

## Asian Elephants and Seasonally Dry Forests

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Elephants, the largest living terrestrial animals, have long captured popular imagination and sparked our fascination. Elephants top most lists of charismatic species, presumably because of their great size, but also for their complex social behavior and the dangers they pose to people (Leader-Williams and Dublin 2000).

Two characteristics of elephant feeding ecology set the species apart from most other herbivores. Elephants consume large quantities of vegetation on a daily basis (for an overview, see Sukumar 2003), and they are mixed feeders, easily switching between grazing and browsing (Sukumar 2003; Dierenfeld 2006). Combined, these factors make the elephant a formidable herbivore, potentially a *keystone species* that might be expected to have an effect disproportionately greater than its biomass (Paine 1995). Most of what scientists and the public know about elephants stems from observations of African savanna elephants (*Loxodonta africana*) in open woodlands, savannas, and grasslands of eastern and southern Africa. In these ecosystems, elephants commonly destroy trees by debarking, uprooting, and breaking branches (Laws 1970; Guy 1989; Holdo 2006; Mapaure and Moe 2009).

Scientists have hypothesized that African elephants are indeed a keystone species, maintaining the structure of open woodlands by destroying a significant proportion of the trees and allowing growth of grasses essential to sustain themselves and diverse communities of herbivore grazers (Dublin et al. 1990), and thus playing an important role in maintaining this ecosystem's biodiversity. This hypothesis has been amplified in recent years through research indicating complex interactions among rainfall, fire frequency, elephants, and other herbivore grazers (Dublin et al. 1990; Ben-Shahar 1996; Mapaure and Moe 2009). Elephant density might be one of the most crucial factors determining the species' ecological role (Holdo 2007; Holdo et al. 2009). At high density, elephants are considered detrimental to biodiversity (Baxter and Getz 2005; Whyte and Fayrer-Hosken 2008). Similar to the effects that overabundant deer populations have along forest ecotones (Alverson et al. 1988; McShea et al. 1997; Augustine and Jordan 1998; McShea 2005), increased densities of browsing elephants can become detrimental to woodland ecosystems by suppressing and reducing the diversity of plant species and other biodiversity components. However, because of the

logistical, ethical, and political difficulties of conducting experiments with an endangered mega-vertebrate, the keystone ecological function of African elephants is often inferred without much proof of the concept, i.e., through exclusion experiments or other experimental designs to link canopy and woodland structure directly to elephant presence or absence and the extent of browsing at the landscape scale (but see Pringle et al. 2007; Asner et al. 2009).

The Asian elephant (*Elephas maximus*) is also frequently called a keystone species (Kurt 1974), but comparative studies and systematic evaluations of its effects on ecosystems are largely nonexistent (but see Mueller-Dombois 1971; Kurt 1974; Ishwaran 1983; Sukumar 1990; Pradhan et al. 2007). Because of the paucity of scientific studies on the Asian species, observations on African elephants are often generalized as holding true in Asia. Such generalization across species is not warranted, and the ecological role of elephants may be even more complex in Asia than in Africa. In Asia, people have played a large role in shaping the ecosystems occupied by elephants, and elephants may have adapted to anthropogenic change more than would be true in many African landscapes. These arguable differences in human-elephant interactions may be somewhat obscured, and further complicated, by the range of socioeconomic, cultural, and even religious differences characterizing human society across the Asian elephant's geographic range.

Indeed, Asian elephant populations may be impacted by their human-affected habitats rather than being themselves the main drivers of habitat successional processes. Asian elephant populations reach their highest density levels along forest–grassland or forest–agriculture ecotones where food plants become more abundant and accessible. These landscapes features are found within seasonally dry forests, where significant human agricultural development has occurred for millennia in conjunction with elephant populations. Perhaps considering humans', not elephants', keystone potential would be most appropriate within most Asian forests.

Generally, population densities of Asian elephants are thought to be higher in savanna-woodland habitats (i.e., seasonally dry forest) than in rain forests that are characterized by closed canopies and tall trees (Leimgruber et al. 2003; Sukumar 2003). This is ascribed to the greater carrying capacity of dry forest–savanna habitats due to a greater abundance of grasses and higher proportion of accessible and edible woody plant species (Sukumar 2003). According to Sukumar (2003) tropical rain forests provide little palatable food to elephants despite their high biomass productivity, whereas savanna-woodlands provide ample and diverse foods ranging from grasses to woody plants and their component parts. Sukumar (2003) states that savanna-woodlands can support elephant densities of 3–5 elephants/km<sup>2</sup>, compared to only about 0.2 elephants/km<sup>2</sup> in rain forest habitats.

Significant elephant populations in remaining dry forests are largely restricted to Sri Lanka, India, and Nepal. In most other areas, seasonally dry forests are now among the most threatened forest ecosystems (Songer et al., this volume; Leimgruber et al. 2005). Remaining areas are often fragmented and have lost their original large- and medium-sized mammal components, including Asian elephants (Myint Aung et al. 2004; Loucks et al. 2009). As awareness increases about the need for conservation of Asian dry forests, we face squarely the question of how important Asian elephants may be as components of dry forest ecosystems.

To assess the relationship between Asian elephants and seasonally dry forests, we have reviewed existing literature and data, in combination with our own research and observations. Specifically, we have explored the following areas:

1. Past and present geographic distribution of Asian elephants relative to the current distribution of dry forest.
2. Asian elephant abundance patterns in dry forest and other habitats.
3. The feeding ecology of Asian elephants and how this relates to their use of dry forest.
4. The role of people in mediating Asian elephant effects in dry forest.

### **PAST AND PRESENT GEOGRAPHIC DISTRIBUTION OF ASIAN ELEPHANTS**

The geographic range of the Asian elephant is thought to have once been contiguous from the Euphrates-Tigris in present-day Iraq through South and Southeast Asia to the Yangtze Kiang in China (Deraniyagala 1955; Olivier 1978; Santiapillai and Jackson 1990; Sukumar 2003). Such an extensive range would only have existed prehistorically, perhaps at the end of the last ice age, 15,000–20,000 years ago. It was then fragmented and reduced by the earliest human civilizations in Mesopotamia, the Indus and Ganges Valleys, and along the Yangtze River (Madella and Fuller 2006; Li et al. 2009). These civilizations established permanent agriculture, specifically rice cultivation, which started in south China along the Yangtze River and spread throughout Asia by 3,000 BCE (Li et al. 2009). Agricultural expansion likely had a significant impact on Asian elephant populations and habitats, and must have resulted in increased human-elephant conflict situations.

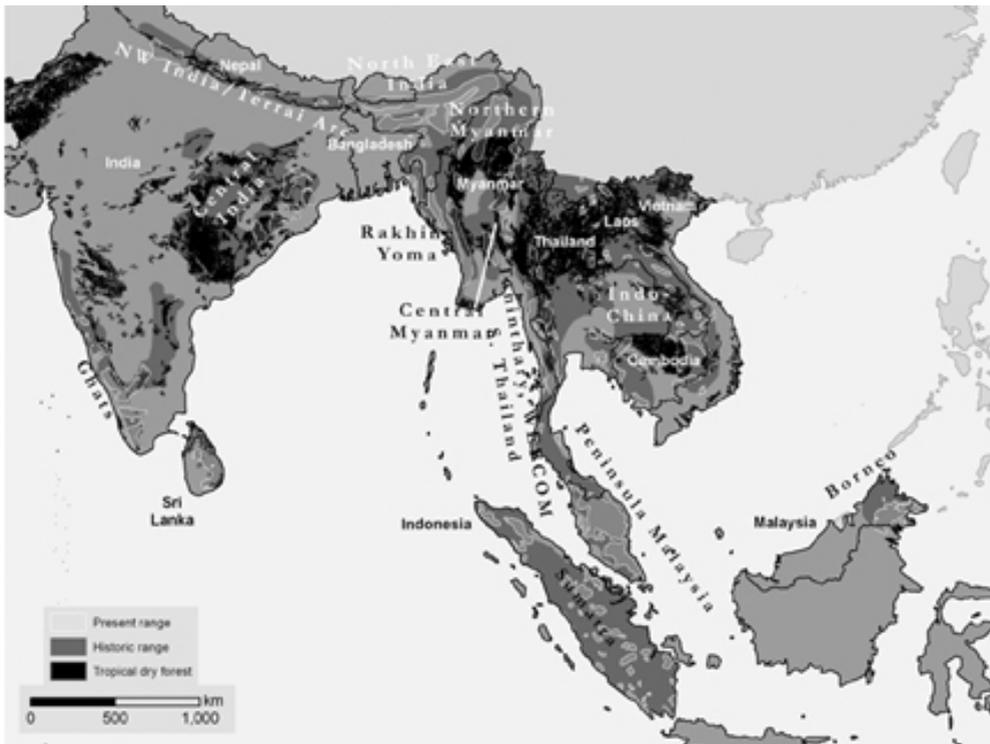
Asian elephant populations persisted through many millennia, but marked declines have occurred since the 1800s, attributable to excessive hunting during colonial periods (Lahiri-Choudhury 1999; Jayewardene 1994) and dramatic increases in agricultural activities (Flint 1994; Sodhi et al. 2004). Widespread agricultural conversions in the past two hundred years have been driven partly by locally increasing human populations requiring more rice and other subsistence crops, and partly by rising global demand for cash crops such as tea, coffee, teak, rubber, oil palm, and coconut (Corlett 1992; Flint 1994; Bryant 1997; Sodhi et al. 2004; Rasul 2007). After colonization, global market demand for tropical timber, especially for valuable dipterocarp species found in dry deciduous and mixed deciduous forests, resulted in large-scale logging and forest conversion to human habitations and cultivations that continues today (see Sodhi et al. 2004). In the early 2000s, deforestation rates in Asia reached a historic high of 1.4 percent annually (Sodhi et al. 2004).

Ultimately, human population growth has been the principal driver of elephant habitat loss by increasing local demand for food acreage and global demand for tropical timber and cash crops. This pattern continues today. Asian elephant range countries hold almost half the world's human population (3.13 billion, or 46 percent; U.S. Census Bureau 2009). Even after exclusion of China as a minor range state, Asian

elephant range countries contain more than a quarter of the world's population (1.79 billion, or 26 percent; U.S. Census Bureau 2009).

To assess the effects of growing human populations and expanding agriculture on Asian elephants and their habitats, we reconstructed the geographic range of Asian elephants in the early 1900s and compared it with a recent range map from the IUCN Asian Elephant Specialist Group (2009). For the 1900s range estimate, we expanded the current range of elephants by adding historical range areas as shown in maps from Stracey (1963). To provide a conservative (i.e., inclusive) range estimate, we adjusted the range polygons to expand into areas that in the 1900s had natural vegetation and low human populations (less than 50 persons/km<sup>2</sup>; History Database of the Global Environment, HYDE; Goldewijk 2001).

In the early 1900s, Asian elephant range probably covered about 2.87 million km<sup>2</sup> and was composed of several large yet discrete populations throughout Asia (Figure 1). In South Asia and mainland Southeast Asia, this range corresponds well with the climatic envelope for dry forests (compare Figure 1 of this chapter with Figure 2 in [Leimgruber et al., this volume](#)). By the early 2000s, the species' geographic range had declined to about 620,000 km<sup>2</sup> (Figure 1), a 78 percent decline in total area in only one hundred years. Asian elephant populations are now restricted to fragmented habitat



**Figure 1.** The historic and current geographic range of Asian elephants in relation to the spatial distribution of seasonally dry tropical forest.

islands dispersed across thirteen South and Southeast Asian states, namely, Sri Lanka, India, Nepal, Bhutan, Bangladesh, Myanmar, China, Thailand, Cambodia, Laos, Vietnam, Malaysia (peninsular and Sabah), and Indonesia (Sumatra and Kalimantan). Current Asian elephant range is highly fragmented and continues to decline in most countries (Leimgruber et al. 2003).

In South Asia and mainland Southeast Asia, elephants were once abundant in the dry forest ecosystems that spanned most of this region. However, human populations have grown more rapidly in these climate zones than elsewhere, with mean human population densities as much as three times higher than in other forest ecosystems in the region (Leimgruber et al., this volume). Consequently, in these areas elephants and dry forest ecosystems have experienced the same fate, disappearing together. Notably, the species is still abundant in some dry forests such as the Eastern and Western Ghats of India, and Sri Lanka's dry zone.

### ASIAN ELEPHANT ABUNDANCE PATTERNS

Most of the diverse definitions of Asian dry forests (see Bunyavejchewin et al., this volume) incorporate the element of seasonal rainfall mediated by monsoon weather patterns. Here we define *dry forest* as “natural vegetation” (including patches of savannah-grassland) occurring in areas with annual rainfall  $\geq 1,600$  mm and monthly rainfall  $\leq 100$  mm during at least six months of the year (Leimgruber et al., this volume). Using a map that combines climate with current forest cover extent (see Figure 2B in Leimgruber et al., this volume), we calculated the amount and percentage cover of dry forest in remaining Asian elephant range (Table 1). Although dry forests make up only 9–12 percent of Asia's land cover (Leimgruber et al., this volume), these forests often serve as important elephant habitat and make up approximately 21 percent of the remaining elephant range (Figure 1; Table 1). Some of the largest elephant populations (more than two thousand elephants) are found in areas possessing large percentages of dry forest, including Sri Lanka, the Ghats in Southern India, central India, the Rakhine Yoma mountain range in Myanmar, and the border region of Thailand and Myanmar (the Western Forest Complex, Tanintharyi, and southern Thailand). As much as 30–40 percent of all living elephants may be found in these areas (Santiapillai and Jackson 1990; Leimgruber et al. 2003; Sukumar 2003).

The estimates of dry forest in elephant ranges are very crude. In all of eastern Sri Lanka, for example, dry forest is the dominant forest type (P. Fernando, personal observation), yet our map shows dry forest only in the northeast and southeast of Sri Lanka. As a consequence, our estimate that 22 percent of the total Asian elephant range is covered by dry forest probably underestimates the extent of overlap between elephant and dry forest ranges.

Asian elephants are generally thought to occur at higher densities in dry forests than in rain forests (Sukumar 2003). These patterns in elephant density are paralleled by a dichotomy between the relative distribution of remaining elephant habitats and elephant populations (Leimgruber et al. 2003). Although systematic and range-wide population estimates don't exist (Blake and Hedges 2004), experts agree that southern India and Sri

**Table 1. Seasonally dry forest extent (km<sup>2</sup>) in the Asian elephant geographic range**

<i>Region</i>	<i>Range Area</i>	<i>Dry Forest Area</i>	
Sri Lanka	33,241	9,818	(30%)
Ghats, India	43,833	9,744	(22%)
Central India	32,043	23,873	(75%)
Terrai Arc / Northwest India	27,628	8,671	(31%)
Northeast India	89,507	0	(0%)
Bangladesh	3,592	0	(0%)
Northwest Myanmar	28,583	10,227	(36%)
Rakhine Yoma	32,075	8,914	(28%)
Bago Yoma / Central Myanmar	21,461	11,459	(53%)
Northeast Myanmar	15,553	9,499	(61%)
Western Forest Complex / Tanintharyi / Southern Thailand	49,982	17,737	(35%)
Eastern Thailand	12,583	5,359	(43%)
Indochina	69,689	17,474	(25%)
Peninsula Malaysia	72,380	0	(0%)
Sumatra	62,284	0	(0%)
Borneo	21,975	0	(0%)
China	4,209	31	(1%)
<b>Total</b>	<b>620,618</b>	<b>132,806</b>	<b>(21%)</b>

Lanka support the largest elephant populations (up to 20 percent of all living wild Asian elephants). Paradoxically these areas are smaller, more fragmented, and more densely populated by people than large elephant habitats in Myanmar and Thailand (Leimgruber et al. 2003). These differences reflect the prevalence of open dry forest in southern India and Sri Lanka. However, these patterns are not simply a function of the differential carrying capacity of habitat types, but are also mediated by national and local differences in hunting and capture of elephants, agricultural practices, cultural attitudes and religious beliefs, and protection of wildlife along with wildlife law enforcement.

## THE FEEDING ECOLOGY OF ASIAN ELEPHANTS

A key to understanding interactions between the environment and elephants is elephant feeding ecology. Elephants are hindgut fermenters with rapid passage times for food and low digestibility and energy intake (Dumonceaux 2006). This, combined with their body size, explains why elephants require such a large daily intake of food. In the wild, elephants have been observed to spend 75–85 percent of the day feeding (Vancuylenberg 1977). Digestive physiology also suggests that elephant feeding strategies consist of consuming enormous quantities of low-quality food, passing this food as rapidly as possible through the gastrointestinal tract, and gaining nutrition from the quantity, rather than quality, of foods (Dumonceaux 2006). Thus, elephants are

generalized feeders, utilizing a vast number of plants and plant parts, ranging from grasses to leaves, branches, roots, seedlings, and fruit (McKay 1973; Sukumar 1989).

Where grass is available, elephants preferentially feed on it, switching to browse only when grasses are unavailable or cannot be consumed because they are mature and unpalatable (Sukumar 1990). Where grasses are unavailable, elephants feed exclusively on browse (Sukumar 1990, 2003). Elephants in mainland Southeast Asia may differ from those in India and rely less on grazing and more on browsing (Chen et al. 2006; Himmelsbach et al. 2006; Campos-Arceiz et al. 2008a, 2008b).

Elephants can be fairly selective when browsing. Although they have a wide breadth of diet, sometimes consuming over one hundred plant species at a site (McKay 1973; Sukumar 1990; Chen et al. 2006; Himmelsbach et al. 2006), usually only a few species are consumed in large quantities (Sukumar 1990).

Asian elephants strip bark (usually the cambium) off trees and may preferentially consume fruits or pods (Sukumar 1989; Campos-Arceiz et al. 2008a, 2008b). Similar to African elephants, Asian elephants can cause tree mortality (Ishwaran 1983; Sukumar 1989; Pradhan et al. 2007). They kill some trees by debarking, but based on our personal observations in Sri Lanka, such behavior appears to be commoner at high elephant densities brought about by restricting elephants to particular areas. Also, it is our observation that some tree species have evolved strategies to cope with intensive browsing by elephants. For example, indigenous trees in Sri Lanka such as *Baobinia racemosa* are resistant to elephant browsing. Damaging the main trunk or debarking does not cause mortality. Instead, the tree responds by sprouting multiple trunks. Other species such as figs (*Ficus* sp.) have convoluted trunks and cannot be ring-barked by elephants. In species such as wood apple (*Limonia acidissima*), elephants strip small branches and twigs of their bark but not larger branches or trunks.

Many elements of Asian elephant feeding ecology resemble patterns observed in northern hemisphere herbivores such as white-tailed deer (Alverson et al. 1988; McShea et al. 1997; McShea 2005), such as switching from herbaceous to woody plant diets, and heavy browsing on trees and shrubs when resources become limited (McCullough 1985; Russell et al. 2001; Fulbright and Ortega-S. 2006). Similar to these deer species, elephants thrive in open forest habitats, early-successional forests, and along forest edges. These feeding strategies could also explain elephants' observed geographic distribution, population density, and habitat choice of dry forests. Grasses and shrubs in the understory are more-common and more-easily accessible in open canopy forests such as dry forest than in moist evergreen forests. Because of their mixed feeding strategy, effectively combining and opportunistically switching between grazing and browsing strategies, elephants are extremely well adapted to open canopy forests, disturbed and early-successional forests, and forest edges.

## **THE ROLE OF PEOPLE IN MEDIATING ASIAN ELEPHANT EFFECTS IN DRY FOREST**

Increasing human densities cause the loss of elephant range, but the relationship is complex and depends on the interactions of people and elephants (Fernando et al. 2005; Fernando 2006). It is likely, though hard to prove, that declines in Asian

elephant populations have occurred in tandem with dry forest declines. Negative effects of dry forest decline on elephant populations may include increased hunting (Hedges et al. 2005; Corlett 2007), conflict with humans, and habitat loss (Fernando et al. 2005; Hedges et al. 2005; Fernando 2006). Conversion of natural habitat to human-dominated habitat results in fragmentation and eventually loss of elephant range (Fernando et al. 2005; Hedges et al. 2005; Fernando 2006). Ironically, elephant populations may initially increase with habitat fragmentation due to increased forest disturbance and edge habitat (Fernando 2006). However, habitat fragmentation also leads to more-frequent encounters and interactions between people and elephants, and intensifying human-elephant conflict, which together with habitat loss ultimately leads to the extirpation of elephants from such areas.

Perhaps the best broad-scale natural experiment testing the hypothesis of Asian elephants as early-successional or edge-adapted species has been taking place in Sri Lanka where, during the past 2,400 years, humans have created thousands of reservoirs and utilized seasonal swidden agriculture (De Silva 1981; Fernando 2006). Today, many of Sri Lanka's rural dry zone landscapes consist of a heterogeneous mosaic of forest and successional lands and abundant edge habitat. As a consequence of these land-use strategies, Sri Lanka (65,610 km<sup>2</sup>; comparable in size to West Virginia [62,755 km<sup>2</sup>] or Lithuania [65,300 km<sup>2</sup>]) has a wild elephant population that may exceed four thousand individuals (Hoffman 1978; Jayewardene 1994) while also supporting over 20 million people (for comparison, West Virginia's population is 1.2 million, and Lithuania's population is 3.3 million; U.S. Census Bureau 2009). In this context, humans are modifying the landscape and artificially increasing its carrying capacity for Asian elephants (Ishwaran 1993; Fernando et al. 2005; Fernando 2006). It is not a coincidence that Sri Lanka, together with India, has the highest yearly numbers of human fatalities from elephants (50–70 people/year; Perera 2009).

Generally, forest habitat modifications by humans, and specifically, land-use activities that create abundant early-successional habitat, produce optimal elephant habitat. Such habitats may be as important as, or more important than, dry forest availability per se. Elephant populations increase in these successional habitats because elephants are attracted to them and because reproductive rates may be higher. With increasing elephant population size, the risk for intense human-elephant conflict and associated elephant mortality also rises. Ultimately, humans take control of the area and elephants are removed, either by being driven out of the habitat or falling victim to human-elephant conflict. This connection is difficult to prove with experimental studies or large-scale habitat manipulations because these areas have been dominated by human activities for a long time. As a consequence, it may be impossible to distinguish whether elephant densities are determined more by ecosystem characteristics of dry forest or by human agricultural practices.

Habitat changes generally viewed as detrimental to conservation—such as swidden agriculture, logging, and forest fires—frequently benefit elephants, as these activities create new habitat similar to forest edge (Fernando 2006). The critical factor is that forest habitat is changed to early-successional habitat by such disturbance and not converted to a land use that excludes elephants. Where habitat loss is caused by conversion of forests to permanent human settlements and cultivations or commercial plantations

such as for oil palm, tea and rubber, elephants will be eliminated (see Fernando et al. 2005; Hedges et al. 2005; Uryu et al. 2008). This is clearly evidenced by the dramatic twinned losses of forest and elephant populations in oil palm plantations in Sumatra (Hedges et al. 2005; Uryu et al. 2008). Conversion of forests to permanent crops, in addition to causing habitat loss, leads to escalation of human-elephant conflict due to crop raiding and increased interaction of elephants with humans, and hence to further loss of elephants (Blake and Hedges 2004; Fernando et al. 2005; Hedges et al. 2005). Increased habitat heterogeneity due to small-scale disturbance often results in better conditions for elephants, while large-scale and homogeneous changes are likely to be detrimental. Therefore, with regard to dry forest and elephants, we should distinguish between habitat disturbance and habitat conversion or loss.

### **KEYSTONE OR EDGE SPECIES? CONSERVATION IMPLICATIONS**

Asian elephant geographic distribution coincides with the distribution of seasonally dry forests. Despite the scarcity of dry forests throughout Asia, these areas continue to harbor the largest wild elephant populations. As dry forests continue to decline, Asian elephants will probably also continue to decline; yet conservation of dry forests might not always benefit elephants.

The importance of habitat succession to the dynamics between forests and elephants, and the observation that habitat suitability for elephants increases with an intermediate disturbance regime, creates a dilemma for those intent on conserving dry forests and elephants. Managers need to assess whether elephants should be maintained as a low-density species in mature dry forests or whether elephant densities should be increased through habitat management, such as an intermediate disturbance regime.

Elephant conservation and management and human-elephant conflict mitigation across Asia have largely been based on the restriction of elephants to protected areas (Fernando 2006; Fernando et al. 2005). The main instrument of such restriction is the “elephant drive,” which attempts to clear elephants out of large areas by driving them into protected areas to which they are subsequently restricted by electric fencing. Yet given the dominant effect of habitat (i.e., carrying capacity) on elephants, the number of elephants in a specific area cannot be increased significantly without a corresponding increase in carrying capacity (Fernando 2006). Habitat management specifically targeting elephants involves activities that may be detrimental to forest conservation, such as cutting and burning of forest (Ishwaran 1993). Thus, increasing the carrying capacity for elephants involves the destruction of forests, which may be counter to conservation objectives. Restriction of elephants to protected areas without a corresponding increase in the areas’ carrying capacities causes habitat degradation and eventually the decline and extinction of those elephant populations (Fernando 2006). Habitat management specifically for elephants in protected areas is not practical in many cases due to logistical constraints and expenses imposed by the necessary scale of management (Fernando 2006), in addition to biodiversity concerns. In Sri Lanka and probably across the Asian elephant range, higher densities of elephants and a larger segment of the elephant population are found outside, rather than inside, protected

areas (Fernando 2006). Therefore, those involved in or interested in conservation of Asian elephants must consider ranges outside the boundaries of protected areas and undisturbed forests.

Artificially high elephant densities, created by driving elephants into small protected areas and fencing them in, may lead to elephants having destructive effects on woodland communities. However, there is little evidence that destructive population levels are reached under natural conditions. Ongoing research in Sri Lanka suggests that artificially high densities often exceed carrying capacity for a park, and are ultimately detrimental to elephants. Elephants so confined suffer high mortality and decreased reproduction and recruitment, leading to population decline (P. Fernando, unpublished data). There is little evidence that Asian elephants serve as a keystone species in Asia's seasonally dry tropical forests. More likely they are a species whose abundance closely tracks the productivity of the habitat; in the context of Asian dry forest, these habitat attributes are mostly anthropogenic.

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