound waves with frequencies as low as about 10 hertz to communicate over long distances (Payne, Langbauer, and Thomas 1986; Poole et al. 1988; Langbauer et al. 1991; Garstang et al. 1995). Both female elephants in estrus and male elephants in musth broadcast unique infrasonic calls to attract mates (Poole et al. 1988). The ability of a matriarch to discriminate between calls of related and unrelated individuals may eventually be crucial for the survival of her family (McComb et al. 2001).

A female elephant in estrus advertises her condition through characteristic behavior (Moss 1983), an infrasonic call (Poole et al. 1988), and chemical signals (Rasmussen 1998). The specific compound released in urine by an estrous Asian elephant has been identified as (Z)-7–dodecenyl acetate, the same compound used by many female insects to attract mates—a remarkable example of convergent evolution (Rasmussen et al. 1996). An adult bull usually detects estrus through a behavior termed *flehmen*. Flehmen involves touching the urogenital orifice of the cow or urine on the ground with the tip of the trunk and transferring a small quantity to the roof of the mouth where a pair of vomeronasal organs assays the substances (Rasmussen et al. 1982).

An important determinant of reproductive success in bull elephants is musth, a physiological and behavioral phenomenon that has been compared to the rut in ungulates (Eisenberg, McKay, and Jainudeen 1971; Poole

1987). Musth was well-known in the Asian elephant and accurately described in ancient Indian literature (Edgerton 1931; Lahiri Choudhury 1992) but was first recognized in the African elephant only in recent times (Poole and Moss 1981). Usually an annual occurrence in adult bulls, musth is manifested through secretion of a fluid from the temporal glands, a sharp rise in the levels of blood androgens (such as testosterone), and behavioral changes such as increased aggression (Jainudeen, Katongole, and Short 1972; Rasmussen et al. 1984; Poole 1987; Niemuller and Liptrap 1991). The nature of the chemical secretion changes with age; younger bulls secrete sweet-smelling compounds such as esters and alcohols while older bulls secrete foul-smelling compounds such as frontalins and nonanone (Rasmussen, Riddle, and Krishnamurthy 2002). Musth bulls broadcast a ketone (cyclohexanone) that seems to serve as a specific male-to-female signal (Rasmussen, Haight, and Hess 1990).

The intensity of musth usually increases with age and also correlates with good body condition. A bull in musth is dominant over non-musth bulls, even older or larger ones, and has much better chances of mating with a cow in estrus than a non-musth bull (Poole 1989a, 1989b). Bulls within a population seem to show distinct spacing in the time of the year they come into musth. The typical pattern seems to be that the older, higher-ranking individuals come into musth during the most favorable period of the year (wet season), while younger bulls come into musth at other times.

High levels of testosterone weaken the immune system of an individual, increasing its vulnerability to parasitism and disease (Folstad and Karter 1992). Thus, musth can be considered within the framework of the handicap principle, as enunciated by Zahavi (1975). A bull surging with testosterone is advertising its genetic quality to female elephants. A female's choice of a bull in musth over one not in musth would thus be adaptive. Similarly, we can also postulate a sexual selection role for tusk size in elephants (Sukumar 2003). An enormous pair of tusks in a bull elephant (or any proboscideans such as the stegodon or the mammoth) can be a significant handicap; female choice for tusk size thus may serve the same adaptive purpose as female selection of a bull in musth (Watve and Sukumar 1997). Indeed, tuskless bulls and tusked bulls could be following alternative evolutionarily stable strategies, defined in game theory as strategies that, over evolutionary time, are able to withstand the invention of new strategies. The tuskless bulls could be diverting resources to body condition and more intense expression of musth, and the tusked bulls could be benefiting from female choice for tusk size (Sukumar 2003).

Foraging Ecology of Elephants

Elephants are generalist herbivores. Their sheer body size and resulting food requirements means that elephants feed on a variety of plant species

and plant parts. Most studies of elephant feeding ecology list well over a hundred species of plants consumed even within one region (Sukumar 2003). Elephants eat leaves, bark, twigs, roots, stem pith, fruits, and flowers. Yet, they select distinctly different plant parts depending on the availability of seasonally changing plant forms, and they show a preference for particular plant families (Sukumar 1989). In quantitative terms, elephants usually prefer grasses, reeds and sedges (Poaceae, Cyperaceae), palms, legumes, many species of the order Malvales, and trees and shrubs of the families Combretaceae, Euphorbiaceae, Rhamnaceae, and Moraceae (Sukumar 2003). In drier habitats such as savanna woodland or deciduous forest, elephant dietary habits usually alternate between predominantly grazing (i.e., feeding on grasses and sedges) during the wet season and browsing (feeding on bamboo, shrubs, and trees) during the dry season (Field and Ross 1976; Sukumar 1989). In moister habitats, such as rain forest, their diet includes several kinds of fruits (Short 1981; White, Tutin, and Fernandez 1993) in addition to the leaves of lianas, vines, shrubs, young trees, and monocots such as palms (Olivier 1978).

Scientists have used the stable carbon isotopic technique to determine the ratio between frequencies of occurrence of different carbon isotopes in elephant bone collagen. These measurements help them determine the dietary ratio of browse or dicotyledonous species to grass or monocotyledonous species (van der Merwe, Lee-Thorp, and Bell 1988; Sukumar and Ramesh 1992) and demonstrate that the contribution of browse plants to elephants' protein synthesis is significantly higher than what could be inferred from the proportion of time they actually spend feeding on browse as compared with grasses (Sukumar and Ramesh 1992). There is a clear positive relationship between rainfall and the extent of browse feeding (Sukumar 2003). Further, elephant populations may be entirely browsers or mixed feeders on browse and grass, but they can never survive entirely as grazers. Thus, browse species are extremely important in the nutrition of elephants (Koch et al. 1995; Sukumar and Ramesh 1995).

Body size is obviously a key determinant of an elephant's foraging strategy. Elephants consume, in dry matter, 1.5–2.0% of their body weight daily. Dentition (Maglio 1973) and gut anatomy and physiology (Clemens and Maloiy 1982) are of equal importance in fostering elephants' strategy as nonruminant "megaherbivores" that subsist on coarse plants of low nutritional quality. They depend on high-crowned molars with a complex pattern of folded plates and occlusal surfaces to grind up the food and rely on hindgut fermentation to digest it.

The elephant's mineral and vitamin requirements are poorly understood. The nutrient requirements for other nonruminants, such as the horse, are usually viewed as adequate for elephants (Dierenfeld 1994). The elephant's appetite for bark may be partly a search for minerals such as cal-

cium (Bax and Sheldrick 1963; Sukumar 1989) or for essential fatty acids (McCullagh 1973). Sodium may also be obtained from bark or from water and soil rich in this mineral (Weir 1972; Ruggiero and Fay 1994). Plant chemical defenses, such as tannins, alkaloids, and cyanogenic compounds also influence the choice of plant species and parts (Rosenthal and Janzen 1979). *Geophagy*—the consumption of soils and clays—may help bind or neutralize certain plant toxins such as alkaloids and thus may aid in digestion (Duquette 1991).

Elephants have been termed a *landscape species*. Because of their body size and food requirements, they have a tremendous impact on large areas, shaping the ecology of entire landscapes. By debarking, damaging, and pushing over trees, elephants can convert woodlands into grasslands (Laws 1970). This transformation favors the increase of grazing ungulate populations. Even in tropical moist forests elephants have created gaps in the forest canopy, and new plant regeneration in these openings may favor smaller ungulates. Ecologists have documented the role of elephants in seed dispersal (Lieberman, Lieberman, and Martin 1987; White et al. 1993), but few plants may have an obligate relationship with the elephant for their dispersal (Hawthorne and Parren 2000).

The dramatic transformation of woodland into grassland in parts of Africa triggered an intense debate over elephant population management through culling. One school of thought considered this habitat transformation as unnatural, caused mainly through human factors such as conversion of habitat for agriculture and compression of elephant populations (e.g., Buss 1977), while the other considered this as part of the natural ecology of the savanna woodland ecosystem (e.g., Caughley 1976; Norton-Griffiths 1979; Sinclair 1981). Ecologists proposed various hypotheses to explain the dynamics of elephants and vegetation. The "stable limit cycle" model of elephants and trees, a predator-prey feedback model for elephant-tree dynamics with oscillation periods of about 270 years, was the one that stimulated the most debate (Caughley 1976). Recent efforts at modeling the limit cycle for elephants and trees have shown that this model is unlikely to operate under realistic conditions of elephant and tree densities (Duffy et al. 1999). Nevertheless, Caughley's model served a very useful purpose; it spurred ecologists to explore the nonequilibrium nature of elephant-vegetation dynamics in semiarid ecosystems such as the savanna woodlands (Sukumar 2003).

Now the dynamic and stochastic nature of elephant-vegetation systems is much better appreciated. Several factors, including climatic fluctuations, fire, and changing populations of browsing and grazing herbivores drive the dynamics of grassland and woodland in semiarid Africa (Western and van Praet 1973; Norton-Griffiths 1979). Studies in the Serengeti-Mara re-

gion exemplify the complex nature of these dynamics. The potential of trees such as *Acacia tortilis* to regenerate, replacing those of their species killed by elephants, may be inadequately realized because of fire damage (Croze 1974), especially in combination with browsing by giraffes (Pellew 1983). Once these factors, in concert, convert enough woodland to grassland, the proliferation of grazers such as wildebeest potentially could lower the standing crop of grass and hence the frequency or intensity of fires. This would give these trees another opportunity to regenerate, or elephants could persistently feed on the tree seedlings, thus locking the system into the grassland stage (Dublin, Sinclair, and McGlade 1990). In fact, the semi-arid regions of Africa could oscillate between two stable states, one where woodlands have relatively few elephants and the other where grasslands have a high abundance of elephants (Dublin et al. 1990). Similarly, I have elsewhere argued that elephant-vegetation dynamics can be expected to vary between a highly fluctuating condition in the markedly seasonal savanna woodlands to a relatively stable condition in aseasonal rain forests (Sukumar 1989, 2003).

The intrinsic dynamics of elephant populations are also of both theoretical and practical interest (Sukumar 2003). As can be expected of a large mammal, the elephant has a late age of sexual maturity (typically 10–15 years old), low reproductive rate (interbirth interval of four to six years), and low juvenile (5–15% per year) and adult mortality (2–3% per year in females). One consequence of these life history traits is the relative stability of elephant populations. When compared with other mammals, elephant populations generally do not intrinsically increase or decrease at high rates. On average, Asian elephant populations are unlikely to grow at greater than about 2% per year (Sukumar 1989); nor African elephant populations (in savannas), at greater than about 4% per year (Hanks and McIntosh 1973). Exceptions to this rule are the Addo and Kruger elephant populations in South Africa that have increased at more than 6% per year for over five decades (Whitehouse and Hall-Martin 2000; see also Whyte and Fayrer-Hosken, Chapter 20 in this volume). Similarly, decreases in population size are unlikely to be drastic, with the exception of the impact of a catastrophic drought, as in the case of Tsavo (Kenya) during 1970–1971 (Corfield 1973).

Elephants are adaptable to a range of conditions. I have argued that demographic traits in elephants, resulting from natural selection, can be expected to vary across environmental gradients. Thus, elephants in the relatively unstable semiarid habitats can be expected to show life history traits indicative of *r*-selection, favoring a reproductive strategy in which many offspring are produced (on a relative scale), while those in the more stable environments of aseasonal rain forests have traits indicative of *K*-selection, favoring a reproductive strategy in which few offspring are produced

(Sukumar 1989, 2003). Observed demographic variables in elephant populations broadly support this expectation; thus, female elephants in semi-arid regions not only have lower mean age at first reproduction and shorter interbirth intervals but also greater variance in these traits as compared with female elephants living in moist forest.

Human-Elephant Interactions

In recent centuries, human interactions with elephants have affected elephant population dynamics. In Asia, elephants have been captured in large numbers over the past 4,000 years, primarily by kings and chieftains for use in armies but also for other purposes, including logging and cultural festivities (Sukumar 1989). The African elephant has been hunted for ivory both historically (Spinage 1973) and in recent times (Douglas-Hamilton 1987). Various models of hunting of African elephants for ivory have clearly shown this to be the major factor in decline of populations over the past two centuries (Pilgram and Western 1986; Caughley, Dublin, and Parker 1990), though one model has also implicated habitat loss until about 1970 in this decline (Milner-Gulland and Beddington 1993). Poaching for ivory and other elephant products, such as hide and meat, has also decimated Asian elephant populations, especially in the region between Myanmar and Vietnam (Menon 2002) or resulted in highly female-biased sex ratios, as in southern India (Sukumar 2003).

One of the most significant effects of elephants on human interests is the destruction of agricultural crops, often accompanied by manslaughter in Asia and Africa (Blair, Boon, and Noor 1979; Sukumar 1989; Barnes 1996; Hoare 1999). These adverse interactions are now commonly referred to as *human-elephant conflict*. Not surprisingly, crops raided by elephants are usually the cultivated analogues of the wild-plant types that elephants consume. Cultivated grasses, palms, and legumes are commonly targeted (Sukumar 1989). There is also considerable selection for plant parts consumed in cultivated fields. Male elephants have a much greater propensity to raid crops than do the female-led family groups (Sukumar and Gadgil 1988; Hoare 1999) and may obtain significant proportions of their annual dietary requirements, both in quantitative and qualitative terms, from agricultural land (Sukumar 1989).

We need to gain a better understanding of the proximate and ultimate causes of crop-raiding behavior to mitigate human-elephant conflicts and the adverse consequences of these conflicts for elephants, specifically the capture or killing of the elephant perpetrators. Studies of human-elephant conflict should be considered within the framework of elephant ecology and should draw on landscape ecology, foraging and movement theory, and studies of social behavior (Sukumar 2003). Habitat loss is probably one of the main proximate causes of crop raiding. Given a certain fidelity to

their home range (Baskaran et al. 1995), elephant family groups or solitary bulls may continue to move into land converted for cultivation. There could be opportunistic raiding related to the seasonal movement pattern of elephants observed in some elephant populations (Sukumar 1989). The same could be true of elephants having to traverse agricultural land to reach water sources (Allaway 1979; Sukumar 1989). One proximate factor that has a fairly clear relationship to raiding is the fragmentation of habitat (Sukumar 1989, 2003; Nath and Sukumar 1998). Habitat fragmentation increases the chances of elephants making contact with cultivated land, while the habitat fragments provide convenient daytime refuges for elephants that raid crops during the night.

In ultimate terms, however, crop raiding can be thought of as a strategy by elephants to maximize their forage intake both quantitatively and qualitatively (Sukumar 1989). Cultivated crops are usually more palatable and nutritious than wild-forage plants (Sukumar 1989; Osborn 1998). They provide more protein and minerals, such as calcium and sodium, as compared with analogous wild species. Raiding involves taking risks because the elephants may have to face hostile farmers. Some elephants may thus opt out of raiding even if they have access to crop fields. The higher propensity of male elephants to raid crops as compared with female elephants may be related to the higher variance in male reproductive success (Sukumar and Gadgil 1988). Selection pressures would favor the evolution of risky strategies by males for enhancing reproductive success. In this instance, the extra nutrition from crop plants would potentially benefit a male elephant through better body condition and more intense expression of musth, thereby increasing its chances of mating. Crop raiding by bulls could thus be a manifestation of a "high risk-high gain" strategy molded by natural selection to enhance reproductive success. Obviously, the realized reproductive success could depend on the interaction with humans; a bull could be injured or killed in the process of raiding.

If learning plays an important role in the development of behavior, including the choice of food plants, it follows that crop raiding could be learned behavior that is transmitted culturally from one generation to the next (Sukumar 1985, 1995a). Extreme climatic events such as severe drought may also trigger the long-distance movement or dispersal of elephants, thus escalating conflict (Sukumar 1995a).

Elephants in Human Culture

It is not surprising that these land giants have played a prominent role in human cultures both symbolically and more directly as beasts of burden (Lahiri Choudhury 1991, Chapter 7 in this volume; Ross 1992). Both Asian and African elephants have been tamed in historical times. With the former species, this culture has continued to flourish to present times, while

with the latter the practice disappeared by about 2,000 years ago and was revived only marginally during the nineteenth century. The elephant has also been deified in Asia, while its role in religion has remained at the totemic level in Africa.

The earliest evidence for elephant taming comes from the seals of the Indus Valley civilization about 4,000 years ago (Carrington 1958), though non-Aryan people in the subcontinent may have tamed it even earlier (Lahiri Choudhury 1991, Chapter 7). The culture of capturing and training elephants in large numbers flourished with the rise of the Aryan republics and kingdoms in northern India and seems to have reached an early peak during Mauryan times (Lahiri Choudhury 1991; Sukumar 2003). Sanctuaries for the protection of wild elephants, presumably to supply the king's army, were set up in ancient India (see the translation of the *Arthashastra,* an ancient manual on statecraft, by Rangarajan 1992); the army of Chandragupta Maurya (late fourth-century BCE) included a 9,000–strong elephant force. During the early centuries of the modern era, we observe the imposition of a taboo on consuming elephant meat and also the rise of the classic elephant-headed deity Ganesha in the Indian subcontinent, reflecting the importance of this animal at least to certain powerful social classes (Sukumar 2003).

The African elephant, possibly a now extinct form from the Atlas Mountains in the north, was tamed by the Carthaginians and used in the Mediterranean wars from around the third century BCE. The elephants that Hannibal marched across the Alps in his much-celebrated campaign against Rome were mostly African (Scullard 1974). This ancient culture of capturing elephants, as well as their use in war, died out in Africa by about 2,000 years ago. On both continents the rise of the elephant culture—specifically the large-scale capture and use of the animal—probably was associated with the rise of major republics and kingdoms. The Carthaginians possibly overexploited a small elephant population already isolated in northern Africa. The Egyptians did not have access to Africa's large, essentially sub-Saharan elephant populations; the few elephants used by the Ptolemies came from Asia or were captured from the Carthaginians. The rulers of the Indian subcontinent, however, could exploit a ready source of abundant elephant populations, virtually at their doorsteps. African elephants could be tamed, as was shown in the erstwhile Belgian Congo during the late nineteenth century, but in modern times, the entire context has changed. It is unlikely that Africa would ever witness an Asian-type elephant culture; even in Asia this culture is on the decline.

Conservation of Elephants

The survival of elephants is linked not merely to biological or ecological factors but also to social, economic, and political forces. Conservation efforts

to save Asian and African elephants face many similar problems, but there are also striking differences, especially with regard to the specific threats to these species (Sukumar 2003).

The population of wild African elephants (ca. 400,000) may be tenfold larger than that of the Asian elephant (ca. 45,000) with a corresponding difference in presently available habitat area; >5 million km² in Africa versus about 0.5 million km² in Asia. Extant Asian elephants are scattered in a series of isolated populations in fragmented landscapes. The majority of these populations may be small and not viable in the long term (Sukumar 1995b). Thus, the availability of sufficient habitat and the maintenance of large, integral landscapes are key to the survival of Asian elephant populations. This factor is also important in some regions of Africa, for instance, in western Africa, where the fragmented habitats and isolated elephant populations resemble the Asian situation. The fragmentation of habitat is not just due to human settlement and agricultural expansion. Roads, railway lines, dams, canals, and other developmental projects are also barriers to elephant movement. The maintenance or augmentation of existing "corridors" or creation of new corridors may thus be key to maintaining landscape integrity.

Human-elephant conflict is an issue of such magnitude that it must be resolved if local people are ever to consider and accept elephant conservation measures. In many regions, people who have traditionally coexisted with elephants have developed simple methods to chase them away from their settlements and crop fields. In the modern world, people's perception of the elephant and their tolerance to its crop raiding is changing. Barriers such as high-voltage electric fences are widely used in Asia and in Africa (Sukumar 1989; Thouless and Sakwa 1995; Nath and Sukumar 1998; O'Connell-Rodwell et al. 2000). These tactics can be reasonably successful if local communities actively participate in their maintenance (see Kiiru, Chapter 19 in this volume; Seneviratne and Rossel, Chapter 17 in this volume). Some form of elephant population management is also needed to contain crop raiding and loss of human lives (Sukumar 1991).

Poaching for ivory and other elephant products is linked to a hierarchy of markets, from local to regional and international (Barbier et al. 1990; Dublin et al. 1995; Menon, Sukumar, and Kumar 1997; Nash 1997; Martin and Stiles 2002; Duffy, Chapter 22 in this volume). Strategies to control poaching should thus include law enforcement by the range states, public education about the value of elephants, and the regulation of illegal international trade through effective enforcement of CITES, the Convention on International Trade in Endangered Species of Wild Flora and Fauna.

One additional factor has only marginal relevance for African ele-

phants but is very important for Asian elephants, namely, the welfare and management of animals in captivity. About 16,000 Asian elephants, or about 30% of the global population, are kept in timber camps, zoos, or temples or are privately owned (Krishnamurthy and Wemmer 1995; Lair 1997). With a few notable exceptions (Kurt 1995; Sukumar et al. 1997; Taylor and Poole 1998), most of these captive stocks are declining because of the paucity or absence of captive births combined with excessive deaths and inadequate welfare.

Elephants can be powerful flagships for the conservation of the rich biodiversity of Asian and African tropical landscapes. It will be an insufficient conservation outcome if elephants merely survive as species. We must conserve elephant populations that actually represent their present diverse genetic makeup (Fernando et al. 2000; Fleischer et al. 2001; Eggert, Rasner, and Woodruff 2002) as well as the spectrum of landscapes they presently inhabit. The complex challenges to elephants' survival can be addressed only through a balanced, pragmatic, and ethical approach to conservation (Sukumar 2003).

References

Abe, E. L. 1994. The behavioural ecology of elephant survivors in Queen Elizabeth National Park, Uganda. DPhil diss., University of Cambridge.

Allaway, J. D. 1979. Elephants and their interactions with people in the Tana river region of Kenya. PhD diss., Cornell University.

Barbier, E. B., Burgess, J. C., Swanson, T. M., and Pearce, D. W. 1990. *Elephants, economics and ivory.* London: Earthscan Publications.

Barnes, R. F. W. 1996. The conflict between humans and elephants in the Central African forests. *Mammal Review* 26: 67–80.

Baskaran, N., Balasubramanian, M., Swaminathan, S., and Desai, A. A. 1995. Home range of elephants in the Nilgiri Biosphere Reserve, South India. In J. C. Daniel and H. S. Datye (eds.), *A week with elephants: Proceedings of the international seminar on Asian elephants, June 1993* (pp. 296–313). Bombay: Bombay Natural History Society and New Delhi: Oxford University Press.

Bax, P. N., and Sheldrick, D. L. W. 1963. Some preliminary observations on the food of elephants in the Tsavo Royal National Park (East) of Kenya. *East African Wildlife Journal* 1: 40–53.

Blair, J. A. S., Boon, G. G., and Noor, N. M. 1979. Conservation or cultivation: The confrontation between the Asian elephant and land development in peninsular Malaysia. *Land Development Digest* 2: 27–59.

Buss, I. O. 1977. Management of big game with particular reference to elephants. *Malayan Nature Journal* 31: 59–71.

Carrington, R. 1958. *Elephants: A short account of their natural history, evolution and influence on mankind.* London: Chatto and Windus.

Caughley, G. 1976. The elephant problem: An alternative hypothesis. *East African Wildlife Journal* 14: 265–283.

Caughley, G., Dublin, H., and Parker, I. 1990. Projected decline of the African elephant. *Biological Conservation* 54: 157–164.

Cerling, T. E., Harris, J. M., MacFadden, B. J., Leakey, M. G., Quade, J., Eisenmann, V., and Ehleringer, J. R. 1997. Global change through the Miocene/Pliocene boundary. *Nature* 389: 153–158.

Clemens, E. T., and Maloiy, G. M. O. 1982. The digestive physiology of three East African herbivores: The elephant, rhinoceros and hippopotamus. *Journal of Zoology* (London) 198: 141–156.

Corfield, T. F. 1973. Elephant mortality in the Tsavo National Park, Kenya. *East African Wildlife Journal* 11: 339–368.

Croze, H. 1974. The Seronera bull problem: Part II. The trees. *East African Wildlife Journal* 12: 29–47.

Dierenfeld, E. S. 1994. Nutrition and feeding. In S. K. Mikota, E. L. Sargant, and G. S. Ranglak (eds.), *Medical management of the elephant* (pp. 69–79). West Bloomfield, MI: Indira Publishing House.

Douglas-Hamilton, I. 1972. On the ecology and behaviour of the African elephant. DPhil diss., Oxford University.

Douglas-Hamilton, I. 1987. African elephants: Population trends and their causes. *Oryx* 21: 11–14.

Douglas-Hamilton, I., and Douglas-Hamilton, O. 1975. *Among the elephants.* New York: Viking Press.

Dublin, H. T., Sinclair, A. R. E., and McGlade, J. 1990. Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *Journal of Animal Ecology* 59: 1147–1164.

Dublin, H. T., Milliken, T., and Barnes, R. F. W. 1995. *Four years after the CITES ban: Illegal killing of elephants, ivory trade and stockpiles.* Gland, Switzerland: International Union for Conservation of Nature and Natural Resources / Species Survival Commission African Elephant Specialist Group.

Duffy, K. J., Page, B. R., Swart, J. H., and Bajic, V. B. 1999. Realistic parameter assessment for a well known elephant-tree ecosystem model reveals that limit cycles are unlikely. *Ecological Modelling* 121: 115–125.

Duquette, J. T. 1991. Detoxification and mineral supplementation as functions of geophagy. *American Journal of Clinical Nutrition* 53: 448–56.

Edgerton, F. (trans.) 1931. *The elephant-lore of the Hindus: The elephant-sport (Matangalila) of Nilakantha.*: New Haven, CT: Yale University Press. Repr., New Delhi: Motilal Banarsidass, 1985.

Eggert, L. S., Rasner, C. A., and Woodruff, D. S. 2002. The evolution and phylogeography of the African elephant inferred from mitochondrial DNA sequence and nuclear microsatellite markers. *Proceedings of the Royal Society, London, B* 269: 1993–2006.

Eisenberg, J. F., McKay, G. M., and Jainudeen, M. R. 1971. Reproductive behaviour of the Asiatic elephant (*Elephas maximus maximus* L.). *Behaviour* 38: 193–225.

Fernando, P., and Lande, R. 2000. Molecular genetic and behavioral analysis of social organization in the Asian elephant (*Elephas maximus*). *Behavioural Ecology and Sociobiology* 48: 84–91.

Fernando, P., Pfrender, M. E., Enclada, S. E., and Lande, R. 2000. Mitochondrial DNA variation, phylogeography, and population structure of the Asian elephant. *Heredity* 84: 362–372.

Field, C. R., and Ross, I. C. 1976. The savanna ecology of Kidepo Valley National Park II. Feeding ecology of elephant and giraffe. *East African Wildlife Journal* 14: 1–15.

Fleischer, C., Perry, E. A., Muralidharan, K., Stevens, E. E., and Wemmer, C. M. 2001. Phylogeography of the Asian elephant (*Elephas maximus*) based on mitochondrial DNA. *Evolution* 55: 1882–1892.

Folstad, I., and Karter, A. J. 1992. Parasites, bright males and the immuno-competence handicap. *American Naturalist* 139: 603–622.

Gadgil, M., and Nair, P. V. 1984. Observations on the social behaviour of free ranging groups of tame Asiatic elephant (*Elephas maximus* Linn). *Proceedings of the Indian Academy of Sciences (Animal Sciences)* 93: 225–233.

Garstang, M., Larom, D., Raspet, R., and Lindeque, M. 1995. Atmospheric controls on elephant communication. *Journal of Experimental Biology* 198: 939–951.

Gheerbrant, E., Sundre, J., and Cappetta, H. 1996. A Palaeocene proboscidean from Morocco. *Nature* 383: 68–70.

Guthrie, R. D. 1984. Mosaics, allelochemics, and nutrients: An ecological theory of late Pleistocene megafaunal extinctions. In P. S. Martin and R. G. Klein (eds.), *Quaternary extinctions: A prehistoric revolution* (pp. 259–298). Tucson: University of Arizona Press.

Hanks, J., and McIntosh, J. E. A. 1973. Population dynamics of the African elephant (*Loxodonta africana*) *Journal of Zoology* 169: 29–38.

Haynes, G. 1991. *Mammoths, mastodonts and elephants: Biology, behavior, and the fossil record.* Cambridge: Cambridge University Press.

Hawthorne, W. D., and Parren, M. P. E. 2000. How important are forest elephants to the survival of woody plant species in Upper Guinean forests? *Journal of Tropical Ecology* 16: 133–150.

Hoare, R. E. 1999. Determinants of human-elephant conflict in a land-use mosaic. *Journal of Applied Ecology* 36: 689–700.

Jainudeen, M. R., Katongole, C. B., and Short, R. V. 1972. Plasma testosterone levels in relation to musth and sexual activity in the male Asiatic elephant, *Elephas maximus. Journal of Reproduction and Fertility* 29: 99–103.

Kiltie, R. A. 1984. Seasonality, gestation time, and large mammal extinctions. In P. S. Martin and R. G. Klein (eds.), *Quaternary extinctions: A prehistoric revolution* (pp. 299–314). Tucson: University of Arizona Press.

Koch, P. L., Heisinger, J., Moss, C., Carlson, R. W., Fogel, M. L., and Behrensmeyer, A. K. 1995. Isotopic tracking of change in diet and habitat use in African elephants. *Science* 267: 1340–1343.

Krishnamurthy, V., and Wemmer, C. 1995. Timber elephant management in the Madras Presidency of India (1844–1947). In J. C. Daniel and H. S. Datye (eds.), *A week with elephants: Proceedings of the international seminar on Asian elephants, June 1993* (pp. 456–472). Bombay: Bombay Natural History Society; New Delhi: Oxford University Press.

Kurt, F. 1974. Remarks on the social structure and ecology of the Ceylon elephant in the Yala National Park. In V. Geist and F. Walther (eds.), *The behaviour of ungulates and its relation to management* (Vol. 2, pp. 618–634). Morges, Switzerland: International Union for Conservation of Nature and Natural Resources.

Kurt, F. 1995. The preservation of Asian elephants in human care: A comparison between the different keeping systems in South Asia and Europe. *Animal Research and Development* 41: 38–60.

Lahiri Choudhury, D. K. 1991. Indian myths and history. In S. K. Eltringham (ed.), *The illustrated encyclopedia of elephants* (pp. 130–147). London: Salamander Books.

Lahiri Choudhury, D. K. 1992. Musth in Indian elephant lore. In J. Shoshani (ed.), *Elephants: Majestic creatures of the wild* (pp. 82–84). Emmaus, PA: Rodale Press.

Lair, R. C. 1997. *Gone astray: The care and management of the Asian elephant in domesticity.* Bangkok: United Nations Food and Agriculture Organization Regional Office for Asia and the Pacific.

Langbauer, W. R., Jr., Payne, K. B., Charif, R. A., Rapaport, L., and Osborn, F. 1991. African elephants respond to distant playbacks of low-frequency conspecific calls. *Journal of Experimental Biology* 157: 35–46.

Laws, R. M. 1970. Elephants as agents of habitat and landscape change in East Africa. *Oikos* 21: 1–15.

Laws, R. M., Parker, I. S. C., and Johnstone, R. C. B., 1975. *Elephants and their habitats: The ecology of elephants in North Bunyoro, Uganda.* Oxford: Clarendon Press.

Leuthold, W. 1977. Spatial organization and strategy of habitat utilization of elephants in Tsavo National Park, Kenya. *Zeitschrift für Säugetierkunde* 42: 358–379.

Lieberman, D., Lieberman, M., and Martin, C. 1987. Notes on seeds in elephant dung from Bia National Park, Ghana. *Biotropica* 19: 365–369.

Lindeque, M., and Lindeque, P. M. 1991. Satellite tracking of elephants in northwestern Namibia. *African Journal of Ecology* 29: 196–206.

Lister, A. M. 1996. Dwarfing in island elephants and deer: Processes in relation to time of isolation. *Symposium of the Zoological Society of London* 69: 277–292.

MacPhee, R. D. E., and Marx, P. A. 1997. The 40,000–year plague: Humans, hyperdisease, and first-contact extinctions. In S. M. Goodman and B. D. Patterson (eds.), *Natural change and human impact in Madagascar* (pp. 169–217) Washington, DC: Smithsonian Institution Press

Maglio, V. J. 1973. Origin and evolution of the Elephantidae. *Transactions of the American Philosophical Society of Philadelphia*, n.s., 63: 1–149.

Mahboubi, M., Ameur, R., Crochet, J. Y., and Jaeger, J. J. 1984. Earliest known proboscidean from early Eocene of north-west Africa. *Nature* 308: 543–544.

Martin, E., and Stiles, D. 2002. *The South and Southeast Asian ivory markets* Nairobi: Save the Elephants

Martin, P. S. 1984. Prehistoric overkill: The global model. In P. S. Martin and R. G. Klein (eds.), *Quaternary extinctions: A prehistoric revolution* (pp. 354–403). Tucson: University of Arizona Press

Martin, P. S., and Klein, R. G. (eds.). 1984. *Quaternary extinctions: A prehistoric revolution.* Tucson: University of Arizona Press

McComb, K., Moss, C., Durant, S. M., Baker, L., and Sayialel, S. 2001. Matriarchs as repositories of social knowledge in African elephants. *Science* 292: 491–494

McCullagh, K. G. 1973. Are African elephants deficient in essential fatty acids? *Nature* 242: 267–268.

McKay, G. M. 1973. Behavior and ecology of the Asiatic elephant in southeastern Ceylon. *Smithsonian Contributions to Zoology* 125: 1–113.

Menon, V. 2002. *Tusker: The story of the Asian elephant.* New Delhi: Penguin Books India.

Menon, V., Sukumar, R., and Kumar, A. 1997. *A God in distress: Threats of poaching and the ivory trade to the Asian elephant in India* Bangalore: Asian Elephant Conservation Centre and New Delhi: Wildlife Protection Society of India.

Milner-Gulland, E. J., and Beddington, J. R. 1993. The exploitation of elephants for the ivory trade: An historical perspective. *Philosophical Transactions of the Royal Society of London*, ser. B 252: 29–37.

Mosimann, J. E., and Martin, P. S. 1975. Simulating overkill by Paleoindians. *American Scientist* 63: 304–313.

Moss, C. J. 1983. Oestrous behaviour and female choice in the African elephant. *Behaviour* 86: 167–196.

Moss, C. J. 1988. *Elephant memories: Thirteen years in the life of an elephant family* New York: William Morrow.

Nash, S. (ed.). 1997. *Still in business: The ivory trade in Asia, seven years after the ivory ban.* Cambridge: Traffic International

Nath, C. D., and Sukumar, R. 1998. *Elephant-human conflict in Kodagu, southern India: Distribution patterns, people's perceptions and mitigation methods* Bangalore: Asian Elephant Research & Conservation Centre, Indian Institute of Science.

Niemuller, C., and Liptrap, R. M. 1991. Altered androstenedione to testosterone ratios and LH concentrations during musth in the captive male Asian elephant (*Elephas maximus*). *Journal of Reproduction and Fertility* 91: 139–146.

Norton-Griffiths, M. 1979. The influence of grazing, browsing, and fire on the vegetation dynamics of the Serengeti In A. R. E. Sinclair and M. Norton-Griffiths (eds.), *Serengeti: Dynamics of an ecosystem* (pp. 310–352). Chicago: University of Chicago Press.

O'Connell-Rodwell, C. E., Rodwell, T., Rice, M., and Hart, L. A. 2000. Living with the modern conservation paradigm: Can agricultural communities co-exist with elephants? A five-year case study in East Caprivi, Namibia *Biological Conservation* 93: 381–391.

Olivier, R. C. D. 1978. On the ecology of the Asian elephant. DPhil diss., University of Cambridge.

Osborn, F. V. 1998. The ecology of crop-raiding elephants in Zimbabwe. DPhil diss., University of Cambridge

Payne, K. B., Langbauer, W. R., Jr., and Thomas, E. M. 1986. Infrasonic calls of the Asian elephant (*Elephas maximus*) *Behavioural Ecology and Sociobiology* 18: 297–301.

Pellew, R. A. P. 1983. The impacts of elephant, giraffe, and fire upon the *Acacia tortilis* woodlands of the Serengeti *African Journal of Ecology* 21: 41–74.

Pilgram, T., and Western, D. 1986. Inferring hunting patterns on African elephants from tusks in the international ivory trade *Journal of Applied Ecology* 23: 503–514.

Poole, J. H. 1987. Rutting behavior in African elephants: The phenomenon of musth. *Behaviour* 102: 283–316

Poole, J. H. 1989a. Announcing intent: The aggressive state of musth in African elephants. *Animal Behaviour* 37: 140–152

Poole, J. H. 1989b. Mate guarding, reproductive success and female choice in African elephants *Animal Behaviour* 37: 842–849.

Poole, J. H., and Moss, C. J. 1981. Musth in the African elephant, *Loxodonta africana Nature* 292: 830–831.

Poole, J. H., and Moss, C. J. 1989. Elephant mate searching: Group dynamics and vocal and olfactory communication. *Symposium of the Zoological Society of London* 61: 111–125

Poole, J. H., Payne, K., Langbauer, W. R., and Moss, C. J. 1988. The social context of some very low frequency calls of African elephants *Behavioural Ecology and Sociobiology* 22: 385–392

Rangarajan, L. N. (ed., trans.). 1992. Kautilya: The *Arthashastra* New Delhi: Penguin Books

Rasmussen, L. E., Buss, I. O., Hess, D. L., and Schmidt, M. J. 1984. Testosterone and dihydrotestosterone concentrations in elephant serum and temporal gland secretions *Biology of Reproduction* 30: 352–362.

Rasmussen, L. E., Schmidt, M. J., Henneous, R., Groves, D., and Daves, G. D., Jr. 1982. Asian bull elephants: Flehmen-like responses to extractable components in female elephant estrous urine. *Science* 217: 159–162

Rasmussen, L. E. L. 1998. Chemical communication: An integral part of functional Asian elephant (*Elephas maximus*) society. *Ecoscience* 5: 410–426

Rasmussen, L. E. L., Haight, J., and Hess, D. L. 1990. Chemical analysis of temporal gland secretions collected from an Asian bull elephant during a four-month musth episode. *Journal of Chemical Ecology* 16: 2167–2181.

Rasmussen, L. E. L., Lee, T. D., Roelofs, W. L., Zhang, A., and Daves, G. D., Jr. 1996. Insect pheromone in elephants. *Nature* 379: 684.

Rasmussen, L. E. L., Riddle, H. S., and Krishnamurthy, V. 2002. Mellifluous matures to malodorous in musth. *Nature* 415: 975–976.

Rosenthal, G. A., and Janzen, D. H. (eds.). 1979. *Herbivores: Their interactions with secondary plant metabolites.* New York: Academic Press.

Ross, D. (ed.). 1992. *Elephant: The animal and its ivory in African culture* Fowler Museum of Cultural History. Los Angeles: University of California

Ruggiero, R. G., and Fay, J. M. 1994. Utilization of termitarium soils by elephants and its ecological implications *African Journal of Ecology* 32: 222–232.

Scullard, H. H. 1974. *The elephant in the Greek and Roman world* Ithaca, NY: Cornell University Press.

Short, J. C. 1981. Diet and feeding behaviour of the forest elephant *Mammalia* 45: 177–185.

Shoshani, J. 1996. Evolution of the Proboscidea In J. Shoshani and P. Tassy (eds.), *The Proboscidea: Evolution and palaeoecology of elephants and their relatives* (pp. 18–33) New York: Oxford University Press

Shoshani, J., and Tassy, P. 1996. Summary, conclusions, and a glimpse into the future. In J. Shoshani and P. Tassy (eds.), *The Proboscidea: Evolution and palaeoecology of elephants and their relatives* (pp. 335–348). New York: Oxford University Press

Sinclair, A. R. E. 1981. Environmental carrying capacity and the evidence for over abundance. In P. A. Jewell and S. Holt (eds.), *Problems in management of locally abundant wild mammals* (pp. 247–257). New York: Academic Press.

Spinage, C. A. 1973. A review of ivory exploitation and elephant population trends in Africa. *East African Wildlife Journal* 11: 281–289.

Sukumar, R. 1985. *Ecology of the Asian elephant (Elephas maximus) and its interaction with man in south India*. PhD diss., Indian Institute of Science, Bangalore.

Sukumar, R. 1989. *The Asian elephant: Ecology and management* (2nd rev. ed., 1992). Cambridge: Cambridge University Press.

Sukumar, R. 1991. The management of large mammals in relation to male strategies and conflict with people. *Biological Conservation* 55: 93–102.

Sukumar, R. 1994. *Elephant days and nights: Ten years with the Indian elephant*. New Delhi: Oxford University Press.

Sukumar, R. 1995a. Elephant raiders and rogues. *Natural History* 104: 52–60.

Sukumar, R. 1995b. Minimum viable populations for elephant conservation. In J. C. Daniel and H. S. Datye (eds.), *A week with elephants: Proceedings of the international seminar on Asian elephants, June 1993* (pp. 279–288). Bombay: Bombay Natural History Society and New Delhi: Oxford University Press.

Sukumar, R. 2003. *The living elephants: Evolutionary ecology, behavior and conservation*. New York: Oxford University Press.

Sukumar, R., and Gadgil, M. 1988. Male-female differences in foraging on crops by Asian elephants. *Animal Behaviour* 36: 1233–1235.

Sukumar, R., Krishnamurthy, V., Wemmer, C., and Rodden, M. 1997. Demography of captive Asian elephants (*Elephas maximus*) in southern India. *Zoo Biology* 16: 263–272.

Sukumar, R., and Ramesh, R. 1992. Stable carbon isotope ratios in Asian elephant collagen: Implications for dietary studies. *Oecologia* 91: 536–539.

Sukumar, R., and Ramesh, R. 1995. Elephant foraging: Is browse or grass more important? In J. C. Daniel and H. S. Datye (eds.), *A week with elephants: Proceedings of the international seminar on Asian elephants, June 1993* (pp. 368–374). Bombay: Bombay Natural History Society and New Delhi: Oxford University Press.

Taylor, V. J., and Poole, T. B. 1998. Captive breeding and infant mortality in Asian elephants: A comparison between 20 Western zoos and 3 eastern elephant centers. *Zoo Biology* 17: 311–332.

Thouless, C. R. 1996. Home ranges and social organization of female elephants in northern Kenya. *African Journal of Ecology* 34: 284–297.

Thouless, C. R., and Sakwa, J. 1995. Shocking elephants: Fences and crop raiders in Laikipia district, Kenya. *Biological Conservation* 72: 99–107.

Todd, N. E., and Roth, V. L. 1996. Origin and radiation of the Elephantidae. In J. Shoshani and P. Tassy (eds.), *The Proboscidea: Evolution and palaeoecology of elephants and their relatives* (pp. 193–202). New York: Oxford University Press.

Turkalo, A., and Fay, J. M. 1995. Studying forest elephants by direct observation: Preliminary results from the Dzanga clearing, Central African Republic. *Pachyderm* 20: 45–54.

van der Merwe, N. J., Lee-Thorp, J. A., and Bell, R. H. V. 1988. Carbon isotopes as indicators of elephant diets and African environments. *African Journal of Ecology* 26: 163–172.

Vartanyan, S. L., Garutt, V. E., and Sher, A. V. 1993. Holocene dwarf mammoths from Wrangel Island in the Siberian Arctic. *Nature* 362: 337–340.

Watve, M. G., and Sukumar, R. 1997. Asian elephants with longer tusks have lower parasite loads. *Current Science* 72: 885–889.

Webb, S. D. 1984. Ten million years of mammal extinctions in North America. In P. S. Martin and R. G. Klein (eds.), *Quaternary extinctions: A prehistoric revolution* (pp. 189–210). Tucson: University of Arizona Press.

Weir, J. S. 1972. Spatial distribution of elephants in an African national park in relation to environmental sodium. *Oikos* 23: 1–13.

West, R. M. 1980. Middle Eocene large mammal assemblage with Tethyan affinities, Ganda Kas Region, Pakistan. *Journal of Paleontology* 54: 508–533.

Western, D., and Lindsay, W. K. 1984. Seasonal herd dynamics of a savanna elephant population. *African Journal of Ecology* 22: 229–244.

Western, D., and van Praet, C. 1973. Cyclical changes in the habitat and climate of an East African ecosystem. *Nature* 241: 104–106.

White, L. J. T., Tutin, C. E. G., and Fernandez, M. 1993. Group composition and diet of forest elephants, *Loxodonta africana cyclotis* Matschie 1900, in the Lopé Reserve, Gabon. *African Journal of Ecology* 31: 181–199.

Whitehouse, A. M., and Hall-Martin, A. J. 2000. Elephants in Addo National Park, South Africa: Reconstruction of the population's history. *Oryx* 34: 46–55.

Zahavi, A. 1975. Mate selection: Selection for a handicap. *Journal of Theoretical Biology* 53: 205–214.