Long-term field studies of elephants: understanding the ecology and conservation of a long-lived ecosystem engineer

Herve Fritz*

Laboratoire Biometrie et Biologie Evolutive, CNRS UMR 5558, Universite de Lyon 1, 43 bd du 11 novembre 1918, 696220 Villeurbanne Cedex, France
Sustainability Research Unit, Nelson Mandela Metropolitan University, George Campus, Saasveld Road, 6529 George, South Africa

* Correspondent: herve.fritz@univ-lyon1.fr

Elephants may live for > 60 years, so it is obvious that long-term studies are necessary if we are to understand their life histories. Here, I review long-term population studies, most based on individual elephants, to show the wealth of detailed mechanisms that such studies can reveal. This review is biased toward African savanna elephants, a reflection of existing long-term studies on elephants worldwide. Besides life histories, there are 2 aspects of elephant biology that are illuminated by long-term field studies (not necessarily those based on individual elephants). First is knowledge of spatial dynamics of populations that occur in response to environmental change (climatic or anthropogenic), such as density dependence that is associated with the distribution of surface water or responses to specific management decisions, and second is the effects these ecosystem engineers have on habitats, landscapes, other species, and ultimately on ecosystems. I also argue that these long-term data are crucial to inform conservation policies and associated management actions, such as changes in water-pumping strategies, landscape management, and control of elephant populations.

Key words: conservation, ecosystem engineer, elephant, *Elephas maximus*, life history, long-term studies, *Loxodonta africana*, *Loxodonta cyclotis*, megaherbivores, wildlife management

With an average generation time close to 25 years (Wittemyer et al. 2013), elephants are very long-lived mammals. They also show a rich and complex social life and potentially have massive short- and long-term effects on their environment. To understand the subtle links they have with one another and the diversity of individual life histories, personalities, culture, and dialects requires time, a "lifetime, both human and elephant," as Moss et al. (2011:2) state in their book on the Amboseli Elephant Research Project in Kenya, which started in 1972 and which has stimulated many others to undertake long-term projects. To some extent, understanding elephant societies requires approaches similar to those used in ethnology or anthropology in studying human societies and their links with their environment. Studies of this type rarely feature snapshot information and instead require long periods of immersion by the researcher in the local environment. Similarly, one needs a sufficiently long time window to understand how these megaherbivores affect their environment through habitat modification (Laws 1970; Guldemond and van Aarde 2008),

tree mortality (O'Connor et al. 2007), seed dispersal (Sekar et al. 2015), and even water use (Chamaillé-Jammes et al. 2007; Valeix et al. 2009), as well as how elephants adapt to these changes. The ripple effects on the functioning of their associated landscapes, foodwebs, herbivore communities, or ecosystems can be massive (Fritz et al. 2002, 2011; Skarpe et al. 2004; Pringle 2008; Haynes 2012), which gives rise to the idea of elephants as ecosystem engineers (sensu Jones et al. 1994). As elephants represent a living example of what may have happened when megafauna dominated all continents, describing and understanding their effect on ecosystems lies beyond the African and Southeast Asian realms (e.g., Bakker et al. 2016 and references therein).

Short-term studies, even very comprehensive ones, only give a snapshot of the ecological, social, and anthropogenic context of elephant life. Elephants have always fascinated humans, and there have been hundreds of short- to medium-term studies but also a few true long-term studies (Wittemyer et al. 2013). Here, I consider as long-term studies those that followed individuals

or populations or both for at least a decade. I include studies that may have had a focus on individuals for < 10 years but that studied whole populations for ≥ 10 years, as well as studies that may have been interrupted but total > 10 years of data. I also include studies of < 10 years that are combined with historical records that allow conclusions to be drawn from long-term longitudinal data. Two categories of studies can be broadly distinguished: those that originally focused on individual behavior and social systems, mostly driven by questions related to life-history strategies and population ecology, and those that focused on population parameters and community or ecosystem effects of elephants, clearly based on management questions.

Decades of long-term studies on elephants have resulted in numerous important insights into their ecophysiology, social behavior, and population dynamics which contributed to their conservation and conservation of their habitats. In this condensed review, I do not aim at being comprehensive, but instead will focus on selected studies. Although I draw examples from all 3 species, 2 African, the savanna elephant (*Loxodonta africana*) and the forest elephant (*Loxodonta cyclotis*), and 1 Asian, the Asian elephant (*Elephas maximus*), there is a bias toward African savanna elephants on which most long-term studies have been done (see Supplementary Data SD1 for an overview of ongoing and past long-term studies). I include trade-offs between energy and behavior, such as for maternal care or individual social ranking, in the "Ecophysiology" section, which thus has a strong behavioral component. In the section "Social System," I cover the very diverse topic of social structure (how individuals interact with each other) and illustrate with some results on social organization. The use of space and of key resources such as water and the role of spatial memory are examined in the section "Population and Community" as these often involve changes in spatial distribution and consequences for population dynamics. Mobility and resource selection also exemplify the response of populations to environmental change, particularly climate change. Similarly, the effects of the number of elephants and their behavior on the ecosystem, with consequences for both vegetation and other animals, are dealt with in the section "Population and Community." The "Conservation" section includes examples of in-depth behavioral studies that are relevant to the interactions of elephants and humans. In this section, I also discuss the potential contribution of long-term studies for management of the various impacts of elephants on ecosystems. The "Cognition" section aims at illustrating the growing body of research on elephant memory and cognitive skills, for which long-term knowledge of individuals and interactions is paramount. The "Future Directions" section offers some topical research questions that require further attention. In each section, I have selectively illustrated some of the key research findings from long-term studies to show the diversity of in-depth knowledge that can only be drawn from long-term field studies.

Ecophysiology

Many physiological studies on elephants have been carried out in captivity, especially on Asian elephants, in particular in relation to reproduction and growth (reviewed by Sukumar 2003). For elephants, which have gestation periods of 620–680 days (Lueders et al. 2012), the effects of environmental conditions on reproduction are likely to be complex. Their high level of cognitive ability and social communication doubtless also play a role in mitigating environmental stress. Therefore, long-term field studies are necessary to relate environmental and social context to breeding and foraging decisions, as well as to relate proximal physiological effects to ultimate fitness. Although yearly population counts recording changes in cohorts of various age classes may be useful in understanding population dynamics (Young and van Aarde 2010), only long-term studies on individual elephants show how individual experience, knowledge, and social status interact to mediate ecophysiological and behavioral responses to environmental change.

In Amboseli National Park, elephant mothers that experienced dry conditions when their calves were ≤ 2 years old tended to show shorter than average time to next conception, which may be an adaptation to the greater risk of losing the calves due to poor body condition. However, mothers that did lose a calf during a drought (here defined as 2 consecutive dry years) were more likely to delay conception, presumably to recover body condition (Lee and Moss 2011). Another difference that was seen was that individuals that started life in a dry year remained smaller than average and delayed their 1st reproduction. Females that experienced 2 dry years in early life tended to have shorter than average lives (Lee and Moss 2011), which suggests a long-lasting effect of initial life conditions on physiology and ultimately on reproduction and survival—and hence on individual fitness. Without long-term field studies these environment–reproduction interactions would not have been discovered.

Combining noninvasive methods for assessing endocrine levels with long-term individual monitoring of adult elephants has brought insights into the determinants of reproductive effort. For example, being able to assess a progesterone metabolite (5α-pregnane-3-ol-20-one) in feces of adult females provided information on ovarian activity (Foley et al. 2001; Wittemyer et al. 2007a). Analysis of estrus and pregnancy rates in individually identified females showed that conception is related to good food resources for a given season (based on maximum levels of the normalized difference vegetation index) and also that there are more conceptions in good years (wetter and with higher vegetation index) than bad years (Foley et al. 2001; Wittemyer et al. 2007a).

An unusual feature of elephants is the existence of a male reproductive cycle, the musth, first described in domestic male Asian elephants (Jainudeen et al. 1972). Although this cycle is well described for captive elephants, details on maturation, seasonality, and its implications for male reproduction in the wild were not well understood for many years (Poole 1987). Now, though, it has been shown that musth is tightly correlated with testosterone levels in wild male savanna elephants (Ganswindt et al. 2005). Further, a benefit of long-term studies is the demonstration that frequency of musth throughout

the life of a male is correlated with the number of young sired (Poole et al. 2011); however, this reproductive success comes with high physiological costs (stress) and physical risks (fights) which can only be sustained by older and larger males in good condition (Ganswindt et al. 2005; Poole et al. 2011). Sources of variation in musth dynamics, such as age at first occurrence, effects of season, and environmental constraint, also require in-depth temporal studies. Variability in number of young sired and proportion of musth bulls in relation to climate and seasonality can only be assessed by long-term studies that can compare known males in different environments. An example of this is the work of Hall-Martin (1987) which compares elephant populations from Addo Elephant National Park in southern South Africa and Kruger National Park in northeastern South Africa. Males in Addo show a weak seasonality associated with less variable rainfall pattern, whereas in Kruger males show a more pronounced seasonality reflecting the sharp contrast in resource availability between the wet and dry seasons. Similarly, the social consequences of musth and the dynamics of male–male interactions require knowledge of the social status of each male and his previous reproductive experience. This can only be accessed through long-term studies of known individuals such as in Etosha National Park in Namibia, Amboseli, or Addo. The Etosha study shows that during dry years a linear hierarchy among males is apparent and controls access to resources, but this hierarchy vanishes in wet years, with more contests occurring (O'Connell-Rodwell et al. 2011). The musth phase can temporarily disrupt dominance. That is because a small male in musth may drive off a large dominant male in a contest because a male in musth is much more aggressive (see review in Sukumar 2003). These patterns could be misleading in terms of interpreting male–male interactions without the context of an individual-based study (O'Connell-Rodwell et al. 2011).

Social System

Because elephants have complex social structure and high cognitive abilities, understanding the complexity of their social behavior requires thorough long-term studies. Only with long-term studies of individuals it is possible to understand the factors that affect their decision-making and ultimately their individual fitness—factors such as social integration, kinship relationships, information transmission, and collective memory.

Savanna elephants use acoustic signals for mate-searching, male–male competition, and maintenance of social bonds (Poole et al. 1988; Poole and Moss 1989). They detect low-frequency "seismic" calls—transmitted through both air and ground—over a range of several kilometers, and use them to mediate inter- and intragroup social encounters (Poole et al. 1988; McComb et al. 2000; O'Connell-Rodwell et al. 2006). A female savanna elephant can know and recognize vocalizations of a mean of 14 different families, including about 100 adult females, enabling her to communicate effectively with over 20% of the population (McComb et al. 2000). Using playback experiments (i.e., playing known sounds on loudspeakers to stimulate a reaction from focal animals) on well-known

individuals and their families, McComb et al. (2001) showed that families with older matriarchs possess greater social networks or greater social confidence, or both, and are more successful in reproducing.

The role of experience, age, and dominance of the matriarch in elephant societies is crucial in many aspects of the group's life. With age comes several advantages for family groups, such as the ability to perceive threats and behave in safe ways (McComb et al. 2011b). In Amboseli, experienced mothers allowed calves to overcome periods of stress, especially in relation to food shortage (Moss et al. 2011). With dominance comes access to resource sites whenever needed, which has considerable influence on spatial distribution of the social units during the lean season (Wittemyer et al. 2007b). The matriarch, with her memory of routes and safe places as well as extended social network, is thus determinant in deciding on actions, such as whether to wait at key drinking or foraging places or whether to aggregate or not (McComb et al. 2001; Wittemyer et al. 2007b; McComb et al. 2011a). In all dimensions, the behavior of matriarchs seems to be beneficial for individuals in the groups as well as for themselves; however, the true value of these decisions in terms of survival and reproduction, and hence individual fitness and inclusive fitness, can only be assessed with very long studies spanning more than the reproductive lifetime of a matriarch (such as those of Moss and Lee 2011a).

In mammals in general, longevity and senescence are poorly understood, more so with regard to behavioral aging than for the effect of age on reproductive outputs. This is probably because the time after prime age is often restricted to very few years in most large mammals, leaving a short time for age-related behavioral changes to be expressed. Thus, with a long period of life after their reproductive prime, comparable to that in humans and other large primates, elephants represent a great opportunity for studying these changes (Moss et al. 2011). Along similar lines, only long, continuous observations of known individuals in equally known contexts can identify the large diversity of gestures and postures (e.g., 83 ritualized displays reported in savanna elephants—Poole and Granli 2011) and the subtlety of acoustic communication (O'Connell-Rodwell et al. 2007; McComb et al. 2011a). Further, these long-term observations have allowed an in-depth understanding of the actual meaning of all these gestures and sounds, the context in which they are used, and associated behavioral responses (Poole and Granli 2011).

Fusion–fission dynamics (the merging or splitting of groups) is a common feature of gregarious and social species. Thus, observed group size often depends on the mechanisms that cause individuals, or a group of individuals, to join or leave a group. In social species such as elephants, with multiple levels of social grouping and associations (i.e., "multitiered" sensu Wittemyer et al. 2005), ecological factors such as food abundance or social factors such as affiliative bonds could lead to fusion or fission (Sukumar 2003; Moss and Lee 2011b). Comparisons of well-studied elephant populations have shown differences between ecosystems in group size, with forest elephants having smaller groups than savanna elephants (reviewed

in Sukumar 2003), and Asian elephants living in dry forest also showing smaller family units as well as looser bonds than the savanna elephant (Fernando and Lande 2000; Vidya and Sukumar 2005). Individual-based studies confirm that individual savanna elephants are more connected to other individuals of their population than are Asian elephants. However, the level of association between individuals in the Asian elephant is much greater than the size of observed groups, which implies a multilevel society, though less structured than that of savanna elephants (de Silva and Wittemyer 2012). Yet, only long-term studies allow the assessment of the relative roles of social, demographic, and environmental drivers of group size and fusion–fission dynamics. Several factors may lead to group fission, the most common ones being low rainfall associated with low food resource and high local competition for food; death of the matriarch; and birth of a calf, which may slow down the mother or create different resource needs (Moss and Lee 2011b). Fusion may be initiated by low competition for resources (in food-rich habitats). It also may be promoted by the need for small family units to join bigger groups for various reasons: to benefit from the leadership of older females, to gain anti-predator benefits (Moss and Lee 2011b), to increase mate-choice opportunities (Poole and Moss 1989), or to enhance information transfer (Lee and Moss 1999). The fusion of family groups is often favored by kinship, with kin more likely to associate than non-kin (Wittemyer et al. 2009). In Amboseli, core groups were more likely to fuse with each other when the oldest females in each group were genetic relatives. The associations between core groups may actually persist for decades, even after the death of the original matriarch, as groups that share mitochondrial DNA haplotypes are more likely to fuse than groups that do not (Archie et al. 2006). The relative influence of social or ecological factors is also dependent on ecosystem; for example, Amboseli elephants seem to be more influenced by social factors (Moss and Lee 2011b) than are elephants in the Samburu National Reserve (also in Kenya—Wittemyer et al. 2005). This may reflect the fact that the major swamp areas in Amboseli provide a good-quality, year-round resource, hence reducing the duration of the dry season, which differs considerably from the arid Samburu ecosystem. In forest elephants, the absence of seasonality and patchy distribution of fruiting trees may explain the small group size, mostly restricted to close family ties (Fishlock and Lee 2013).

The social life of males is animated by the permanent quest for social dominance, which increases access to females and to water (O'Connell-Rodwell 2015), and the bonding of "buddies" can serve as information exchange centers. Fusion–fission between individual males and groups of males also tends to be based on kinship and similar age classes, but older males play a pivotal role in social networks, suggesting that older males influence the cohesion of male social groups (Chiyo et al. 2011a). A genetic study on over 500 known individuals in Amboseli showed that males display courtship behavior and mating more frequently with non-kin females, which contributes to inbreeding avoidance (Archie et al. 2007). This may reflect that the cost of reproduction for these males may be very high because of energy spent in male–male contests for acquiring dominance and access to reproduction and also for time spent in mate guarding. Relatedness between local males in Indian elephants may suggest some adaptive behavior that could further minimize aggression between males and the contest costs of acquiring dominance (Vidya and Sukumar 2005).

POPULATION AND COMMUNITY ECOLOGY

Population dynamics in space and time.—Understanding population dynamics requires knowledge of age structure, age-dependent survival, age at first reproduction, and length of interbirth intervals, and in elephants all of these require long-term studies of individuals (Gough and Kerley 2006 for Addo elephants). The fascination for elephants has generated a number of demographic studies (see Wittemyer et al. 2013:table 2 for key demographic parameters). The estimated maximum intrinsic growth rate of elephants is about 7% (Calef 1988), which is rarely reached except in populations recovering from severe poaching (7.1% in Tarangire National Park in Kenya—Foley and Faust 2010) or massive culling operations (6.6% in Kruger—Whyte 2001). Populations in more arid areas (< 400 mm annual rainfall) show much lower growth rates (Samburu, 2.9%—Wittemyer et al. 2013; Amboseli, 3.75%—Moss 2001). However, neither mean calving interval nor mortality seems to be correlated with average annual rainfall (Wittemyer et al. 2013).

Useful data have been generated by long-term field studies with continuous monitoring of population numbers and distribution of elephants in space and time. Although these data do not give any insight into demographics processes, they represent unique sources of data for population modeling over large areas and can lead to understanding temporal and spatial dynamics (Chamaillé-Jammes et al. 2008; Young et al. 2009). They also contribute substantially to our understanding of the spatial response of elephant populations to changes in resources (Chamaillé-Jammes et al. 2007), in particular in a context of climate change and anthropogenic modification of landscapes. Recently, research on these topics has benefited immensely from the use of satellite collars (Chamaillé-Jammes et al. 2013; Wall et al. 2013), although these studies do not yet span decades (but see Roever et al. 2013). Long-term continuous monitoring of populations is a major source of information that should be encouraged, especially for analyzing the effect of management initiatives. Using such data, Chamaillé-Jammes et al. (2007) showed the importance of waterholes in limiting elephant distribution, and ultimately their role in driving the population dynamics of elephants in Hwange National Park in Zimbabwe through spatial trade-offs between acquisition of water and food (Chamaillé-Jammes et al. 2014). In Kruger as well, long-term data showed the effect of closing waterholes on population dynamics: though the response of the population was complex, with elephants congregating in many areas, the broad-scale monitoring of elephant distribution over a large number of years still showed that riverine habitats were used more than other areas, and thus their integrity was of greater

concern because of their cumulative number of hosted elephants (Smit and Ferreira 2010).

Habitat change and ecosystem effects.—Elephants are often referred to as ecosystem engineers because of the level of influence they can have on the functioning of most components of their ecosystem, from vegetation dynamics to habitat structure, and structure and dynamics of herbivore communities. Elephants can alter plant diversity and are a major cause of loss of trees in savanna systems, especially of tall trees (O'Connor et al. 2007; Asner and Levick 2012; Rutina and Moe 2014). These ecosystem-level effects have caused decades-long major debates over how to deal with these changes, especially in protected areas (Laws 1970; O'Connor et al. 2007). However, these effects are often amplified or mediated by other factors, such as anthropogenic disturbances or local climate (Guldemond and van Aarde 2008; Sankaran et al. 2013). The use of exclosures that exclude herbivores, especially those that exclude large herbivores, is valuable in developing an understanding of the effects of large herbivores on plant communities. Such exclosures can reveal the role of megaherbivores in shaping structure in plant heights, species composition, and other plant traits, information that can shed light on the mechanisms involved and on long-term demographic responses and the evolution of adaptive traits in plants. Durable commitments to maintain such long-term exclosures are needed. Long-term exclosure studies in Addo Elephant Park, Kruger National Park, and Laikipia (Kenya) have also shed light on effects of elephants on possible trajectories for landscape change, including community-wide changes in vegetation and on key vulnerable plant species (Penzhorn et al. 1974; Sankaran et al. 2013; Wigley et al. 2014, 2015). Similarly, elephants are known key seed dispersers (Campos-Arceiz and Blake 2011), but assessing their effects on the maintenance of plant diversity and life history through seed dispersal not only requires experiments (Sekar et al. 2015) but also long-term monitoring of landscapes (Vijver et al. 1999 in Tarangire, Tanzania; Sukumar et al. 2005 in Mudumalai, India), and if possible in areas presenting contrasting levels of elephant use (Cochrane 2003). Our ability to understand the effects of elephants on the dynamics of wooded savannas has been strengthened by repeated observations on browsing behavior of elephants, the impact of their browsing on plants, and the rate at which elephants fell trees (Asner et al. 2015).

Elephants can have significant effects on the diversity and ecology of other animals, mostly indirectly through habitat modification, either negatively (Cumming et al. 1997) or positively (Skarpe et al. 2004; Valeix et al. 2011). They may affect other herbivores directly through interference or scramble competition (Fritz et al. 2002; Valeix et al. 2009) or facilitation (Makhabu et al. 2006). Studying these effects requires enough time to assess how habitat changes impact other organisms and how permanent is the signature of elephant effects. For instance a short-term benefit of habitat change (e.g., increase of forage through re-sprouting of lateral branches from broken stems or coppicing) could have long-term costs with loss of cover. Comparing data from sequences of years separated by an interval with no data may be adequate for investigating such questions, but long-term continuous tracking of changes is more likely to unravel processes (Valeix et al. 2008), especially experimental studies using selective exclosures (Young et al. 2005). For more thorough analyses on multiple facets of the influence of elephants, see du Toit et al. (2003) for Kruger, Sukumar (2011) for Asian elephants, Skarpe et al. (2014) for Chobe, and Fishlock and Breuer (2015) for forest elephants.

CONSERVATION

Elephants are emblematic of most challenges facing conservation. The 3 species have variable levels of vulnerability in various African subregions and in Asia, ranging from critically endangered to being of least concern (Blanc 2008). Information on population parameters and conditions of recovery is therefore crucial. It is important that we pursue in-depth demographic studies on all elephant species in the largest possible array of ecosystems (see Turkalo et al. 2013 for forest elephant, Katugaha et al. 1999 and de Silva et al. 2011 for Asian elephants in Sri Lanka, and Sukumar 2003 in India). Elephant populations thrive in some well-managed protected areas while declining in others, but they also use large areas outside conservation areas (e.g., Graham et al. 2009), which creates conflicts in agricultural areas. Consequently, understanding the choices made by elephants that raid crops should give perspectives into the selection pressure driving them to take such a high-risk behavior (e.g., being shot as problem animals or subject to retaliatory killing). Long-term behavioral and genetic studies can provide the foundation for such understanding by looking at individual benefits of crop-raiding (Chiyo et al. 2011b). Because crops are a much higher quality food than wild plants for part of the year (Sukumar 1990), the nutritional benefits of crop-raiding for male elephants translate into larger body size and ultimately greater fitness (Chiyo et al. 2011b). In parallel, long-term follow-up of people and practices involved at the interface is necessary to fully grasp the dynamics of the interactions and identify possible ways for coexistence (Guerbois et al. 2012). A long-term experiment with beehive fences in northern Kenya has provided new insights into mitigation tactics (King et al. 2011; Soltis et al. 2014). Several hundred people are killed by elephants each year, increasing the intensity of human–elephant conflicts (Lamarque et al. 2009). It is mostly in areas with high human populations, in Asia in particular, that fatal encounters are most common, often associated with raids by elephants on village fields or granaries (Sukumar 2003). Even though savanna elephants have been shown to discriminate potentially threatening human categories from non-threatening ones (McComb et al. 2014), our understanding of causes and early warnings for dangerous encounters remain very fragmented and anecdotal.

In places where elephant populations are increasing in size, their impact on the local ecosystem is of concern to local conservationists and park managers, and managers seek options to best deal with a sometimes embarrassing ecosystem engineer that does not shape the system in line with the views of managers

and local stakeholders (Whyte et al. 1998). The benefits of long-term studies lie in shedding light on the effect of management practices. For instance, significant social disruption caused by culling has been documented through the long-term monitoring of individuals, with, for instance, young traumatized males killing other species, black rhinoceros (*Diceros bicornis*) in particular (Poole 1989; Shannon et al. 2013). This is particularly true for translocated males (Slotow et al. 2000). Social consequences of large-scale poaching has also been shown, with orphaned females that survive poaching raids tending to form less structured groups than orphaned females from other causes (Gobush et al. 2009). On the ecosystem side, the use of botanical reserves (with elephant-proof exclosures) within elephant ranges inside protected areas also requires long-term commitments to assess how efficient it would be to preserve endemic and emblematic vegetation sensitive to elephants (Lombard et al. 2001).

COGNITION

The cognitive abilities of elephants are high, and their intelligence has often been admired. They can memorize large amounts of information. For instance, they have the ability to discriminate between familiar and unfamiliar individual sounds (O'Connell-Rodwell et al. 2007), or threatening human voices (McComb et al. 2014), and they are also able to keep track of out-of-sight family members (Bates et al. 2007). The associated level of information exchange between individual elephants depends on the degree to which elephants distinguish between call types (such as alarms, greetings, bonding vocalizations); de Silva (2010) distinguishes 14 call types in Asian elephants, but also "combination calls" that combine several types of information within a call (de Silva 2010). Ultimately, the relevance and use of this ability depends upon its significance to reproduction and survival, and hence this can only be understood through longitudinal studies of individuals. The amount of knowledge elephants have acquired during previous movements through an area seems to be used in navigating landscapes, and only long-term studies of individual spatial behavior can unravel the link between this acquired environmental knowledge and the behavioral adjustments they make, and then ultimately the transfer of information to other related individuals of the family or kin-related elephants (Byrne and Bates 2011). There is a major challenge here for researchers; the combination of high mobility and high cognitive skills in elephants provides many possible adaptive responses to environmental changes (climatic or anthropogenic). New ideas for conservation areas have been proposed, such as open landscape conservation areas (i.e., without fences) and areas that are located in adjoining countries such as Trans-Frontiers Conservation Areas or other forms of megaparks (van Aarde and Jackson 2007), which elephants could use in many different ways. Putting such concepts into action would require long-term monitoring if we are to understand the mechanisms underlying the success or failure of these initiatives to conserve elephant populations. This obviously also applies to populations of many other large and mobile mammals.

FUTURE DIRECTIONS

The areas of social cognition, information transfer, and behavioral manipulation of other individuals such as deception also require more investigation in order to show a clear link between the adaptive and fitness significance of elephant cognitive abilities and associated communication capabilities, social behaviors, and mobility. To my knowledge none of the existing long-term studies have adequately investigated the link between cognition and the memory of environmental features, although it has been partially explored. This is a major task for years to come, both for our understanding of the ecology of these megaherbivores as well as for their conservation. Indeed, the landscapes are likely to be increasingly reshaped by human activities, including conservation practices: some migration routes will be blocked and others opened, spatiotemporal dynamics of resource will be modified, and safe habitats may change attributes.

In the area of conservation, much more needs to be done on long-term mechanisms of coexistence between elephants and humans in shared landscapes. Indeed, a lot of attention has been paid to symptomatic remedies for human–elephant conflict, whereas coexistence requires integrating cultural, symbolic, and economic values of elephants with people and a better understanding of tolerance determinants. This implies an ethnographic approach to human–elephant interactions. From the elephant viewpoint, integrating human activities into their landscape and adapting to them requires predictable cues associated with disturbance and risk. Further, these cues should be easy to memorize and even to transfer between individuals and generations.

Because of their effect on the landscape, elephants have been described as ecosystem engineers—agents of habitat change that affect basic functions and processes of ecosystems. As illustrated previously, their role in changing the way the ecosystem functions goes beyond landscapes, and it requires long-term studies to track the likely consequences of these megaherbivores in the various foodwebs with which they are associated. Secondary production can indeed be massively influenced by elephants in savannas on poor soils (Fritz et al. 2002). Elephants could even change the ecosystem identity in the sense of resilience theory, i.e., its functions, structure, and feedback (Walker et al. 2004). Recent studies on the influence of megafauna call for even better understanding (Bakker et al. 2016), because the presence of these elephants may fundamentally affect the trajectory of change of the systems they live in. Only long-term studies will give us the necessary insights.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Significant long-term studies on elephants.

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Special Feature Editor was Barbara H. Blake.