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African elephants
Loxodonta africana
and human–elephant interactions: implications for conservation

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African elephants face an uncertain future. Politics, war, sustained media campaigns, corrupt, weak or absent institutions supporting conservation, land-use planning or general governance, and greed are all bringing elephants into direct conflict with humans. Although elephant populations have declined considerably relative to their historical size and range, human populations have expanded to occupy and intensively use remaining elephant areas. Strategies to minimize perceptions of conflict and the implementation of land-use planning with biodiversity protection as its goal could help to sustain at least some populations of elephants. Here, we review threats to elephants, with an emphasis on those resulting from human perceptions of conflict, and suggest some mechanisms for grappling with these threats.

Key words: African elephant, conflict, crop-raiding, human–elephant interaction, land use, poaching, population status

Charismatic, intelligent, social, long-lived, strong and very large; these traits underlie the complex and at times conflicted relationship between elephants and humans. African elephants *Loxodonta africana* and Asian elephants *Elephas maximus* have provided humans with meat, ivory and a workforce over recorded history. At the same time, there are millennia-old records of crop-raiding by elephants in both the African and Asian continents (Osborn, 1998). While the elephant is used as a flagship species to gain public sympathy for species and habitat conservation (e.g. the logo of African Wildlife Foundation), for many subsistence foresters, farmers and pastoralists, elephants represent a threat to livelihoods and lives. This category of human–elephant interaction is exclusively negative and includes human death, injuries and illness, financial losses as a result of crop-raiding, livestock mortality and constraints on general day-to-day human activities (e.g. reported restrictions on collecting firewood or water, travelling to school and loss of time because of farm guarding).

When the colonial African national parks were created, the aim was to protect inviolate sanctuaries, from which people were excluded, and these landscapes became frozen in time. This exclusion further contributed to negative perceptions of highly visible wild species, such as elephants, which were seen as having a political, economic or land-use advantage over local people (see Anderson & Grove, 1987). The outcome of negative interactions between people and elephants are inevitably bleak as far as elephants are concerned. Indeed, some contemporary language used to describe elephants and, in particular, human–elephant interaction is determinedly hostile (e.g. conflict, pests, compensation, valuing resources or commodities) firmly places people in control of the outcomes of interactions, whether or not conflict actually occurs. In addition, much current conservation emphasis is on the maintenance of sustainable ecosystems in the context of sustainable eco-

nomic systems, with all the implied expectations of a market economy and rewards thus anticipated. The role and place of charismatic mega-fauna within evolving conservation paradigms need to be considered carefully as long as some humans aesthetically or emotionally value these animals, while others live in a state of permanently engaged hostilities and still others are reaping the financial rewards of their exploitation.

Here, we briefly review elements of the conflict paradigm and its consequences for elephant conservation, with an emphasis on savannah African elephants, although the issues of loss of livelihood and human life from elephants, and elephant population declines are as relevant to Asian elephants (Sukumar, 1989) as they are to the African species, including African forest elephants *Loxodonta cyclotis*.

ELEPHANT POPULATIONS: IVORY & HUMANS

Early European travellers and explorers in Africa reported a conspicuous absence of elephants and other large mammals in specific areas of appropriate elephant habitat, suggesting that hunting by local populations had contributed to localized extinctions (Selous, 1881; Thomson, 1885; von Höhnel, 1894; Neumann, 1898). Such accounts might support a narrative of 'competitive exclusion' between people and elephants (e.g. Parker & Graham, 1989) but they may also reflect the chronic negative human impact on mega-fauna populations (see Surovell *et al.,* 2005). Historical demands for ivory among early civilizations are thought to have contributed to the extinction of elephants from Syria around the 4th century A.D. and from the rest of North Africa by the 7th century (Spinage, 1994). By the 15th century a profitable trade with the Middle East, China, India and, subsequently, Europe facilitated the extensive settlement of Swahili ivory and slave traders along the East African coast (Hakansson, 2004). Between 1500 and 1700 A.D. Europe was importing *c.* 100–200 tonnes of ivory per year and by the late 19th century, European ivory imports may have been as high as 700 tonnes (Spinage, 1994), representing a potential 60 000 elephants killed per annum (Blanc *et al.,* 2003). The 'ivory crisis' describes the period from the early 1970s until the early 1990s after the 1989 CITES (Convention on the International Trade in Endangered Species of Wild Fauna and Flora) ban on the ivory trade took effect. During this recent period, African elephant populations again declined dramatically in response to intense hunting for ivory, which was used to fuel wars (Draulans & Krunkelsven, 2002) and to fund local development and individualized wealth. Uganda's elephant numbers fell from an estimated 17 600 to 1800, Kenya's from 130 000 to 19 000 and Tanzania's from 185 000 to 87 000, declines that were thought to be mirrored throughout elephant range states (Douglas-Hamilton, 1987).

The effect of the CITES ban on the trade in elephant products (including ivory), while debated (see Stiles, 2004), has been to reduce poaching pressure on many savannah populations. As a result some populations have increased, such as those in Kenya (thought to have increased from 19 000 to 29 000: Kenya Wildlife Service 2005 estimates) and Tanzania (thought to have increased from 87 000 to *c.* 130 000: Tanzania National Parks Authority 2005 estimates), although they may still be below their pre-poaching levels (see also Blanc *et al.,* 2005). Other populations have grown relatively continually as a result of effective anti-poaching enforcement and management strategies over the longer term (South Africa, Botswana). However ongoing war and political instability within Central Africa has helped sustain the illicit trade in ivory, and many populations of forest elephants are thought to be under intense poaching pressure (see Blanc *et al.,* 2003). The CITES MIKE (Monitoring the Illegal Killing of Elephants) Programme was

established in 1999 to assess the extent and effect of poaching Africa-wide, although it has yet to produce regional reports on current elephant status or mortality. It is known that some countries, notably Nigeria, Côte d'Ivoire and Senegal (Courouble *et al.,* 2003), are still producing more ivory artefacts than there are elephants in those countries. Extensive poaching and cross-border 'mining' of elephants (see Stephenson, 2004; Dublin, 2005) thus still appears to be a significant problem in West, Central and some parts of Eastern Africa; for example, between Sudan and Democratic Republic of the Congo. The most recent assessments of elephant population status by region and country (Blanc *et al.,* 2003) suggest that there are now between 420 000 and a speculative total of 660 000 African elephants, when some pre-poaching estimates were as high as 1·6 million (Douglas-Hamilton, 1987).

LAND USE AND ELEPHANTS

The availability of modern weapons has made it far easier for people to kill large mammals and has contributed to marked declines in elephant numbers. Periods of intense hunting resulted in major transitions in the spatial occurrence of human–elephant conflict as elephants shifted their range beyond those hunting spheres that were supplying the ivory market. Some elephants responded to intense hunting by moving into protected areas and other secure refuges. In some cases this has resulted in the incidence of human–elephant conflict where little or none had been reported previously (Thouless, 1994; Tchamba, 1996). Settlements surrounding refuges record the most incidents of human–elephant conflict (Naughton-Treves, 1997). In areas where security has recently improved, elephants move beyond refuges and are now coming into conflict with people who may have only recently settled in these surrounding areas (Sitati, 2003). Thus, the mobility and adaptability of elephants has contributed to both their persistence and to a dynamic and shifting interface in the interactions between people and elephants across Africa.

Parker & Graham (1989) developed a model of elephant populations that suggested that human population growth and settlement expansion were more significant threats to elephant populations over the long term than was the trade in ivory. However, the coarse scale of their investigations may have overlooked important elements of the relationship between people and elephants at finer scales. Hoare & du Toit (1999) carried out similar analyses of the effect of human density on elephant numbers in the Sebungwe region of Zimbabwe. This region was included in Parker & Graham's (1989) model but at the district level, while Hoare & du Toit (1999) carried out their analysis at the ward level, representing the smallest unit of administration in Zimbabwe. This finer level of analysis found that while elephant density and human density were indeed negatively correlated, the relationship was not linear. Elephant density is unrelated to human density until a threshold is reached at about 15·6 persons/km^2, representing a transformation of land use to about 40–50% human activities, at which point elephants vanish. Hoare & du Toit (1999) concluded that the sudden disappearance of elephants in areas above this threshold could be attributed to elephants moving to less disturbed habitats rather than elephants dying *in situ*. They also suggested that when the total area of land transformed by human settlement exceeds a critical point, 'the size and connectivity of the remaining patches of elephant habitat are then the determinants of whether or not elephants remain as residents or move away' (Hoare & du Toit, 1999). These conclusions bring to light the role of both habitat transformation and elephant ecology in determining the ability of elephants to persist in human dominated landscapes.

The impact of people on the ability of wild animals to endure in a given landscape relates to factors including direct mortality and injury to elephants, and the fragmentation of habitats through conversion into crop-fields, settlement and livestock pasture. The creation of barriers to movement (fences or zones of high mortality risk) is fundamental to understanding wild species persistence. Obviously, barriers deprive elephant populations of genetic exchange and critical access to seasonal food and water resources.

Managers and/or conservationists have attempted to address these constraints on wildlife persistence using a range of landscape 'tools' based on ecological principles. For example, corridors are one particular land-use feature relevant to connectivity and broad issues of wildlife population decline. Corridors are often considered as continuous linear strips and dispersal is the main movement along such strips. However, there are other types of connecting habitats (e.g. stepping stones, habitat mosaics) and other types of animal movement (daily foraging or migratory movements; see Douglas-Hamilton *et al.,* 2005) that can facilitate connectivity and which are sometimes ignored in the corridor debate (Bennett, 2003). The behavioural components of connectivity, such as which individual elephants use specific areas, which sex or age group incurs or avoids risks and which sex or age group moves or is resident, are likely to have significant implications for the persistence of populations. Connectivity between habitat patches ensures that individuals in a population have access to resources that are seasonally distributed, such as water or high-quality browse, or that are patchy in space as well as time, such as shelter from risk.

Despite the importance attributed to corridors in facilitating the persistence of wildlife populations in the context of habitat fragmentation, barriers or areas of mortality risk (Simberloff & Cox, 1987; Armbuster & Lande, 1993; Beier, 1993), empirical data on corridor use by elephants are lacking (but see Johnsingh & Williams, 1999 for India). In Africa, the debate over the need for corridors, their size and location is, however, unlikely to alter any politically driven process of land tenure and land-use change (Osborn & Parker, 2003). Reconciling the ecological principles needed in order to ensure the persistence of wild-elephant populations with the short-term political and socio-economic goals of developing nations, is an enormous challenge, although it is a priority for ensuring elephant conservation (see also Hoare, 2002).

CROP RAIDING, ELEPHANTS AND HUMAN ATTITUDES

The 'Pleistocene' African landscape has been characterized as small, scattered human settlements existing in a sea of elephants (Parker & Graham, 1989). As noted above, however, a continuous distribution of elephants was by no means certain. The presence of elephants at high densities in pre-colonial Africa is assumed, although few data exist, to have acted a major constraint on cultivation (Parker & Graham, 1989; Barnes, 1996; Hoare, 1999). The wide stone walls surrounding ancient villages in Zimbabwe may have been constructed to deter crop-raiding elephants (Clutton-Brock, 1999), indicating that crop-depredations by elephants have long been a significant problem in the African savannas. Subsistence farmers have abandoned villages as a result of conflict with wildlife in parts of modern-day Zambia and Malawi (Bell, 1984), supporting suggestions for enhanced vulnerability of pre-colonial African farmers. In equatorial forests, elephants may long have been a limiting factor for agricultural settlement (Barnes, 1996) and there are early colonial records of small-scale farmers suffering extensive depredations by elephants (Schweitzer, 1922). A shifting pattern of cultivation in forests actually encourages a mixture of

secondary growth highly favourable to elephants (Barnes, 1991).

While not new, reported incidents of conflict between people and large mammals have increased of late (Kangwana, 1995) and human–wildlife conflict in general is *perceived* to be increasing (Kiiru, 1995; Treves & Karanth, 2003) and to be more widespread (Hoare, 1999). This perception, however, may be unsubstantiated and human–wildlife conflict is perhaps more accurately described as neither increasing nor decreasing but dynamic and dependent on the local temporal and spatial extent of interactions. For example, in Uganda, where elephant range has decreased from 70% to less than 7% of the country between the 1920s and 1990s there has been a concomitant decline in the area at risk from crop-raiding by elephants (Naughton-Treves, 1997), but no decline in the attention that raids receive. Human population distributions thus underlie perceptions of conflict.

In the Sebungwa region of north-west Zimbabwe (15 000 km^2) the intensity of human–elephant conflict was explored in relation to elephant density, proximity to a protected area, area of human settlement, human density and local rainfall (Hoare, 1999). None of these were found to be predictive, which confounds our ability to predict when and where conflict is likely. The absence of spatial correlates was attributed to the high number of incidents involving ♂ elephants (79%). Hoare speculated that a few individual ♂♂ could be responsible for high levels of problem incidents in these areas although the actual level of raiding could match those in areas where there are many occasional raiders. The 'male behaviour hypothesis' has been supported by empirical observations elsewhere, and especially in Asian elephants (Sukumar & Gadgil, 1988; Sukumar, 1991; Osborn, 1998).

In the Kenyan Tsavo ecosystem, human–elephant conflict (measured as numbers of incidents per km^2 per year) was significantly associated with distance to permanent water, mean elevation and the length of the protected area frontage (Smith & Kasiki, 2000). The clear spatial correlates found in this study may be the result of the preponderance of ♀ elephants involved in incidents. In the Kenyan Mara ecosystem, Sitati *et al.* (2003) suggested that occurrence and intensity of crop-raiding by ♀♀ was predicted by percentage of area under cultivation (representing opportunity costs for ♀♀ that are willing to travel further to gain food), but for ♂-led groups the key factor was proximity to settlements (representing mortality risk because raiding close to settlements is associated with a greater likelihood of being shot). In addition, elephant-induced human injury or death was unrelated to either factor influencing elephant distributions, but rather proximity to roads and 'unfortunate spatial coincidence'. The important point is that the risks and opportunities from crop-raiding differ between the sexes of elephants and for humans.

In Laikipia District in northern Kenya, distance from elephant refuges (ranches) and permanent water predicted the spatial occurrence of crop-raiding by elephants (M. D. Graham, pers. obs). In addition crop-raiding intensity was highest at sites with low to intermediate levels of crop-cover and lower at sites of intense cultivation. This illustrates the vulnerability of small-scale farmers living in land-use mosaics where for many reasons, although principally climatic, settlements and cultivation are 'patchy'. Clearly small, scattered settlements surrounded by natural bushland are more vulnerable to crop depredation by elephants than are consolidated 'barriers' of agricultural land. In yet another Kenyan study, government records indicated that levels of human injury and mortality were accentuated during times of drought (Thouless, 1994). This may reflect heightened levels of conflict between elephants and pastoralists over access to scarce watering points

(Kangwana, 1993; Thouless, 1994) as well as competition over grazing on high-quality forbs (Young & Gadd, 2005).

All these examples highlight the importance of land-use planning in order to predict and manage human–elephant conflict.

Crop raiding by elephants can have a temporal pattern linked to seasonal declines in the availability of wild foods, specifically high-quality wild grasses (Osborn, 2004). Around Kibale National Park, Uganda, however, the attractiveness of maize to crop-raiders in this region is independent of the availability of wild foods (Naughton-Treves *et al.,* 1998), suggesting selection for specific crop traits (high density and large patch size), ripeness stage or nutrient density (high sugars, low fibre). An understanding of the local dynamics of wild food availability in the context of crop ripening is a further factor that could help in mitigation of conflict over crops (Chiyo *et al.,* 2005).

Local people rate crop-raiding by wildlife as the biggest problem associated with living next to protected areas (Hill, 1997; Naughton-Treves, 1997; De Boer & Baquete, 1998; Gillingham & Lee, 1999). Farmers' perceptions of crop-raiding reflect a focus on extreme events and there is often a significant mismatch between damage reality and perception of loss or rank of pest species (Naughton-Treves, 1997; Gillingham & Lee, 2003; Lee & Priston, 2005). Regular field assessments found that smaller-bodied pests, such as rodents, bush pigs and birds, living within settlement areas and not large mammals from the protected area were responsible for most crop-damage (Gillingham & Lee, 2003). However the ranking of 'pests' may also represent a form of local resistance and protest over the negative impacts of protectionist conservation strategies (Gillingham, 1998).

The propensity of respondents to exaggerate depredation by wildlife reflects important social dimensions to human–wildlife conflict. Exaggerated complaints can result from concern over resource-use constraints imposed by conservation legislation, regional land-tenure systems or their administrative representatives (Madden, 2004). The development of a compensation culture has a consequence such that rather than viewing wildlife, including elephants, as part of the system within which farming or cattle ranching occurs, any effects of wildlife on crops, waterholes or other land uses is seen as a direct cost to local people, which must be made up from central government funds as long as the government retains custodianship of the wildlife. In some cases, elephants may be used as lightening rods for a range of unrelated grievances associated with poverty or exclusion from social benefits (Gillingham, 1998). As a result of these factors, tension between local farmers and wildlife authorities can run high. Politicians are often able to effectively exploit these tensions by publicly blaming wildlife personnel for the problems.

The media are also extremely effective at using human–elephant conflict incidents to construct narratives of inequality, fear and political struggle. The combination of pressure on wildlife authorities from politicians and the national media can be played out in dramatic fashion. For example, in 2004, several days after the President of Kenya publicly criticized the Kenya Wildlife Service for not protecting farmers from wildlife, three elephants were shot to control 'problem' animals adjacent to Aberdares National Park. The media were invited to attend the operation and subsequently scenes of trapped elephants being shot repeatedly with unsuitable low-calibre guns in daylight were broadcasted on national television in what might subjectively be described as an 'execution'.

It has been suggested that if local people are given custodianship of wildlife and are able to make decisions about the 'use' of wildlife, then perceptions of conflict may be reduced (Barbier, 1992; Metcalfe, 1994). However, the success of

projects that have used this approach, such as CAMPFIRE in Zimbabwe and ADMADE in Zambia, is debatable (Gibson & Marks, 1995; Murombedzi, 2001; Adams, 2004). The danger of community-based utilization is that it may encourage a pattern of wildlife 'use' that, in the absence of meaningful institutions, will be unsustainable, as appears to be happening in a context of political instability in Zimbabwe. In addition the policy of consumptive use is based on simple farming principles (fences, management units, maximum yields, monocultures) that diverge significantly from an emerging systems view of the environment among ecologists and conservation biologists (open landscapes, ecological and evolutionary resilience, diversity and connectivity).

As a final note, even with regard to protected areas, the so-called 'elephant problem' (too many elephants, concentrated in refuges, altering the inviolate protected areas) continues to influence managers' strategies towards elephants (see also Gillson & Lindsay, 2003). This perceived 'problem' encouraged the emergence of systematic elephant culling as a management tool for various conservation areas in Africa. In Kenya's Tsavo National Park in the late 1960s, the impact of conservation policies and effective protection from poachers resulted in an apparently rapidly growing elephant population over the short term of the biological censuses, which had a visible impact on the park's woodlands. This impact, combined with a persistent drought, created the appearance of a devastated landscape and caused scientists to propose management intervention through culling (Parker, 1983). Without culling, it was argued, elephants would eat everything in their region and cause irreparable damage to the habitat. However, a prolonged drought combined with subsequent unpredicted poaching reduced the Tsavo population from 20 000–30 000 to <5000 by the late 1980s. Similar concerns over habitat destruction in Murchison National Park resulted in a cull of 2000 out of 14 000 elephants in the late 1960s (Laws *et al.,* 1975). Because of political instability and intense poaching only 1500 elephants remained by 1980 (Eltringham & Malpas, 1980). In Queen Elizabeth National Park, only 150 of the original 3500 elephants remained after poaching, with genetic consequences for the isolates (Nyakaana *et al.,* 2001). Similar to human–elephant conflict, the language of 'habitat destruction' rather than sound ecosystem science seems paramount in these historical debates (see also Gillson & Lindsay, 2003).

The point here is that as a management tool, culling often produces unexpected results; combined with the ethical and welfare issues associated with mass killings of elephants, culling may not represent a particularly effective or attractive management strategy (Whyte *et al.,* 1999). Culling may also create markets for inappropriate trade, such as moving orphaned elephant calves into captivity, which again has major ethical as well as conservation implications (e.g. recent public controversies in Swaziland and Kenya about the export of 'surplus' young elephants to various zoos in North America and Thailand). There are ongoing debates about needs to cull in South Africa, Botswana and Zimbabwe. However, in the absence of incentives or spin-offs from culling, the creation of mega-parks and meta-reserves and especially those extending transnationally may represent the next wave of potential successful non-lethal management options for some populations of elephants (van Aarde, 2005). For other isolated, fenced or relict populations, surrounded by a sea of human-dominated landscapes, considered management of reproduction, population size or movements might be the only options.

CONCLUSIONS

It is humans, not elephants, who define the problems, set the agenda for solutions

and maximize their own returns. The trade in ivory, human–elephant interactions and landscape management are all of critical importance to the fate of elephants on the African continent (Stephenson, 2004). These issues can be considered to be risk factors potentially leading to elephant population declines (Table 1). The ban on the ivory trade has been a partial solution to elephant poaching when associated with effective enforcement and monitoring (e.g. CITES MIKE Programme), and appropriate land-use planning is necessary as a first step towards addressing both human–elephant conflict and the so-called 'elephant problem' of too many elephants in the humanly-defined 'wrong' areas.

Effective land-use planning that takes account of the needs of wildlife in the context of human livelihoods and future development is urgently needed, and not only for the maintenance of elephant populations but also for biodiversity more generally. In order to offset the cost of conservation measures, benefits resulting from consumptive and non-consumptive utilization of wildlife have been realigned to provide advantages specifically to local people. Despite the positive aims of these conservation mechanisms, few have been successfully implemented and, as yet, even fewer have published measurable long-term impacts on species-specific conservation problems. It is time to reconsider the problems confronting elephants in increasingly human-dominated landscapes and design solutions that integrate the needs of both the human and the elephant into land-use plans. It should also be possible to find sustainable solutions that do not involve consumptive utilization, because elephants seldom benefit from such use.

Remove economic incentives from hunting, culling or live sale for export to zoos, and in the absence of crop-raiding conflicts, the managers of the future might feel confident enough to leave elephants to manage their own populations especially in a mega-park context. This can only occur, however, with the support of local media, where communities lack economic incentives for exploitation, and in communities with high levels of participation and social inclusion. Where there is conflict within a community as a result of social exclusion, differential distribution of benefits and perceptions of disenfranchisement from those benefits, then even in the absence of direct conflict with elephants, positive attitudes are unlikely to thrive either in the media or within the local population (e.g. Gillingham & Lee, 1999). If people, both western conservationists and local populations with traditions of living with wildlife (e.g. Kuriyan, 2002), wish to see elephants per-

REGION	DEFINITE	POSSIBLE	THREATS
East	117 716	22 511	conflict with humans for resources (space, food and water), isolation, poaching
South	246 592	26 098	crop-raiding, compression, poaching, trophy or meat hunting
Central	16 450	64 477	poaching for ivory and bushmeat, large-scale habitat loss as a result of extractive industries (mining, logging)
West	5458	3039	poaching, habitat fragmentation as a result of human activities, conflict with humans

Table 1. Estimates of elephant numbers for African regions from the *African Elephant Status Report 2002* **(Blanc** *et al.,* **2003): definite. known or 95% confidence intervals on minimum counts or population estimates; possible. difference between counts and upper estimates (Blanc** *et al.,* **2003). Threats are ranked in priority by region from Stephenson (2004).**

sisting in some areas in the future, it may be time to find the land and political will to create either sensitively managed multi-use areas or the mega-parks of the future.

As a final note, political instability has dominated post-colonial Africa with 20 African states experiencing civil war since 1960 (Draulans & Krunkelsven, 2002). In the absence of political stability it becomes extremely challenging to maintain conservation institutions (although the Parc des Virungas is a notable exception; see Adams, 2004). Many of the declines in African elephant populations in the last 30 years have occurred in the context of civil war and/or the breakdown in political and institutional governance. Debates over consumptive utilization, land-use planning and the ivory trade are meaningless in the context of wars, where years of conservation investment become worthless. This context underlies the sharp decline in Garamba National Park's elephant population and the virtual extinction of the Northern white rhinoceros *Ceratotherium simum cottoni.* Without informed discussion and active international engagement to address the impact of war on elephants and biodiversity conservation, the future of populations in some areas is bleak.

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REFERENCES

van Aarde, R. (2005): *A conservation alternative for African elephants: the mega-parks and meta-population metaphor.* Grahamstown, South Africa: Cecily Niven Memorial Lecture, Sasol Scifest.

Adams, W. M. (2004): *Against extinction: the story of conservation.* London: Earthscan.

Anderson, D. & Grove, R. (1987): *Conservation in Africa: people, policies and practice.* Cambridge: Cambridge University Press.

Armbuster, P. & Lande R. (1993): A population viability analysis for African elephant: how big should reserves be? *Conservation Biology* **7:** 602–610.

Barbier, E. (1992): Community based development in Africa. In *Economics for the wilds: wildlife, wildlands, diversity and development:* 103–135. Swanson, T. M & Barbier, E. B. (Eds). London: Earthscan.

Barnes, R. F. W. (1991): Man determines the distribution of elephants in the rainforests in north-eastern Gabon. *African Journal of Ecology* **29:** 54–63.

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

Beier, P. (1993): Determining minimum habitat areas and habitat corridors for cougars. *Conservation Biology* **7:** 94–108.

Bell, R. H. V. (1984): The man–animal interface: an assessment of crop damage and wildlife control. In *Conservation and wildlife management in Africa:* 389–415. Bell, R. H. V. & McShane-Caluzi, E. (Eds). Lilongwe, Malawi: US Peace Corps Office of Training and Program Support.

Bennett, A. F. (2003): *Linkages in the landscape: the role of corridors and connectivity in wildlife conservation.* Gland: IUCN.

Blanc, J. J., Thouless, C. R., Hart, J. A., Dublin, H. T., Douglas-Hamilton, I., Craig, G. C. & Barnes, R. F. W. (2003): *African elephant status report 2002. Occasional Paper of the IUCN Species Survival Commission 29.* Gland: IUCN/SSC African Elephant Specialist Group.

Blanc, J. J., Barnes, R. F. W., Craig, G. C., Douglas-Hamilton, I., Dublin, H. T., Hart, J. A. & Thouless, C. R. (2005): Changes in elephant numbers in major savannah populations in East and Southern Africa. *Pachyderm* **38:** 19–28.

Chiyo, P., Cochrane, E. P., Naughton, L. & Basuta, G. I. (2005): Temporal patterns of crop raiding by elephants: a response to forage quality or crop availability. *African Journal of Ecology* **43:** 48–55.

Clutton-Brock, J. (1999): Cattle, sheep and goats south of the Sahara: an archaezoological perspective. In *The origins and development of African livestock: archaeology, genetics, linguistics and ethnography.* Blench, R. & MacDonald, K. (Eds). London: University College London Press.

Courouble, M., Hurst, M. & Miliken, T. (2003): *More ivory than elephants: domestic ivory markets in three West African countries. Traffic Online Report* No. 8. Cambridge: TRAFFIC International. http://www.traffic.org/news/press-releases/WestAfricanIvory.pdf

De Boer, W. & Baquete, D. (1998): Natural resource use, crop damage and attitudes of rural people in the vicinity of Maputo Elephant Reserve, Mozambique. *Environmental Conservation* **28:** 208–218.

Douglas-Hamilton, I. (1987): African elephants: population trends and their causes. *Oryx* **21:** 11–24.

Douglas-Hamilton, I., Krink, T. & Vollrath, F. (2005): Movements and corridors of African ele-

phants in relation to protected areas. *Naturwissenschaften* **92:** 158–163.
Draulans, D. & Krunkelsven. E. V. (2002): The impact of war on forest areas in the Democratic Republic of Congo. *Oryx* **36:** 35–40.
Dublin, H. T. (2005): African elephant specialist group report. *Pachyderm* **38:** 1–10.
Eltringham, S. K. & Malpas, R. C. (1980): The decline of elephant numbers in Rwenzori Kabalega Falls National Parks, Uganda. *African Journal of Ecology* **18:** 73–86.
Gibson, C. C. & Marks, S. A. (1995): Transforming rural hunters into conservationists: an assessment of community-based wildlife management programs in Africa. *World Development* **23:** 941–957.
Gillingham, S. (1998) *Giving wildlife a value: a case study of community wildlife management around the Selous Game Reserve, Tanzania.* PhD thesis, University of Cambridge, UK.
Gillingham, S. & Lee, P. C. (1999). The impact of wildlife-related benefits on the conservation attitudes of local people around the Selous Game Reserve, Tanzania. *Environmental Conservation* **26:** 218–228.
Gillingham. S. & Lee, P. C. (2003) A preliminary assessment of perceived and actual patterns of wildlife crop-damage in an area bordering the Selous Game Reserve, Tanzania. *Oryx* **37:** 316–325.
Gillson, L. & Lindsay, W. K. (2003): Ivory and ecology: changing perspectives on elephant management and the international trade in ivory. *Environmental Science and Policy* **6:** 411–419.
Hakansson, N. T. (2004): The human ecology of world systems in East Africa: the impact of the ivory trade. *Human Ecology* **32:** 561–587.
Hill, C. M. (1997): Crop-raiding by wild vertebrates: the farmer's perspective in an agricultural community in western Uganda. *International Journal of Pest Management* **43:** 77–84.
Hoare, R. E. (1999): Determinants of human–elephant conflict in a land-use mosaic. *Journal of Applied Ecology* **36:** 689–700.
Hoare, R. E. (2002): Update on the study and management of human–elephant conflict in Africa. *Pachyderm* **33:** 91–92.
Hoare, R. E. & du Toit, J. T. (1999): Coexistence between people and elephants in African savannas. *Conservation Biology* **13:** 633–639.
von Höhnel, L. (1894): *Discovery of Lakes Rudolph and Stephanie: a narrative of Count Samuel Teleki's exploring and hunting expedition in Eastern Equatorial Africa in 1887 and 1888.* London: Longmans and Green.
Johnsingh, A. J. T. & Williams, A. C. (1999): Elephant corridors in India: lessons for other elephant range countries. *Oryx* **33:** 210–214.
Kangwana, K. F. (1993): *Elephants and Maasai: conflict and conservation in Amboseli, Kenya.* PhD thesis, University of Cambridge, UK.
Kangwana, K. F. (1995): Human–elephant conflict: the challenge ahead. *Pachyderm* **19:** 11–14.
Kiiru, W. (1995): The current status of human–elephant conflict in Kenya. *Pachyderm* **19:** 15–19.
Kuriyan, R. (2002): Linking local perceptions of elephants and conservation: Samburu pastoralists in Northern Kenya. *Society and Natural Resources* **15:** 949–957.
Laws, R. M., Parker, I. S. C. & Johnstone, R. C. B. (1975): *Elephants and their habitats: the ecology of elephants in North Bunyoro, Uganda.* Oxford: Clarendon Press.
Lee, P. C. & Priston, N. J. (2005): Human attitudes to primates: perceptions of pests, conflict and consequences for primate conservation. In *Primate–human interaction and conservation:* 1–23. Patterson, J. D. & Wallace, J. (Eds). Toronto: American Society of Primatologists Publications.
Madden, F. (2004): Creating coexistence between humans and wildlife: global perspectives on local efforts to address human–wildlife conflict. *Human Dimensions of Wildlife* **9:** 247–259.
Metcalfe, S. (1994): The Zimbabwe Communal Areas Management Programme for Indigenous Resources. In *Natural connections: perspectives on community-based conservation:* 161–193. Western, D. Wright, P. M. & Strum, S. C. (Eds). Washington, DC: Island Press.
Murombedzi, J. (2001): Why wildlife conservation has not economically benefited communities in Africa. In *African wildlife and African livelihoods: the promise and performance of community-based conservation:* 208–226. Hulme, D. & Murphee, M. (Eds). Oxford: James Currey.
Naughton-Treves, L. (1997): Farming the forest edge: vulnerable places and people around Kibale National Park, Uganda. *The Geographical Review* **87:** 27–46.
Naughton-Treves, L., Treves, A., Chapman, C. & Wrangham, R. W. (1998): Temporal patterns of crop-raiding by primates: linking food availability in croplands and adjacent forest. *Journal of Applied Ecology* **35:** 596–606.
Neumann, A. H. (1898): *Elephant-hunting in East Equatorial Africa.* London: Rowland Ward Ltd.
Nyakaana, S., Abe, E. L., Artander, P. & Siegsmund, H. (2001): DNA evidence for elephant social breakdown in Queen Elizabeth National Park, Uganda. *Animal Conservation* **4:** 231–237.
Osborn, F. V. (1998): *The ecology of crop-raiding elephants in Zimbabwe.* PhD thesis, University of Cambridge, UK.
Osborn, F. V. (2004): Seasonal variation of feeding patterns and food selection by crop-raiding elephants in Zimbabwe. *African Journal of Ecology* **42:** 322–327.
Osborn, F. V. & Parker. G. E. (2003): Linking two elephant refuges with a corridor in the communal lands of Zimbabwe. *African Journal of Ecology* **41:** 68–74.
Parker, I. S. C. (1983): *Ivory crisis.* London: Chatto & Windus.

PARKER, I. S. C. & GRAHAM, A. D. (1989): Men, elephants and competition. *Symposium of the Zoological Society of London* No. 61: 241–252.
SCHWEITZER, A. (1922): *On the edge of the primeval forest.* London: Adams & Charles Black.
SELOUS, F. C. (1881): *A hunter's wanderings in Africa.* London: Richard Bentley & Son.
SIMBERLOFF, D. & COX, J. (1987): Consequences and costs of conservation corridors. *Conservation Biology* **1:** 63–71.
SITATI, N. W. (2003): *Human–elephant conflict in TransMara district adjacent to Masai Mara National Reserve.* PhD thesis, University of Kent, Canterbury, UK.
SITATI, N. W., WALPOLE, M. J., SMITH, R. J. & LEADER-WILLIAMS, N. (2003): Predicting spatial aspects of human–elephant conflict. *Journal of Applied Ecology* **40:** 667–677.
SMITH, R. J. & KASIKI, S. (2000): *A spatial analysis of human–elephant conflict in the Tsavo ecosystem, Kenya.* Gland: IUCN/SSC African Elephant Specialist Group.
SPINAGE, C. A. (1994): *Elephants.* London: T. & A. D. Poyser.
STEPHENSON, P. J. (2004): The future for elephants in Africa. In *Terrestrial ecoregions of Africa and Madagascar: a conservation assessment:* 133–136. Burgess, J. D. A. H., Underwood, N. E., Dinerstein, E., Olson, D., Itoua, I., Schipper, J., Ricketts, T. & Newman K. (Eds). Washington, DC: Island Press.
STILES, D. (2004): The ivory trade and elephant conservation. *Environmental Conservation* **31:** 309–321.
SUKUMAR, R. (1989): *The Asian elephant: ecology and management.* Cambridge: Cambridge University Press.
SUKUMAR, R. (1991): The management of large mammals in relation to male strategies and conflict with people. *Biological Conservation* **55:** 93–102.
SUKUMAR, R. & GADGIL, M. (1988): Male–female differences in foraging on crops by Asian elephants. *Animal Behaviour* **36:** 1233–1255.
SUROVELL, T., WAGUESPACK, N. & BRANTIGLAN, P. J. (2005) Global archaeological evidence for proboscidian overkill. *Proceedings of the National Academy of Sciences USA* **102:** 6231–6236.
TCHAMBA, M. (1996) History and present status of the human/elephant conflict in the Waza-Logone region, Cameroon, West Africa. *Biological Conservation* **75:** 35–41.
THOMSON, S. W. (1885): *Through Maasailand.* London: John Taylor.
THOULESS, C. (1994) Conflict between humans and elephants on private land in northern Kenya. *Oryx* **28:** 119–127.
TREVES, A. & KARANTH, K. (2003) Human–carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology* **17:** 1491–1499.
YOUNG T. P. & GADD M. E. (2005): Competition and compensation among cattle, zebras, and elephants in a semi-arid savanna in Laikipia, Kenya. *Biological Conservation* **122:** 351–359.
WHYTE, I. J., BIGGS, H. C., GAYLARD, A. & BRAACK, L. E. O. (1999): A new policy for the management of Kruger National Park's elephant population. *Koedoe* **42**(1):111–132.

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