Megaparks for metapopulations: Addressing the causes of locally high elephant numbers in southern Africa

Rudi J. van Aarde [a] and Tim P. Jackson[a]

[a]Conservation Ecology Research Unit, Department of Zoology and Entomology, **University of Pretoria,** Hatfield 0028, South Africa

Abstract

Conservation management options for southern African elephants range from local to regional scales. Here we review these options and argue in favour of actions that will deal with the causes rather than symptoms of elephant numbers that are locally high. Metapopulation theory ensures population persistence, while our approach extends this in order to stabilise elephant numbers regionally. By allowing for the development and maintenance of regional sinks, we may also limit numbers in sources. This application of the metapopulation metaphor is a powerful ecological platform from which to manage elephant numbers and impact through southern Africa. Our approach engages the causes of the apparently high abundance of elephants in parts of southern Africa. It moves away from the practice of dealing only with numbers (symptoms) when managing the impact of elephants on other species. While providing an ecological basis for the development of elephant management options, this needs to be melded with social, political and economic realities through southern Africa. In this regard we are encouraged by the ongoing development of several Transfrontier Conservation programmes and Peace Parks across the region.

Article Outline

1. Introduction

The management of Africa's elephants is complex – they are vulnerable to extinction in some regions but appear over-abundant in others (Blake and Hedges, 2004 and Stephenson, 2004). Overall, southern Africa's populations grew significantly from 1994 to 2002 (Blanc et al., 2005) and this trend probably continues. Across the sub-region, increasing elephant numbers may threaten other species and their habitats (Chafota and Owen-Smith, 1996, Lombard et al., 2001 and Whyte et al., 2003), while elephants that roam beyond conservation areas come in to conflict with people (e.g. Barnes, 1996, Hoare, 1999, Osborn and Parker, 2003 and Sitati et al., 2005). It is not surprising that elephant management has fuelled well-worn debates for almost half a century.

The elephant problem, as it is known, has its roots in the locally high numbers of elephants in conservation areas and their perceived consequences for vegetation (see Pienaar et al., 1966, van Wyk and Fairall, 1969, Brooks and Buss, 1962, Caughley, 1976, Hanks, 1979, Barnes, 1983 and Foggin, 2003). More specifically, such high numbers have been blamed for degrading vegetation to the detriment of other species (e.g. Buechner and Dawkins, 1961, Laws, 1970 and Caughley, 1976). Factors that cause locally high numbers are induced principally by people and include water supplementation, fencing and the reduction and fragmentation of landscapes that detract from more natural movements of elephants. More recently the focus on elephants has broadened in both scientific and political circles to include conflict between humans and elephants.

Management practices that address local impact by curbing high numbers actually deal with the symptoms and not the underlying causes of the elephant problem. Here, we advance an approach that addresses the causes of locally high elephant numbers using elephant spatio-temporal dynamics. Specifically, we advocate applying metapopulation principles to elephant management as this could limit numbers at a regional scale while also reducing their local ecological impact. In addition, we advocate changing management practices that lead to locally high numbers and interfere with spatio-temporal dynamics.

Traditionally metapopulation theory ensures population persistence (e.g. Hanski, 1999, Broome, 2001, Ferreras, 2001, Wikramanayake et al., 2004 and Hellgren et al., 2005). Here we extend this approach to manage local numbers of an abundant species, the savanna elephant (*Loxodonta africana*), across the southern African sub-continent. Essentially, we may reduce impact by allowing dispersal from sources into sinks.

2. The present scenario

While elephants are widely distributed over sub-Saharan Africa this once continuous population is now fragmented and often confined to formal protected areas that account for only 16% of their distributional range (see Blanc et al., 2003). Today, almost 70% of Africa's elephants occur in southern Africa (Blanc et al., 2003). Here many populations are increasing at rates of 4–5% per annum, while in small reserves rates of increase are often higher (Slotow et al., 2005).

Elephants are long-lived and we have little understanding of the factors that limit populations. We know that survival amongst adults is high (Owen-Smith, 1983) but varies considerably for sub-adults <10 years old (Leuthold, 1976 and Haynes, 1987; Shrader et al., unpublished data). Poaching (Stiles, 2004) and periodic droughts (see Walker et al., 1987 and Dudley et al., 2001) challenge survival while protection and the provisioning of water may enhance population growth.

Dispersal may also limit elephant populations (Chafota and Owen-Smith, 1996), though fences impair movement. Fences enclose several reserves, demarcate international borders and act as veterinary cordons. Human settlements around reserves also provide effective barriers to movements (see Hoare and du Toit, 1999) that could compromise dispersal. When confined, protected, or provided with water elephant densities reach levels that may adversely affect vegetation (see Gaylard et al., 2003, Whyte et al., 2003, Skarpe et al., 2004 and de Beer et al., 2006) and transform landscapes (see Western and Gichohi, 1989, Dublin et al., 1990, Herremans, 1995, Cumming et al., 1997, Gillson and Lindsay, 2003, Pickett et al., 2003 and Western and Maitumo, 2004). Given this scenario, controlling local elephant numbers may reduce the degradation of vegetation (see Chafota and Owen-Smith, 1996, Whyte et al., 1999 and Whyte, 2004). Alternatively, there may be no ecological basis for artificially controlling elephant numbers (see Gillson and Lindsay, 2003 and Skarpe et al., 2004).

3. Past and present management practices deal with symptoms

Early approaches to conservation management focused on numbers (Hanks et al., 1981). For instance active management by the addition of water and manipulation of fire may have instigated changes in the ranging behaviour of herbivores and induced high local impacts (Owen-Smith, 1996, Gaylard et al., 2003, Grainger et al., 2005 and de Beer et al., 2006). Historical sentiment primarily considered management issues at a political and not a conservation level (see Buss, 1977 and Cumming, 1981), thereby distancing conservation practices from our present day understanding that conservation should focus on maintaining heterogeneity (e.g. Rogers, 2003).

Elephant management aimed to stabilise numbers at levels for which it was assumed that vegetation would not be degraded, thereby maintaining biodiversity (Caughley, 1983, Walker et al., 1987 and Gillson and Lindsay, 2003). The concept of *economic* carrying capacity supports this practice (Caughley, 1983 and Gillson and Lindsay, 2003) and consequently agricultural rather than ecological paradigms drove many early management actions. These included measures to increase and then stabilise numbers at levels below their so-called carrying capacity. Consequently, elephant numbers in some southern African parks were reduced to levels considered lower than those dictated by *ecological* carrying capacity. Under these circumstances, resources no longer limited numbers (Chafota and Owen-Smith, 1996 and Gillson and Lindsay, 2003). Those that thought this would maintain woodlands clearly ignored the many other factors that induce changes across woodlands (e.g. Pickett et al., 2003).

Some consider landscape transformation as detrimental for the conservation of biological diversity. In doing so they ignore that many woodlands developed in response to historical disturbances driven by man (see Walker, 1989). Here the ivory trade was pivotal as it decimated elephant populations and reduced their impact on woodlands. This could have been amplified by the rinderpest pandemic that devastated browser populations across eastern and southern Africa, thereby providing for the further development of woodlands (see Prins and van der Jeugd, 1993 and van de Koppel and Prins, 1998). From here stems the misconception that woodlands must be maintained (e.g. Skarpe et al., 2004). This mind set would certainly make elephants a problem as many people enjoy woodlands for their aesthetic values. Despite this history, elephant management often involved the control of numbers. Before setting out our ideas to address the underlying causes of the elephant problem we briefly evaluate the success of culling, contraception and translocation in controlling numbers, as well the economic, ethical and logistical constraints of these methods.

3.1. Culling

With the adoption of culling during the mid-1960s, elephant target densities were set arbitrarily (van Wyk and Fairall, 1969 and Laws et al., 1970) – densities supported by the concept of economic carrying capacity. This pre-dated the modern ethos that landscape diversity moulds population numbers. Culling targets were therefore whimsical and had no theoretical basis (see Caughley, 1983 and Owen-Smith, 1983).

Culling may disrupt population dynamics. For instance, culling may give rise to immigration. This occurred in the Kruger National Park, where movement into culled areas increased numbers (van Aarde et al., 1999). In this case, the increase in densities after culling (van Aarde et al., 1999) may have intensified the local impact of elephants. Culling is only effective in limiting growth when applied continuously. For instance, following the cessation of culling in the Kruger, growth rates increased dramatically (see Whyte et al., 2003). Since the cessation of culling in 1995 elephant numbers in Hwange National Park (Zimbabwe) almost doubled in just six years, while elsewhere in Zimbabwe numbers grew about 28% over the same period (Foggin, 2003). Even so culling does reduce numbers, albeit temporarily.

Selective culling targeting bulls or animals of certain age classes also may distort age structures and enhance, rather than suppress growth rates (see Gordon et al., 2004) and so negate the intention of culling. In addition, at lower densities population growth rate may increase (see Sinclair, 2003), so culling could effectively increase growth rate.

3.2. Contraception

Birth control has been hailed as a tool to limit elephant numbers. We can control birth rates with hormones and their derivates, or with immuno-contraceptives (Pimm and van Aarde, 2001). Contraceptives may lengthen inter-calving intervals or increase the age of first calving (Dobson, 1993). This could reduce population growth and the impact that further increases in numbers can have for vegetation. Unlike culling, contraception does not reduce elephant numbers – instead it relies on natural mortality.

Contraception, like culling, raises ethical questions, especially when unplanned sterilization of cows excludes them from the gene pool (Whyte et al., 1998) and induces abortion (see Allen et al., 2002). Moreover, despite initial optimism, all contraceptives may have side effects on the health and behaviour of cows (Whyte et al., 1998 and Pimm and van Aarde, 2001). Hormonally treated cows may remain in sexual heat and be harassed by bulls (Whyte and Grobler, 1997). Reducing reproductive rates may also destabilise the age and social structures of breeding herds and possibly influence the wellbeing of cows and their calves (see McComb et al., 2001 and Pimm and van Aarde, 2001).

While we may debate the ethics of contraception, the limitations imposed by the logistics of such a programme are more tangible. The efforts needed to stabilise elephant numbers in large populations through birth control are not realistic. They are both laborious and costly (Pimm and van Aarde, 2001). At the population level, birth control is constrained by the number of females needing treatment (Whyte et al., 1998). For instance, age at first calving will only increase effectively if almost 50% of pregnant cows less than 15 years old are on birth control or forced to abort (Dobson, 1993). Worse, in Kruger, growth will only stabilize at zero if we treat nearly 75% of adult cows continuously for 11 years (van Aarde et al., 1999). To effectively maintain zero growth contraception would need to be ongoing. Treated cows need to be marked individually in order to locate them for booster treatment. Most African countries do not have the finances or infrastructures to sustain such operations (see Pimm and van Aarde, 2001). Indeed, we agree with Bertschinger et al. (2003) who concluded that immuno-contraception is only suitable for small, confined populations.

3.3. Translocation

While ethically appealing, translocation is not a practical solution to reduce numbers in large populations. Transporting elephant herds is both costly and cumbersome (Foggin, 2003 and Hofmeyr, 2003). More importantly, few existing conservation areas in southern Africa can accommodate extra elephants (Hofmeyr, 2003 and Whyte, 2004), while small-scale translocations to other continents are fraught with ethical issues (Roberts and

Travers, 2004). On several reserves, reintroduced elephants have exhibited behavioural abnormalities, due mainly to disrupted social structure (Slotow et al., 2000, Garaï et al., 2004 and Bradshaw et al., 2005). To be effective, translocation must also continue for as long as managers wish to keep local numbers at specific levels.

In turn, we must even manage translocated populations to prevent undesirable impact – particularly as most translocations are from larger to smaller reserves (Garaï et al., 2004). Most of the 30 populations founded on small estates across South Africa over the past 20 years now need control (Slotow et al., 2005). We conclude that translocating elephants cannot limit numbers, either in a target area or across the region.

3.4. Do nothing

Historically, crisis management rather than evidence-based management clouded elephant conservation (Lindsay, 2003). The obvious alternative is to do nothing. Some argue that this approach provides the best compromise solution, however, politically unacceptable this might seem (see Griffiths, 2004). In principal, we do not agree with this approach for systems that are manipulated or artificially isolated. Under such conditions it is only by altering population numbers in a controlled way and closely monitoring the responses of populations that we can hope to understand the outcomes of our management actions (see Pullin et al., 2004). Consequently "doing nothing" does not advance our understanding of management. While many elephant-related studies have been conducted, comprehensive studies using replicated, controlled designs are few. We need such information in order to make informed management decisions.

4. Consequences of control

Stabilizing elephant numbers may induce complications, given that African savannas are not stable. Here disturbances modulate resilience and resistance (Walker, 1989, Rogers, 2003, Scholes et al., 2003, Gillson and Lindsay, 2003 and Gillson, 2004a). Elephants disturb savannas (see Western, 1989) and static numbers may compromise local habitat heterogeneity and species richness (Walker et al., 1987, Cumming et al., 1997, Gillson and Lindsay, 2003 and Whyte et al., 2003). Static numbers may also reduce the spatial patchiness that buffers species against drought (Illius and O'Connor, 2000). Savannas may not benefit, therefore, from static elephant numbers – ultimately, resilience may be weakened (Caughley, 1983, Walker et al., 1987, Illius and O'Connor, 2000 and Ogutu and Owen-Smith, 2003). While we can theorise, it is impossible to specify elephant densities that do not interfere with biological diversity (Chafota and Owen-Smith, 1996, Ben-Shahar, 1997 and Whyte et al., 2003). We, like others, argue that maintaining elephant numbers at predefined levels is not a sensible management goal. Indeed, numbers should vary, through both space and time in response to both density dependent and environmental forces (Bulte et al., 2004 and Gillson et al., 2005).

5. Addressing the causes of the problem

Conservation actions derived from population and landscape principles could address the causes of the elephant problem. Therefore, where possible, we need to focus on restoring forces that limit elephant numbers and modulate their impacts on vegetation under natural conditions. To deal with the causes of the problem means we need to tackle the artificial manipulation of limiting resources. Here, specifically, we address the other key aspects central to the issue of locally high elephant numbers – range fragmentation and restriction. To do so we must reinstate dispersal as a process that moderates densities both temporally and spatially. This calls for an ecological framework against which to develop and assess the outcomes of such elephant management. Inherently, such a paradigm will address the persistence and diversity of system processes where elephants occur.

Gillson and Lindsay's (2003) proposal for a non-equilibrium approach offers a fresh theoretical basis for elephant management. At the appropriate temporal and spatial scales their approach becomes even more attractive (see Gillson, 2004b and Bulte et al., 2004). It is also consistent with our understanding of the African savanna in a non-equilibrium state (Dublin et al., 1990, Gillson, 2004a, Gillson, 2004b, Skarpe et al., 2004 and Birkett and Stevens-Wood, 2005). A non-equilibrium approach focuses on demographic and ecological processes, recognizing the interactive role of elephants in savanna systems. We wish to augment Gillson and Lindsay's (2003) approach by adding the metapopulation metaphor as a platform to manage the elephant problem across southern Africa.

6. The metapopulation metaphor

Metapopulation theory (Hanski, 1999) provides a conceptual framework for population management (Groot-Bruinderink et al., 2003 and Hanski, 2004). The metapopulation is one of several models that explore demographic responses to spatial scale (see Thomas and Kunin, 1999). It relies on the spatial discontinuities in a population imposed by landscape heterogeneity. Following local extinctions, the dynamics of sub-populations differ enough to induce dispersal and the recolonisation of patches. Under these conditions, local populations are driven by dispersal events. Local populations could fluctuate in numbers, while the sum total of numbers across the region will remain relatively stable (Pulliam, 1988).

Dispersal may also be intrinsic, due to differences in landscape quality, and therefore differences in source and sink habitats (Dias, 1996). Here, mortality in sinks will occur deterministically and provides a mechanism through which populations could be limited across regions (e.g. Novaro et al., 2005). We may arrange such demographic responses along two axes that combine per capita birth–death and emigration–immigration rates (Thomas and Kunin, 1999). The classical metapopulation functions at the point where the sum total of the differences between births and deaths, and between immigration and emigration is zero – in other words where the regional population is stable despite local instabilities.

Catering for landscape heterogeneity is important as it provides the key processes that maintain populations across space and time. To operate, metapopulations essentially require vacant habitats, dispersal between these, and asynchrony in the dynamics of the local populations. Here we argue that these conditions hold for elephants across southern Africa.

6.1. Habitat vacancy

Since the end of the 19th century elephant range has declined dramatically throughout Africa (Brooks and Buss, 1962, Parker and Graham, 1989, Roth and Douglas-Hamilton, 1991 and Stephenson, 2004). Currently, elephants occur over some 5 million km^2 and well beyond the boundaries of protected areas, which account for only 16% of their range (Blanc et al., 2003). Elephant ranges, however, are poorly documented – in southern Africa for instance, they are believed to extend over ∼1.7 million km^2 of which only 39% has been confirmed (Blanc et al., 2003). At a continental scale, up to 50% of potential elephant range has not been surveyed and only 15% is covered by systematic surveys (Blanc et al., 2003).

Clearly, we have a very poor understanding of elephant ranges. Presently, elephants do not occupy all potential range across southern Africa. In some areas people inhabit land not occupied by elephants (Hoare and du Toit, 1999), while in others they share their land with elephants. Often overlooked is the fact that across much of southern Africa human densities seldom exceed five persons per km^2 (Mittermeier et al., 2003). Much of this land is relatively untransformed (Mittermeier et al., 2003) and, given the opportunity, could be colonised by elephants. These areas incorporate private land, communal land, forest reserves and wildlife management areas – vacant habitats that are key to metapopulation dynamics.

6.2. Dispersal and range use

The present distribution of elephants is patchy, though most occur in conservation areas. They disperse readily into vacant habitats. For instance, historical records show that elephants moved from Mozambique into South Africa’s Kruger National Park, which in the early 1900s supported fewer than 10 elephants. Dispersal at annual rates of 7–10 km meant that the Park’s 20,000 km^2 was colonised within 50 years (Whyte et al., 2003). Similarly, in 1955 elephants were recorded in the Serengeti National Park (Tanzania) after an absence of at least 40 years. Here numbers increased over a 10-year period, mainly through immigration, to some 2000 individuals (Lamprey et al., 1967).

In other areas, where managers manipulated water availability, elephant populations expanded rapidly and at rates that exceed their reproductive capacity. For instance, Etosha National Park’s population approximated 50 individuals in 1950 and increased to some 2000 by 1980 (see Lindeque and Lindeque, 1991). Following water supplementation in the Khaudum Game Reserve (Namibia), its population increased from around 80 in 1976 to some 3400 in 2004 (B. Beytell, pers. commn.). Civil unrest in southern Angola may have contributed to this increase in Khaudum, which at ∼13% per year is almost double that typical of populations with a stable age structure (see Calef, 1988).

In Kruger, culling induced dispersal of elephants onto areas where densities were reduced (van Aarde et al., 1999). It follows that elephants do disperse when given the opportunity or when circumstances allow. This is critical to the application of the metapopulation model to the conservation management of elephants, since the metapopulation can only operate with dispersal.

6.3. Asynchrony in dynamics

Within southern Africa elephant population growth rates differ. Numbers fluctuate when populations are driven by local events, such as droughts, outbreaks of disease and disturbances induced by people (Leuthold, 1976, Haynes, 1988, Lindeque, 1991 and Dudley et al., 2001). Most widespread is the apparent increase over a five-year period of elephant numbers in conservation areas including the Kruger, northern Botswana and Khaudum Game Reserve (Blanc et al., 2005). Over the same time period, in other areas such as Etosha National Park (van AStephenson, 2004arde et al., 2003), the Caprivi Region in Namibia (Blanc et al., 2005), Hwange National Park (S. Chamaillé-Jammes, unpublished data) and Sebungwe in Zimbabwe (Blanc et al., 2005) numbers appear relatively stable. Particularly through Zambia’s national parks, including South Luangwa and Kafue and in Malawi’s Kasungu National Park, elephant numbers may have declined over recent years (see Blanc et al., 2005, Ferreira et al., 2005 and Guldemond et al., 2005). This variation in trends may partly be ascribed to intra- as well as inter-population differences in inter-calving intervals, ages at sexual maturity and survival rates. Thus, population numbers vary in time, both between and within southern Africa’s elephants.

7. From theory to practice

We support the development of one or more networks of conservation areas that will allow the southern African sub-region’s elephants to be driven by metapopulation dynamics. Inevitably, our model must provide for both source and sink populations. This can be achieved by allowing dispersal from sources, including many existing conservation areas, to sinks. In doing so, our approach links source populations within a megapark context. We advocate that the landscape matrices between conservation areas act primarily as sinks. By the very nature of sinks, here elephant mortality rates must be greater than birth rates, while populations are maintained by immigration from sources. Such immigration should limit numbers in source populations. In restoring this type of metapopulation structure, elephant numbers could be prevented from increasing locally to levels that are deemed undesirable in sources.

Sink populations must be limited and while we advocate natural control, there may be a need for people to reduce numbers in sinks. We see this as natural given that human predation is considered a major historical source of impact on elephant numbers (Surovell et al., 2005). To manage sinks effectively local communities could be allowed to hunt elephants in a controlled and authorised manner. This must be seen in the context of sustainable resource use and must provide tangible benefits (for instance in the form of meat or revenue from sports hunting) to these communities. Ultimately, maintaining sink areas effectively will benefit regional elephant conservation. It is unclear how sinks will perform, or even whether they will need overt management. These issues need thorough investigation before implementing a metapopulation approach to manage regional elephant numbers.

By defragmenting the landscape and encouraging elephant range expansion, our metapopulation approach addresses the underlying causes of locally high elephant numbers. While metapopulation theory may underlie wildlife population dynamics elsewhere in Africa (for instance of wildebeest *Connochaetes taurinus* in the Serengeti/Mara system; see Sinclair, 2003), this paradigm has not been advanced formally as a management tool to limit numbers regionally. Perhaps Owen-Smith (1983) advocated the most similar approach when he put forward the idea of creating dispersal sinks for white rhinoceros *Ceratotherium simum* in the form of "vacuum zones", where off-take was controlled – though his idea was specifically conceived for enclosed areas. In essence, we encourage the maintenance of a widely distributed elephant population, where the demographics and dynamics of sub-populations differ across space and time. Here, the dynamics of these sub-populations should be managed within a metapopulation framework. To do so, we envisage a conservation matrix comprising a range of land use options across international boundaries at a sub-continental scale.

To achieve this goal we must develop a far better understanding of the spatial, population and conflict dynamics of elephants within southern Africa, as well as the consequences of defragmenting populations for the spread of contagious disease (see Hess, 1994). Conceptually, our ideas are at variance with management practices such as fencing, the provisioning of artificial water, culling in source areas and contraception. Conversely, our approach has a relatively simple ecological platform, which considers the population as a spatial entity. From a social perspective the establishment of megaparks will inevitably meet with negative sentiment from local communities, as people are naturally concerned about the increase in elephant numbers outside formal reserves (see O'Connell-Rodwell et al., 2000). These people can only be expected to support this conservation idea if the benefits of elephants outweigh the perceived costs (see Gillingham and Lee, 2003) – addressing this issue must be integrated in the establishment of megaparks (also see Newmark et al., 1994). Furthermore, before implementation and for the megapark approach to be effective, decision-makers need to be informed of its sound scientific basis (see Pullin et al., 2004).

Nevertheless, the development of the network of conservation areas we envisage for southern Africa, is a reality. The process is complex and involves local government authorities, national wildlife management agencies, non-governmental organizations and local communities. It underlies international collaboration and the ethos of Peace Parks and the establishment of Transfrontier Conservation Areas (TFCAs) (see Hanks, 2001, Wynberg, 2002 and Western, 2003). From a political and financial standpoint, the Southern African Development Community supports these initiatives and plans are in place for the establishment of several TFCAs throughout southern Africa. For example, in 2002 an agreement was signed by member countries to create the Greater Limpopo Transfrontier Park. This will eventually unite major conservation areas and adjoining landscape matrices in Mozambique, South Africa and Zimbabwe. The proposed Kavango–Zambezi Transfrontier Conservation Area (KAZA TFCA) involves five countries and incorporates 36 national parks, game reserves and wildlife management areas. It extends over an area of more than 300,000 km^2 that supports about 200,000 elephants. To put this into perspective, this is an area some 20 times larger than the Serengeti National Park, while the KAZA TFCA contains about one third of all Africa's elephants.

By allowing elephant numbers to fluctuate locally through dispersal, we may reduce impact on vegetation and other taxa. Under our scenario, conservation areas serve as components of a regional landscape mosaic, not as isolated entities in which elephants must occur all the time in "acceptable" numbers. This relieves individual parks of the onus to stabilise local elephant populations. Consequently, transient changes within regional conservation clusters would represent a shifting mosaic of resources over space and time. We propose conservation managers should accept local instability of elephant numbers, as long as relative stability can be assured through regional conservation initiatives. Such an option develops regional conservation initiatives that focus on elephants – it makes ecological sense and should have political, sociological and economic benefits.

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