

ELEPHANT POPULATION BIOLOGY AND ECOLOGY

Lead author: Rudi van Aarde

Authors: Sam Ferreira, Tim Jackson, and Bruce Page

Contributing authors: Yolandi de Beer, Katie Gough, Rob Guldemon, Jessi Junker, Pieter Olivier, Theresia Ott, and Morgan Trimble

INTRODUCTION

THE ELEPHANT debate deals largely with population size, how elephant numbers change over time, how they may affect other species (e.g. Owen-Smith *et al.*, 2006; Van Aarde *et al.*, 2006), and how elephants should be managed (e.g. Whyte *et al.*, 2003; Van Aarde & Jackson, 2007). Changes in elephant numbers are the basis of many management plans and policies. For instance, the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) utilises trends in numbers and poaching data to inform ivory trade decisions (Hunter & Milliken, 2004). Past decisions to cull elephants in several parks across the southern African subcontinent have also been motivated by numbers and trends in numbers over time (Cumming & Jones, 2005).

The focus of past management on numbers, rather than impact, may have detracted from the ultimate goal of controlling or reducing the effect elephants had on vegetation, other species, and people. The limited options available when managing numbers (see chapters on contraception, translocation and culling) and the emotive issues that surround this may also detract from its popularity and effectiveness. However, a multitude of options exists and can be developed to manage impact (see Chapter 12). Ultimately, the effectiveness of management hinges on monitoring the outcomes for impact, which include the response of affected species, ecological processes, elephant range utilisation, and elephant numbers. This monitoring may be done on a local scale (e.g. around waterholes), at the park level (e.g. to monitor the effectiveness of contraception and culling), or on the regional scale (e.g. to monitor the effectiveness of restoring seasonal and large-scale movement patterns). Therefore it is important to unravel and understand the mechanisms that determine spatial utilisation patterns and how numbers vary across space and time. This chapter focuses on assessing our understanding of the factors that determine these variables.

In this chapter we compare the social, spatial, and demographic profiles of South Africa's elephant populations to those of elephant populations elsewhere in Africa. We also make a concerted effort to explain similarities and differences, and we use these to evaluate the response of elephant populations to their living conditions in South Africa's conservation areas. For the spatial aspects, we compare South Africa's elephants with those living across the environmental gradient typical of southern Africa. For the demographic component, we compare data on South Africa's populations to all other information available from elephant populations in Africa. We also provide brief summaries of elephant sociology (box 1) and intelligence (box 2) that may modify our understanding of the spatial and dynamic responses of elephants to the environment, people, and management. Additionally, we discuss the effects of various management actions on population biology. We conclude this chapter with recommendations on how to accommodate elephant population responses to management in South Africa. We consider all of this as relevant to the assessment of South Africa's elephant populations.

SPATIAL UTILISATION

Distribution

Elephants need to drink regularly and therefore occur where surface water is available (e.g. Smit *et al.*, 2007a; Harris *et al.*, 2008). Through southern Africa, 70–80 per cent of elephant range occurs outside protected areas (Blanc *et al.*, 2007; Van Aarde & Jackson, 2007). Fencing partly restricts regional distributions in southern Africa (Van Aarde *et al.*, 2005; Mbaiwa & Mbaiwa, 2006). In unfenced areas, human population density and agriculture influence elephant distribution (Hoare & Du Toit, 1999), but elephants and humans continue to coexist across most of the southern African distributional range of elephants (Jackson *et al.*, 2008). This is not the case in South Africa, where elephants are fenced off to live on land set aside for conservation and where people do not inhabit the land.

Historically, elephants ranged through much of South Africa (Hall-Martin, 1992). However, by 1920, human population growth, expanding settlement, the ivory trade, and crop protection decimated elephant numbers in the country to an estimated 120 (Hall-Martin, 1992). These few elephants were restricted to areas around Knysna, Addo, Tembe, and the Olifants Gorge (later proclaimed as part of Kruger) (Hall-Martin, 1992).

Box 1: Social aspects of African savanna elephants

Elephants live in a well structured and complex society. Their so-called fission-fusion social structure influences the way they interact with each other and with their natural environment (McComb *et al.*, 2001; Wittemyer *et al.*, 2005a; Archie *et al.*, 2006; Wittemyer & Getz, 2007). It is therefore critical that conservation management efforts consider the consequences for elephant society (Couzin, 2006). For instance, destroying part of a social unit may have consequences for the surviving members of that unit. Furthermore, by keeping elephants in relatively small areas their social structuring may not provide for behavioural inbreeding avoidance (see Archie *et al.*, 2006), or for the spatial segregation of herds based on dominance (Wittemyer *et al.*, 2007a).

Cows form the foundation of the social structure – they generally spend their entire lives in tightly knit social groups and live in a specific area (Moss, 1988). Adult bulls, on the other hand, are generally solitary though they associate with female groups (breeding herds) for brief periods of travel and to mate (Moss & Poole, 1983; Poole & Moss, 1989). The female social structure has been described as comprising six hierarchical tiers of organisation. From lower to higher levels of organisation, these tiers include mother-calf units, families, bond groups, clans, subpopulations, and populations (Wittemyer *et al.*, 2005a). The basic unit of social structure, however, is the matriarch-led family unit, typically consisting of 1–20 adult cows, their daughters, and immature male offspring (Archie *et al.*, 2006).

Families are highly stable across time and season (Wittemyer *et al.*, 2005a). Because most female elephants remain with the group into which they were born, relatedness within families is high (Archie *et al.*, 2006). Though permanent fissions are rare, families may break up into smaller subgroups for short periods, or fuse with other families to form larger groups (Wittemyer *et al.*, 2005a; Archie *et al.*, 2006). Families that consistently fuse to form larger groups are known as bond groups. Similarly, coalitions of bond groups are known as clans. Sub-populations and populations are higher-order tiers that group lower-order tiers together based on geography.

This multi-tiered structure probably evolved to balance the costs and benefits of sociality (Wittemyer *et al.*, 2005a). Potential benefits include the defence of resources and territories, joint protection from predators, shared parenting duties, collective social and ecological knowledge, and increased

inclusive fitness (Archie *et al.*, 2006). Higher tiered structures such as bond groups and clans might also enable the exchange of ecological information over relatively long distances (Foley, 2002). However, social living also has costs; it may intensify competition. The balance of the costs and benefits of associating at various tiers in the hierarchy differs temporally and seasonally in response to resource variability, the number of individuals in each group, and the spatial distribution of groups (Wittemyer *et al.*, 2005a).

Therefore, size and composition of social units may be influenced by human manipulation of resources such as the availability of water or the reduction of habitable space. Other interventions, such as culling, hunting, poaching, contraception, and translocation may also alter size and composition of groups (Ferreira *et al.*, 2008). The implications of these influences at the population level are poorly understood and require more research. However, McComb *et al.* (2001) show that families with older matriarchs have greater reproductive success, potentially due to the superior ability of older matriarchs to distinguish between the calls of known and unknown elephants. Therefore, hunters or poachers focusing their efforts on large tusked individuals may disproportionately affect the population through the removal of a few key individuals (McComb *et al.*, 2001). Furthermore, kinship is a primary driver of social relationships, and bond groups consist largely of related families (Archie *et al.*, 2006). Therefore, when population control measures remove a family's close relatives in other family units, the bond group and any associated fitness benefit may dissolve. Archie *et al.* (2006) recommend that elephant conservation measures strive to maintain patterns of maternal kinship.

Additionally, group dominance, primarily determined by the age of the matriarch (Wittemyer & Getz, 2007), plays an important role in spatial structuring (Wittemyer *et al.*, 2007a). Dominant groups enjoy disproportionate access to preferred habitats during the dry season, thereby minimising exposure to predation and conflict with humans and expending less energy than subordinate groups. Conversely, subdominant groups are relegated to marginal areas often outside protected reserves (Wittemyer *et al.*, 2007a). This research highlights the importance of social mechanisms and open ecosystems to population control and to the mitigation of the impacts elephants may have on ecosystems (Van Aarde & Jackson, 2007).

Within the southern African region, the local distribution of elephants varies seasonally. This can be ascribed to variation in resource availability across space and time (O'Connor *et al.*, 2007). For example, towards the end of the dry season when surface water is scarce, elephant density increases near rivers (Stokke & Du Toit, 2002; Jackson *et al.*, 2008). Similar effects occur around artificial waterholes (De Beer *et al.*, 2006), where dry season elephant densities are related to the density of added water points (Chamaillé-Jammes *et al.*, 2007). Thus, elephant distribution varies in space and time and is modified by water provision.

Factors determining the distribution of elephants

Within regions where elephants occur, several factors influence their local distribution. These factors include landscape type, food and water availability, rainfall-related changes in food quality and water availability, elephant density, social structures, management, and people.

Landscape type affects distribution because elephants do not move randomly through the terrain. Some landscape types, such as riparian environments and wetlands, support more elephants than others (e.g. Ntumi *et al.*, 2005; Kinahan *et al.*, 2007; Smit *et al.*, 2007a; Harris *et al.*, 2008), whereas steep hills tend to be avoided by elephants (Nellemann *et al.*, 2002; Wall *et al.*, 2006), despite their ability to negotiate such terrain under exceptional conditions.

Food and water are key requirements of elephants and affect their distribution. The water requirements of elephants are central to understanding patterns of their spatial use. For instance, in Kruger elephants drink on average every two days during the dry season (Young, 1970). In drier environments, bull elephants probably drink every 3–5 days and breeding herds every 2–4 days (Viljoen, 1988; Leggett, 2006b). Elephants, especially breeding herds, therefore seldom roam far away from drinking water.

Across southern Africa, we generally distinguish between dry and wet seasons. During the wet season, food resources are more abundant and higher in quality (Owen-Smith, 1988). Water is also distributed widely during the wet season and may not therefore restrict elephant spatial use and roaming distances (Leuthold, 1977; Western & Lindsay, 1984; Verlinden & Gavor, 1998; Gaylard *et al.*, 2003; De Beer *et al.*, 2006). In the dry season, however, the quality of food resources deteriorates, and seasonal water sources dry up. Therefore, elephants may use different habitats in a different part of their range

Box 2: Elephant intelligence

Once corrected for body size, the African elephant has a brain comparable in size and complexity to those of humans and other primates (Cozzi *et al.*, 2001). This certainly contributes to the popular belief that elephants have exceptional brainpower. Observations of elephants helping others and their apparent grief when facing dead conspecifics may strengthen the belief that elephants possess almost human-like awareness and intelligence. However, recent literature suggests that elephants are not extraordinarily intelligent but are, like many species, well adapted to cope with the natural spatial and temporal variability they face (Hart *et al.*, 2007).

Hart *et al.* (2008) also suggest that elephants perform poorly when compared to chimpanzees and humans in cognitive feats such as the use of tools, visual discrimination learning, and tests of 'insight behaviour' such as solving puzzles to reap rewards. However, elephants do have long-term, extensive spatial and temporal memory (Foley, 2002; Hakeem *et al.*, 2005; Leggett, 2006a). For herds to survive it is critical that there should be individuals within the herd that can successfully find isolated water holes and new foraging grounds over vast distances. Thus, long-term memory may enhance the ability to find scarce resources. Additionally, elephants, like many other species, can discriminate between different sounds. They can recognise individual calls from 1–1.5 km away (McComb *et al.*, 2003), and know the individual calls of about 100 other elephants (McComb *et al.*, 2000). Such auditory recognition may enable social associations between groups (McComb *et al.*, 2000). African elephants use olfaction and vision to identify different types of people in their local area and to vary their reactions appropriately to probable danger (Bates *et al.*, 2007). This may also be the case for other species that have not yet been studied.

Another aspect of elephant behaviour is their reaction to other elephants that are disabled or dead (Hart *et al.*, 2007). They can distinguish between elephant remains and those of other species, and often spend time investigating elephant corpses (Moss, 1988; McComb *et al.*, 2006). Responses to the death of an elephant calf include exploratory behaviour, fear and alarm behaviour, support efforts to lift the dying calf, body-guarding reactions and even aggression towards the body (Payne, 2003). There are many anecdotes of elephants trying to help others disabled by immobilisation drugs or bullets (see Douglas-Hamilton *et al.*, 2005). Behaviour consistent

with Post-Traumatic Stress Syndrome in humans has been observed in elephants (Bradshaw *et al.*, 2005). Inferences that such instances represent higher-order emotional expression or intelligence are subjective.

at the height of the wet season compared to the dry season (Western & Lindsay, 1984; Verlinden & Gavor, 1998; CERU, unpublished data).

In theory, if home range size is dependent on habitat productivity (see Harestad & Bunnell, 1979), elephants should range further during the dry season to include food resources otherwise available within smaller areas during the wet season. Contradictory to this expectation, elephants tend to concentrate their foraging activities in relatively small ranges close to water during the dry season (Gaylard *et al.*, 2003; Osborn & Parker, 2003; Redfern *et al.*, 2003; De Beer *et al.*, 2006; Leggett, 2006a; Smit *et al.*, 2007a). This suggests that elephants seek key resources such as water (see Scoone, 1995; Illius, 2006), regardless of the spatial distribution of other resources. Thus, in the dry season, water availability is a determinant of elephant spatial use (De Beer *et al.*, 2006) while selection for vegetation is often secondary (Harris *et al.*, 2008; Chamaillé-Jammes *et al.*, 2007).

Elephants also seek vegetation that is available near water; consequently, they may avoid water sources that are not associated with suitable vegetation (Harris *et al.*, 2008). In the arid Etosha National Park (Namibia), vegetation is sparsely distributed, and elephants select areas near water with high vegetation cover. However, here they will move greater distances during the dry season to obtain food (Harris *et al.*, 2008). In the evergreen savannas of Maputo Elephant Reserve (Mozambique), high vegetation cover is often associated with the distribution of water, and during the dry season, elephants do not have to move far from water to obtain food (Harris *et al.*, 2008). Thus, elephants meet their nutritional requirements within the constraints set by the location of water sources (Redfern *et al.*, 2003).

In savannas, there is a relationship between rainfall and primary productivity (e.g. Coe *et al.*, 1976). More recently, the remotely sensed Normalised Difference Vegetation Index (NDVI) has been used as a surrogate for primary productivity (e.g. Pettorelli *et al.*, 2005). Primary productivity (measured by NDVI) does apparently influence elephant spatial use, and during the dry season elephant densities tend to be higher in more productive areas, though the relationship is weak (Chamaillé-Jammes *et al.*, 2007; Young *et al.*, 2008).

Temporal (time) scales determine our interpretation of the way that elephants utilise the landscapes where they live. For instance, on a short time scale (hourly), the relative position of food resources (the distribution of individual forage and non-forage plants), water and shade can explain elephant movements. To study these movements, the distribution of path lengths and turn angles might be related to these resources (Dai *et al.*, 2007). Scaling up to a daily interval, movements usually consist of elephants foraging and travelling to and away from water and shade (De Villiers & Kok, 1988; Kinahan *et al.*, 2007). On a seasonal scale, within the same locality, elephants travel daily over longer distances during the wet than the dry season (Wittemyer *et al.*, 2007a; CERU, unpublished data).

Distribution across the landscape is also affected by the density of elephants (their number per unit area). As elephant numbers increase, distribution may change in two ways. First, local densities may remain relatively constant while the population extends its range. This may be the case in northern Botswana, where Junker *et al.* (2008) show that increased elephant numbers were associated with expansion of their range, whereas elephant densities did not increase. Here, space was not limiting, and elephants were able to extend their distribution outwards into unoccupied areas. Alternatively, if fencing, human populations, or other factors limit the area elephants can occupy, density may increase within specific areas. Young *et al.* (2008) studied elephant populations in Kruger and observed that as numbers increased after culling stopped, at a time when increases in land area were limited (the study period was prior to the removal of parts of the fence between Kruger and Limpopo National Park in Mozambique), the number of patches occupied by elephants increased. Thus, as densities increased, elephants became more evenly distributed across Kruger.

Furthermore, the social hierarchy of elephants may underlie spatial use, with dominant herds in Kenya having a greater proportion of their range within protected areas compared to subordinate herds (Wittemyer *et al.*, 2007a; see box 1). Here, dominant herds also spend more time near water and move shorter distances when measured at hourly, daily, or seasonal time intervals (Wittemyer *et al.*, 2007a). We are not aware of similar studies in any South African parks. In South Africa, fences limit temporal patterns of spatial use – all 63 populations in the country live in fully or partially fenced areas (see later). Consequently seasonal changes in the location and sizes of ranging areas (home ranges) in fenced-in populations were less pronounced than in free-ranging populations elsewhere in Africa (CERU, unpublished data).

As most of the elephant range in Africa occurs outside protected areas (Blanc *et al.*, 2007), human and elephant ranges overlap in many places. Inevitably, this leads to interactions between elephants, people, and their livelihoods (Van Aarde & Jackson, 2007). Elephants come into greater contact with people where their ranges increase. In northern Botswana, for instance, an increase in the distributional range of elephants led to a substantial increase in conflict between people and elephants (Alexander *et al.*, 2006).

Elephants appear to use space in a manner that reduces contact with people. On a daily basis, they achieve this by altering their drinking behaviour. For instance, along the Okavango River in north-western Botswana, people are active in fields during the day, while elephants visit areas close to the river at night only (Jackson *et al.*, 2008), thereby limiting overlap in times that elephants and people are in the same area. Spatially, elephants may avoid areas close to human settlements and leave areas entirely when human densities reach a particular threshold (Hoare & Du Toit, 1999). Hoare (1999) suggests that breeding herds are more likely than bulls to avoid people. When the distributions of people and elephants do overlap, conflict is often reported. Incidences of conflict, therefore, appear to be correlated with spatial factors such as human density, land transformation, agriculture, roads, and proximity to protected areas (Hoare & Du Toit, 1999; Parker & Osborn, 2001; Sitati *et al.*, 2003).

Elephant home ranges

The home range of an elephant represents the area it traverses in its normal activities of food gathering, mating, and caring for young. Home ranges can be measured on various time scales (e.g. monthly, seasonally, annually), and provide a measure of elephant spatial use in relation to various biotic and abiotic factors. Rainfall apparently plays an important role in determining home range size and location (Thouless, 1995; Osborn, 2004). Furthermore, across southern Africa, rainfall generally increases from southwest to northeast, creating a gradient of vegetation types (e.g. Sankaran *et al.*, 2005). In dry areas towards the west of the subcontinent where rainfall is relatively low, elephants tend to have larger home ranges than in wetter areas to the east (Van Aarde *et al.*, 2005).

Resources such as water, food, and shelter are unevenly distributed across the landscape, which gives rise to a mosaic of different land type patches (habitats or vegetation classes) (Forman & Godron, 1986). Heterogeneity refers to the complexity and variability of the spatial pattern contained by these patches within this landscape mosaic (Li & Reynolds, 1994). At the landscape

scale, some aspects of heterogeneity influence the location and/or size of elephant home ranges (Grainger *et al.*, 2005; Murwira & Skidmore, 2005; De Beer, 2007; Ott, 2007). In general, elephants favour areas where vegetation patches are more complex and diverse (Ott, 2007). Relatively high levels of heterogeneity, due to an increase in the length of habitat edges (Tufto *et al.*, 1996; Saïd & Servanty, 2005), may further benefit elephants by providing better opportunities to obtain resources (De Beer, 2007; Ott, 2007). In relatively wet (mesic) savannas (see Sankaran *et al.*, 2005), cows tend to occur in areas with higher levels of heterogeneity than where bulls occur, and for both sexes, heterogeneity levels are higher within their wet season ranges than within dry season ranges (Ott, 2007).

In Kruger, only one measure of heterogeneity that Grainger *et al.* (2005) examined explains variability in elephant home range sizes, possibly because the distribution of artificial water resources (e.g. dams, drinking troughs and waterholes maintained by water from boreholes) masks patterns in landscape use. Here, the areas of elephant home ranges tend to decrease as the density of waterholes increases (Grainger *et al.*, 2005), as is also the case in the Etosha National Park and the Khaudum Game Reserve in northern Namibia (De Beer, 2007). This once again points to water and the distribution thereof being an important determinant of the manner in which elephants utilise landscapes. Tampering with the distribution of water through the construction of dams and waterholes therefore will alter the ranging behaviour of elephants.

In South Africa fences that separate conservation areas where elephants live from the surrounding landscape influence the home range. Consequently, elephants in South Africa have relatively small home ranges (breeding herds mean = 595 km², range: 21 km²–2 766 km², $n = 51$; bulls mean = 153 km² range: 32 km²–1 707 km², $n = 43$; figure 1), compared to those of elephants throughout the rest of the region (breeding herds mean = 1 678 km², range 4 km²–10 738 km², $n = 73$; bulls mean = 2 095 km², range 3 km²–12 800 km², $n = 23$; figure 1). Home range sizes of both bulls and breeding herds are smaller in South Africa compared to those of elephants in other areas of southern Africa with similar rainfall (figure 2). Significantly, all South Africa's elephants (at least for the time these data were available) occur in fenced areas, while the movements of those in the rest of the region, except for Etosha in Namibia, are not restricted in the same way.

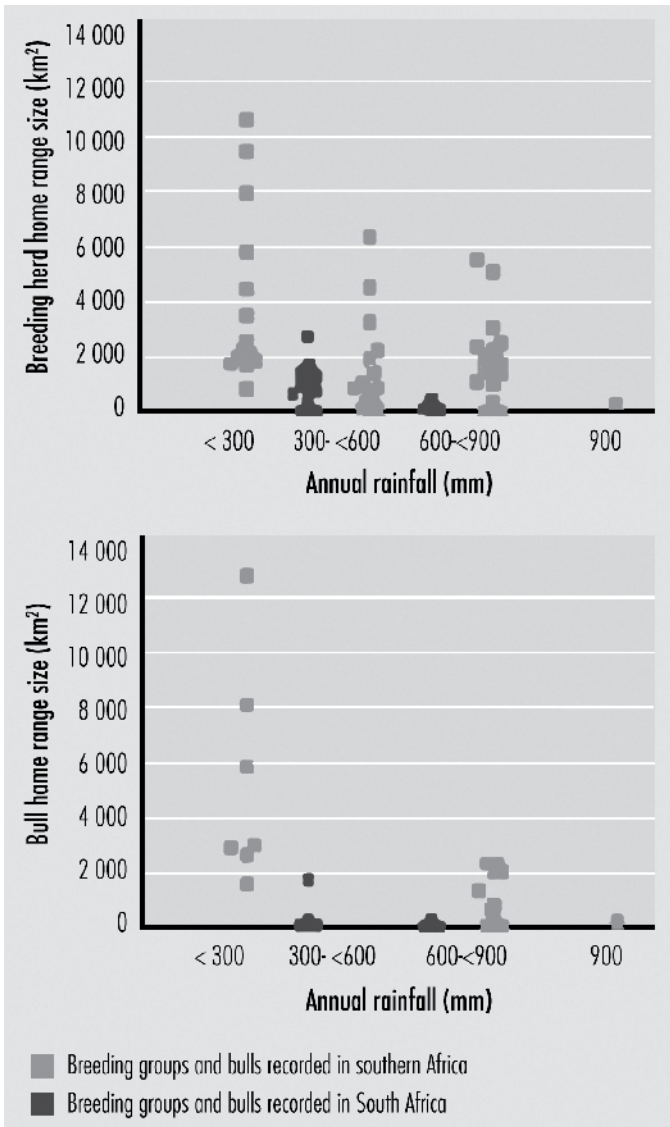


Figure 1: The home range sizes of elephant bulls and breeding herds in South Africa (dark symbols) compared to those recorded elsewhere in southern Africa (light symbols), within different annual rainfall classes. We recognise that this comparison may be confounded by factors such as season. Even so, for both bulls and cows in South Africa, home range sizes appear to be smaller and to vary less in area than those of elephants elsewhere in the region. This leads to concerns about management practices in South Africa, such as fencing, that restrict elephant range use, with consequences for the intensity at which they will use the landscape (figure adapted from Guldemond, 2006)

This raises three principal concerns regarding the home ranges of elephants in South Africa. First, home ranges here are relatively small compared to those of elephants throughout the rest of the region. Second, given the relatively small sizes of most protected areas in South Africa, the home ranges of individual elephants here may cover a greater proportion of these protected areas than elsewhere. Third, unlike some other areas, there may be little spatial segregation in land use between the dry and wet seasons (see Western & Lindsay, 1984; Verlinden & Gavor, 1988).

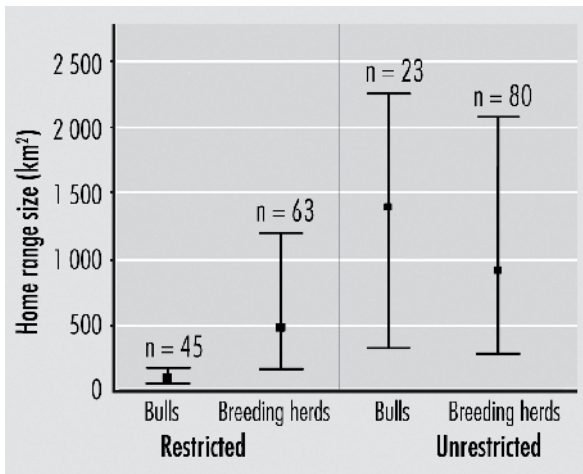


Figure 2: The home range sizes (range [min, max] with mean) across southern Africa of elephant bulls and breeding herds whose movements are restricted by fencing, compared to those whose movements are unrestricted. The comparison is limited to areas within the annual rainfall ranges similar to that in South African study sites (376–748 mm per year). All elephants in South Africa occur in areas where fences restrict movements, while those in the rest of the region do not. Thus, grouping elephants into areas where their movements are compromised by fencing, also groups them into South African and non-South African populations and underlies a fundamental reason for the small ranges characteristic of elephants in South Africa (figure adapted from Guldmond, 2006)

Together, these factors suggest that elephants in South Africa make more intensive use of the land available to them than elsewhere. In turn, the impact they have on vegetation is likely to be more severe, giving vegetation little chance to recover from elephant damage (see Van Aarde *et al.*, 2006). A decrease in home range area induced by fencing thus will enhance the impact that elephants can have on the landscapes where they live.

Our present understanding of the distribution and spatial use patterns of elephants in South Africa are incomplete. However, technological improvements have enhanced our ability to track the movements of elephants over vast areas and for extended periods, thus expanding our capacity to address important research questions. Such research, especially when conducted as parts of an adaptive management strategy that manipulates landscape variables such as the distribution of water and fences, should allow us to assess why spatial use patterns of elephants in South Africa differ from patterns throughout the rest of southern Africa. This could also address the impact elephant spatial use may have on the landscape, vegetation, and other species. However, preventing elephants from moving outside small fenced reserves precludes the application of management options that restore their large-scale spatial use patterns, as suggested by Van Aarde *et al.* (2006) and Van Aarde & Jackson (2007).

POPULATION BIOLOGY

Understanding elephant population biology can empower conservation managers to predict the response of populations to various management actions. As part of population biology, studies of the dynamics of populations focus on factors that change their attributes over time and explain how such changes determine population numbers. These population attributes include the size, density (numbers per square kilometre or per square mile), distribution, birth rates, death rates, and dispersal rates of a collection of individuals that share space. For research purposes, a population must comprise enough individuals from which to collect data to estimate these vital rates and provide for statistical limitations of analytical procedures (Akçakaya, 2002). Populations that comprise only a few breeding herds and bulls therefore do not lend themselves to estimates of vital rates. This certainly holds for most of the newly established populations confined to relatively small areas in South Africa. The factors that influence births, deaths, immigration, and emigration determine population size and change in numbers over time (population growth). In this section we compare the attributes of elephant populations and discuss the factors that may limit population sizes. We also compare the dynamics of South Africa's elephant populations to populations elsewhere in Africa.

Box 3: Assigning ages to elephants

Monitoring population changes is important for implementing appropriate management actions and evaluating their effectiveness (Gibbs, 2000). Authorities could use demographic parameters, such as age at first calving, calving interval, and survival rates to predict population changes over time. They seldom do so. One reason is that estimates of these population parameters require accurate determination of the ages of individuals within a population.

Methods to determine the chronological ages of elephants include measuring molar tooth wear and progression (e.g. Laws, 1966; Sikes, 1966; Fatti *et al.*, 1980; Jachmann, 1988), elephant tusk dimensions (Hanks, 1972; Sukumar *et al.*, 1988), back lengths (Croze, 1972), shoulder heights (e.g. Laws, 1966; Douglas-Hamilton, 1972; Jachmann, 1988; Lee & Moss, 1995; Shrader *et al.*, 2006a), hind foot lengths (Western *et al.*, 1983; Lee & Moss, 1995), and dung boli diameters (e.g. Reilly, 2002; Morrison *et al.*, 2005). All these methods rely on the relationship between a particular morphological feature and age to determine the age of an individual elephant. Only three body size measures have formally been related to known age. Lee & Moss (1995) provided a relationship between footprint diameters and known age while Morrison *et al.* (2005) did that for dung boli in Amboseli National Park. Shrader *et al.* (2006a) showed that the Addo Elephant National Park and Amboseli elephants had the same relationship between shoulder height and known age elephants. These relationships are the best available to assign ages for cows up to age 15 and for bulls up to age 25.

Several factors may impede the success of age determination techniques. Dense vegetation may hamper direct measurements of free-ranging elephants, and many earlier measurements could only be taken from captive or immobilised animals (Lee & Moss, 1995). Measuring tusk dimensions requires close access to elephants (Hanks, 1972). Studies examining the rates of tooth eruption have yet to be carried out on living, free-ranging elephants, though studies of the lower and upper jaw tooth rows of shot elephants in Uganda (Laws, 1966; Laws *et al.*, 1975) saw the development of age determination techniques based on eruption and wear patterns. Measurements of footprints are subject to terrain, substrate, incline and other environmental factors (Western *et al.*, 1983; Reilly, 2002; Morrison *et al.*, 2005). Measuring the back length or shoulder height of elephants in the field is only practical where

visibility is good and animals can be photographed (Morrison *et al.*, 2005). Furthermore, this technique requires expensive equipment such as digital range finders and cameras, may be time-consuming, and may be prone to measurement error (Jachmann, 1980; Morrison *et al.*, 2005; Shrader *et al.*, 2006a). However, digital photogrammetry, a recently developed method to measure shoulder heights of elephants (Shrader *et al.*, 2006b), requires less time and produces more accurate and precise results than other measuring techniques.

Births

The number of calves that an average cow will have in her lifetime is determined by the ages at which cows have their first and last calves, and the years that elapse between births. The number of calves produced by each cow influences the rate at which a population grows. Generally populations will grow faster when cows have their first calves when relatively young, when the time that elapses between births (calving intervals) is short, and when they continue to breed to old age. The age at first calving, calving interval, and age at last calving, are therefore key traits of a population. Quantifying these traits and understanding how they vary across space, time, between elephants of different ages, and between populations, enables us to decipher the dynamics of a population.

Scientists use different methods to estimate age at first calving. Some of them study elephants over a long time to follow individual life histories (e.g. Whitehouse & Hall-Martin, 2000; Moss, 2001; Wittemyer *et al.*, 2005b; Gough & Kerley, 2006); others observe family units and identify cow-calf associations (e.g. Jachmann, 1980; Jachmann, 1986); others examine breast development in cows (e.g. McKnight, 2000), or note the reproductive activity of killed cows by assessing whether a cow is pregnant and counting how many placental scars (i.e. pigmented scars on the uterus that represent the number of times a cow has been pregnant) she carries (e.g. Hanks, 1971; Lewis, 1984; Lindeque 1991; Whyte 2001). All these methods rely on assigning ages accurately to individual elephants (see box 3).

Long-term observations and cow-calf associations return the age at which a cow had her first calf, while the other methods give the age at which she conceived or is likely to conceive. Age at first conception can be converted to age at first calving by adding 22 months, the gestation period in

elephants (Hodges *et al.*, 1994). Estimates of the length of calving intervals can be influenced by the deaths of calves, incorrect assignment of the ages of elephants, and allomothering – when cows look after calves that are not their offspring (Lee, 1987). Comparisons are limited when considering that different techniques were used to estimate age (see box 3) and age at first calving.

Published estimates (table 1) show a wide range of ages at which cows have their first calf. For instance, in Addo some cows can conceive when seven years old, thus giving birth at nine (Gough & Kerley, 2006). The mean ages of first calving tend to be lower for South African populations compared to elsewhere in Africa (figure 3A). Cows in South Africa tend to have their first calves at an average age of 11.3 years (median = 11.9, $SD = 1.8$, $n = 8$ estimates). Those elsewhere have their first calves at an age of 14.1 years (median = 13.5, $SD = 3.0$, $n = 16$ estimates). In addition, the range and confidence limits of estimates of age at first calving tend to be wider for populations elsewhere compared to populations in South Africa (figure 3B). This suggests that most cows in South African parks may have their first calf at younger ages than those living elsewhere. Thus, if all the other traits are the same, populations in South Africa will increase faster than elsewhere.

Why would cows in South Africa mature earlier than elsewhere? We know that, for mammals, resource quality affects the age at sexual maturity and therefore the age when they may have their first calves (e.g. Owen-Smith, 1990). This suggests that elephants in South African parks have better resources available than elephants living elsewhere. This could be due to dams and waterholes that are constructed in these parks enabling access to additional resources by allowing elephants the opportunity to forage in otherwise inaccessible areas. Elephants living here may therefore not be constrained by resources and this could be one of the reasons why elephant cows in South African populations may have their first calves at a relatively young age.

Elephant cows across Africa give birth at intervals of 1.8–13.5 years (table 1). The calving intervals of 10.3, 11.0, 11.5, and 13.5 years for elephants in the Tsavo National Park, Kenya (McKnight, 2000), the Amboseli National Park, Kenya (Moss, 2001), the Murchison Falls National Park, Uganda (Buss & Smith, 1966), and the Budongo Forest Reserve, Uganda (Laws *et al.*, 1975), respectively, are exceptionally long when compared to values from elsewhere. Additionally, the 1.8 years noted for an elephant in Amboseli (Moss, 2001) is exceptionally short (table 1). The 22-month gestation period combined with apparent infertility induced by suckling places a lower limit on the length of the calving interval (Hodges *et al.*, 1994). Thus, the extremely short calving interval noted in Amboseli may be due to the early death of the previous calf. However, infertility

during suckling has not been confirmed in free-ranging elephants, but indirectly inferred from observation in Amboseli where birth intervals of 3.2 years for cows whose calves died before 2 years of age is shorter than the median of 4.5 years (Moss, 2001). No single factor yet has been identified that can explain the variability in calving intervals in elephants, but Laws *et al.* (1975) suggest that calving intervals tend to increase with density. This observation needs further study but is supported by some South African data (CERU unpublished records).

Calving intervals for elephants varied considerably across Africa (table 1). Mean values for South African populations tend to be similar to the lower end of mean values recorded elsewhere in Africa (figure 3C). Elephants living in South African populations have calves on average every 3.6 years (median = 3.8, $SD = 0.7$, $n = 10$ estimates), while those elsewhere have calves every 4.2 years (median = 3.8, $SD = 1.8$, $n = 22$ estimates). The length of calving intervals tends to vary less in South African populations than elsewhere in Africa (figure 3D). This may be related to regional rainfall differences. Even so, the confidence intervals and ranges of values of calving intervals suggest that most cows in South Africa tend to have calves more often than those living elsewhere in Africa. The reasons for this are not known, but may be related to the relatively low calf mortalities noted in South Africa (see later), or by resources not being limited as a result of management interventions such as water provision, as we discussed earlier. Compared to age at first calving and calving interval, age at last calving is less well known. We found three estimates in the published literature: (1) 60 years in Kruger, based on ovarian activity noted for killed elephants aged using tooth eruption criteria (Smuts, 1975), (2) 48–55 years in Addo, based on individual life histories with guessed ages (Whitehouse & Hall-Martin, 2000), and (3) guesstimates of 52–56 years for elephants in Amboseli (Moss, 2001). This suggests fertility may begin to decrease in a cow's late forties. Too little information is available to compare elephants from different regions.

The onset and end of breeding are not abrupt in a population. Typically, the age at which cows have their first calf differs from population to population, but the age-specific birth rate remains relatively constant for adult cows within a population, and then declines around the age when elephants stop breeding (Whitehouse & Hall-Martin, 2000; Moss, 2001).

Various measures serve as indices of age-specific reproductive output, which usually is expressed as fecundity, defined as yearly production of female calves per cow of a given age group. In table 2 we present data for different populations on the percentages of cows that were pregnant and/or lactating among culled specimens of a specific age, or the percentage of cows that

gave birth. Values for Kruger and Etosha seem similar, but much higher than those for other populations, probably due to the different information being recorded by different workers. We have no comparable statistics on this aspect of reproductive output for different populations.

Locality	Method	Age at first calving (years)						Reference
		Mean	Median	SD	SE	95% CI	Range	
South African populations								
Addo	Individual histories	13.0	–	–	–	–	–	Woodd, 1999
	Individual histories	13.0	–	2.03	0.3	12.5–13.5	10–16	Whitehouse & Hall-Martin, 2000
	Individual histories	12.3	–	1.73	0.2	11.7–12.7	–	Gough & Kerley, 2006
	Cow-calf associations	13.8	–	–	0.8	12.1–15.4	–	Ferreira & Van Aarde, 2008
Kruger	Culled samples	–	–	–	–	–	11.0–17.0	Smuts, 1975
	Culled samples	–	–	–	–	–	9.0–14.0	Whyte, 2001
Mabula	Cow-calf associations	12.3	12.0	–	0.6	11.2–13.4	–	Mackey <i>et al.</i> , 2006
Phinda	Cow-calf associations	10.3	10	–	0.6	9.2–11.4	–	Mackey <i>et al.</i> , 2006
Pilanesberg	Cow-calf associations	9.2	9	–	0.2	8.8–9.6	–	Mackey <i>et al.</i> , 2006
Pongola	Cow-calf associations	8.4	8	–	0.5	7.3–9.5	–	Mackey <i>et al.</i> , 2006
Tembe	Cow-calf associations	11.5	–	–	0.5	10.4–12.5	–	Morley, 2005
Other populations								
Amboseli	Individual histories	13.7	14.1	–	–	–	8.9–21.6	Moss, 2001
	Cow-calf associations	13.6	–	–	0.5	12.5–14.6	–	Ferreira & Van Aarde, 2008
Bugongo	Placental scars	22.4	–	–	–	19.9–24.9	–	Laws <i>et al.</i> , 1975
Etosha	Placental scars	12.5	–	–	–	–	10.8–12.8	Lindeque, 1988
	Placental scars	13.7	–	–	–	–	12.8–13.8	Lindeque, 1988
	Puberty	13.8	–	–	1.2	11.5–16.2	–	Lindeque, 1988
	Puberty	12.6	–	–	1.5	9.7–15.6	–	Lindeque, 1988
	Culled samples	15.3	–	–	–	–	13.8–17.8	Lindeque, 1988
	Culled samples	13.3	–	–	–	–	9.8–17.8	Lindeque, 1988
Kasungu	Cow-calf associations	12.8	–	2.6	–	–	–	Jachmann, 1986
Kidepo	Cow-calf associations	–	–	–	–	–	8.8–13.8	Croze, 1972
Luangwa	Placental scars	15.8	–	–	–	–	13.0–19.0	Hanks, 1972

Locality	Method	Age at first calving (years)						Reference
		Mean	Median	SD	SE	95% CI	Range	
Maputo	Cow-calf associations	9.8	–	–	0.5	9.3–10.3	–	Morley, 2005
Mkomazi	Placental scars	12.2	–	–	–	11.3–13.1	–	Laws <i>et al.</i> , 1975
Mkomazi East	Placental scars	12.2	–	–	–	11.0–13.4	–	Laws <i>et al.</i> , 1975
Murchison North	Culled samples	–	–	–	–	–	8.8–12.8	Buss & Smith, 1966
	Placental scars	16.3	–	–	–	15.5–17.1	–	Laws <i>et al.</i> , 1975
Murchison South	Placental scars	17.8	–	–	–	16.9–18.6	–	Laws <i>et al.</i> , 1975
Tsavo	Cow-calf associations	–	–	–	–	–	12.8–16.8	McKnight, 2000
	Cow-calf associations	–	–	–	–	–	12.8–16.8	McKnight, 2000
	Placental scars	11.7	–	–	–	10.8–12.6	–	Laws <i>et al.</i> , 1975
Zambezi	Culled samples	–	–	–	–	–	15.8–16.8	Dunham, 1988
	Culled samples	–	–	–	–	–	12.8–14.8	Dunham, 1988

Table 1A: The ages at first calving for elephant populations across Africa. We present published statistics and the method that yielded estimates of these values. Counts of placental scars are for cows culled for either research or management purposes

Locality	Method	Calving interval (years)						Reference
		Mean	Median	SD	SE	95% CI	Range	
South African populations								
Addo	Individual histories	3.8	–	–	–	–	–	Woodd, 1999
	Individual histories	3.8	–	1.29	0.1	3.6–4.0	–	Whitehouse & Hall-Martin, 2000
	Individual histories	3.3	–	0.77	–	–	–	Gough & Kerley, 2006
	Cow-calf associations	4.0	–	–	0.3	3.3–4.6	–	Ferreira & Van Aarde, 2008
Kruger	Placental scars	4.5	–	–	–	4.0–5.0	–	Smuts, 1975
	Culled samples	3.7	–	–	–	–	–	Whyte, 2001
Mabula	Cow-calf associations	2.4	–	–	0.1	2.3–2.5	–	Mackey <i>et al.</i> , 2006
Phinda	Cow-calf associations	3.9	–	–	0.2	3.5–4.3	–	Mackey <i>et al.</i> , 2006
Pilanesberg	Cow-calf associations	3.3	–	–	0.1	3.1–3.5	–	Mackey <i>et al.</i> , 2006
Pongola	Cow-calf associations	3.1	–	–	0.2	2.7–3.5	–	Mackey <i>et al.</i> , 2006

Locality	Method	Calving interval (years)					Reference	
		Mean	Median	SD	SE	95% CI		
Tembe	Cow-calf associations	4.6	–	–	0.6	3.4–5.8	–	Morley, 2005
Other populations								
Amboseli	Individual histories	4.5	4.2	–	–	–	1.8–11.7	Moss, 2001
	Cow-calf associations	4.6	–	–	0.2	4.1–5.1	–	Ferreira & Van Aarde, 2008
Bugongo	Culled samples	7.7	–	–	–	5.4–13.5	–	Laws <i>et al.</i> , 1975
Etosha	Culled samples	3.8	–	–	–	–	–	Lindeque, 1988
	Placental scars	2.1	–	–	–	–	–	Lindeque, 1988
	Placental scars	2.5	–	–	–	–	–	Lindeque, 1988
Kasungu	Cow-calf associations	3.9	–	1.1	–	2.2–5.3	–	Jachmann, 1986
	Cow-calf associations	3.3	–	1.3	–	–	–	Jachmann, 1986
Kidepo	Culled samples	2.2	–	–	–	–	–	Croze, 1972
	Culled samples	3.2	–	–	–	–	–	Croze, 1972
Luangwa	Culled samples	3.0	–	–	–	–	–	Hanks, 1972
	Placental scars	4.0	–	–	–	–	–	Hanks, 1972
Maputo	Cow-calf associations	3.1	–	–	1.1	3.0–4.2	–	Morley, 2005
Mkomazi	Culled samples	2.9	–	–	–	2.6–3.4	–	Laws <i>et al.</i> , 1975
Mkomazi East	Culled samples	4.2	–	–	–	3.1–5.0	–	Laws <i>et al.</i> , 1975
Murchison North	Culled samples	–	–	–	–	–	2.6–5.8	Buss & Smith, 1966
	Culled samples	9.1	–	–	–	7.5–11.5	–	Laws <i>et al.</i> , 1975
Murchison South	Culled samples	5.6	–	–	–	4.8–6.8	–	Laws <i>et al.</i> , 1975
Tsavo	Cow-calf associations	4.6	–	–	–	–	–	McKnight, 2000
	Cow-calf associations	5.0	–	1.8	0.9	3.2–6.8	–	McKnight, 2000
	Culled samples	6.8	–	–	–	5.1–10.3	–	Laws <i>et al.</i> , 1975
Zambezi	Culled samples	2.8	–	–	–	–	–	Dunham, 1988
	Culled samples	3.4	–	–	–	–	–	Dunham, 1988
	Placental scars	3.8	–	–	0.4	3.0–4.6	–	Dunham, 1988

Table 1B: Lengths of calving intervals (B) for elephant populations across Africa. We present published statistics and the method that yielded estimates of these values. Counts of placental scars are for cows culled for either research or management purposes

When combining reproductive output with the survival likelihood of a cow of a specific age (see table 3), a reproductive value can be assigned to each age group. This so-called reproductive value gives the relative contribution that each age group makes to the increase in population size. Our analyses suggest that the overall pattern is the same for all populations for which we have information (figure 4). Furthermore, in all these populations, elephants that are 15–25 years old contribute most to future growth of populations.

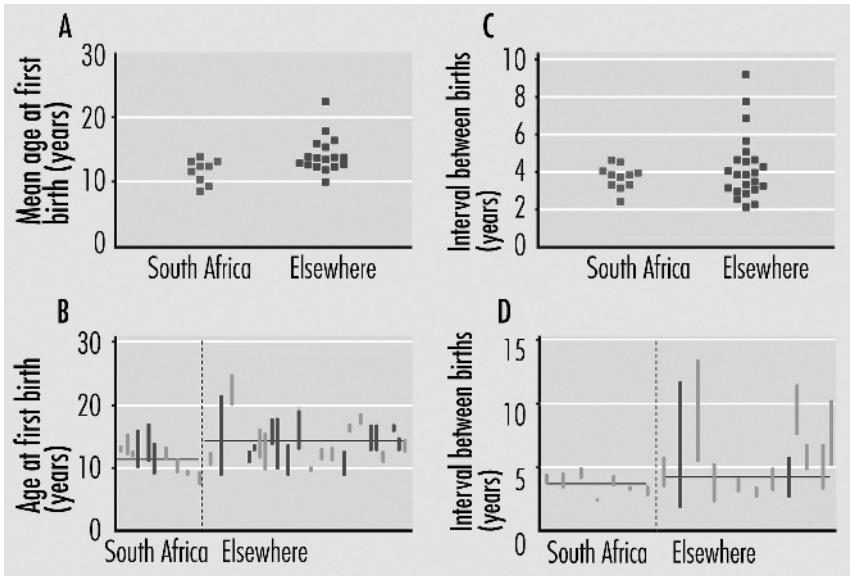


Figure 3: A comparison of reproductive variables of elephant populations living in South Africa with those for elephants living elsewhere in Africa. A) The mean age at first calving recorded for each population. B) The lower and upper confidence limits (lighter lines) or range between minimum and maximum values (darker lines) of age at first calving for each population, depending on published information. The horizontal black lines are the mean values calculated from estimates. South African elephant populations (those at the left of the dotted line) tend to give birth when younger than elephants elsewhere in Africa. C) The mean calving interval for each population. D) The lower and upper confidence limits (lighter lines) or range between minimum and maximum values (darker lines) of birth intervals recorded for each population. The horizontal black lines are the mean values calculated from estimates available for populations. The ranges for South African elephant populations tend to be at the lower end of those elsewhere and suggest that cows living in South Africa have calves more often than cows elsewhere in Africa

Deaths

Under natural conditions elephant populations typically have relatively low yearly death rates. These are usually expressed as high survival rates (Laws, 1969; Hanks, 1979; Whitehouse & Hall-Martin, 2000; Dudley *et al.*, 2001; Moss, 2001; Whyte, 2001; Wittemyer *et al.*, 2005b; Gough & Kerley, 2006). Age- and sex-specific survival values have been published for several populations (table 3). These are often calculated from age distributions of culled samples, but long-term studies of individuals of known age provide the most reliable information (e.g. Whitehouse & Hall-Martin, 2000; Moss, 2001). More recently Ferreira & Van Aarde (2008) developed survey and calculation protocols that are not invasive and that yield estimates comparable to those from long-term studies.

Age (yrs)	South Africa		Populations elsewhere in Africa		
	Kruger Pregnant or lactating	Amboseli Giving birth	Etosha Pregnant or lactating	Luangwa Pregnant	Murchison Lactating
0–4	0	0	0	0	0
5–9	5.5	0	3.6	0	2.0
10–14	52.0	14.0	32.2	5.2	3.0
15–19	91.0	21.0	76.7	56.6	20.0
20–24	80.5	23.0	94.1	50.6	50.0
25–29	93.0	23.0	98.8	50.6	65.0
20–34	86.5	23.0	89.6	50.0	66.0
35–39	93.7	23.0	93.3	50.0	76.0
40–44	92.9	20.0	100.0	42.1	60.0
45–49	94.7	18.0	93.3	42.1	57.0
50–54	89.3	14.0	86.7	33.3	37.0
55–59	85.7	10.0	56.7	33.3	0
60–64	–	0	–	–	–
Reference	Smuts, 1975	Moss, 2001	Lindeque, 1988	Hanks, 1979	Laws <i>et al.</i> , 1975

Table 2: Age-specific reproductive rates (given as percentages) as indices of age-specific fecundity for selected elephant populations across southern Africa

Lee & Moss (1995) suggest that in Amboseli many elephants die during the first two years of life, fewer during the next one to two years, and more after they are weaned when about four years old. This is supported by studies on elephants in Addo where survival rates for young elephants tend to be lower than for adults,

particularly for juveniles in the first few years of life (Whitehouse & Hall-Martin, 2000; Moss, 2001).

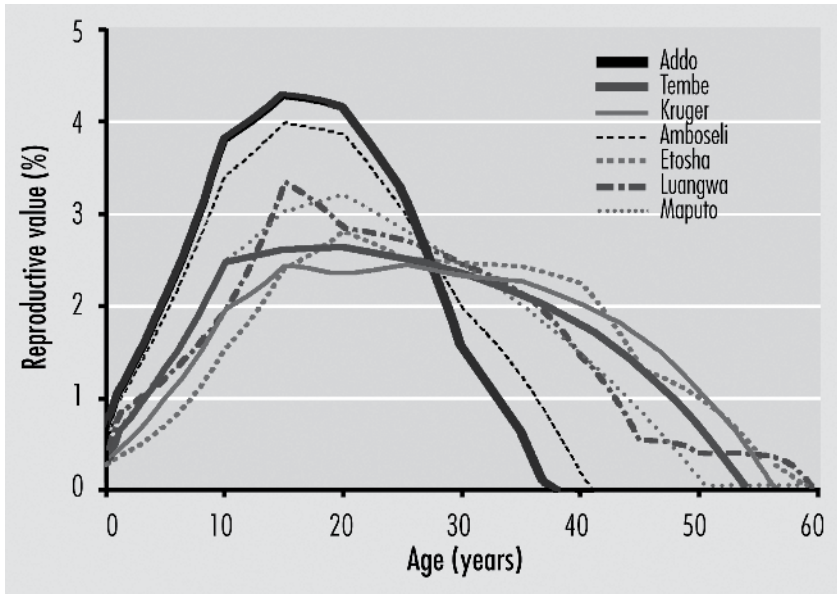


Figure 4: Reproductive values (the percentage contribution of different age groups to future population growth) as a function of age for South African (solid lines) and other (broken lines) populations. We extracted data from the literature and standardised the value for each age class as a fraction of the maximum value across all age classes for each population. We then used survival estimates (table 3) to calculate survival likelihoods (the probability at birth that an individual will survive to a specific age). Combining fecundity and survival likelihood with an independent estimate of population growth yielded the reproductive values following the equations of Case (2000)

Survival rates are relatively high across all ages (table 3). Here a comparison of values we have for South African populations with those for populations elsewhere in Africa yields valuable insights. For instance, for the first age class we note that the lowest survival value for South African populations (0.90) is higher than the lowest value of 0.59 noted for elephants elsewhere in Africa. Survival rates for elephants in older age classes are slightly less variable for South African populations than for populations elsewhere. Some may deem these comparisons invalid because different methods were employed to obtain data for the different populations. Nonetheless, our Assessment suggests that survival is relatively high in South African populations, compared to some

populations elsewhere in Africa. If so, and if other population traits remain constant or higher, as has been shown earlier in this chapter, then population sizes should also increase faster here than elsewhere in Africa.

		Age (years)						
		Population	0	1–9	10–19	20–29	30–44	45–60
South African populations	Addo ¹	0.94	0.99	0.99	0.99	0.99	0.98	0.00
	Kruger ²	0.97	0.97	0.97	0.97	0.97	0.97	–
	Tembe ³	0.90	0.99	0.99	0.99	0.99	0.99	–
	Amboseli ⁴	0.94	0.99	0.98	0.99	0.97	0.95	–
Populations elsewhere in Africa	Buganga ⁵	0.97	0.97	0.97	0.97	0.97	0.97	–
	Etosha ⁶	0.84	0.87	0.9	0.93	0.92	0.88	0.84
	Kasungu ⁷	0.94	0.96	0.96	0.94	0.91	0.86	0.67
	Luangwa ⁸	0.59	0.92	0.89	0.87	0.86	0.50	0.00
	Maputo ³	0.82	0.94	0.95	0.97	0.97	0.97	–
	Mkomazi ⁵	0.95	0.95	0.95	0.95	0.95	0.95	–
	Murchison ⁵	0.97	0.97	0.97	0.97	0.97	0.97	–
	Sambura ⁹	0.98	0.99	0.98	0.98	0.97	0.97	–
	Tsavo ⁵	0.95	0.95	0.95	0.95	0.95	0.95	–

¹ Calculated from individual histories. Extracted from Whitehouse & Hall-Martin (2000)

² Calculated from the difference between observed and expected population growth rates. Extracted from Whyte (2001)

³ Calculated from age distributions and fecundity estimates. Extracted from Morley & van Aarde (2006)

⁴ Calculated from individual histories. Extracted from Moss (2001)

⁵ Calculated from age distributions assuming that exponential growth is zero. Extracted from Laws *et al.* (1975)

⁶ Calculated from age distributions assuming that exponential growth is 0.1. Extracted from Lindeque (1988)

⁷ Calculated from age distributions assuming that exponential growth is zero. Extracted from Jachmann (1980, 1984)

⁸ Calculated from age distributions assuming that exponential growth is zero. Extracted from Hanks (1979)

⁹ Calculated from individual histories. Extracted from Wittemyer *et al.* (2005b)

Table 3: Annual survival rates for elephants in different age classes and populations. To compare estimates we grouped estimates into age classes and calculated mean annual survival rates for each group from the published information. Some studies assumed constant survival across all ages

Ivory poaching (e.g. Gillson & Lindsay, 2003; Stiles, 2004; Reeve, 2006; Wasser *et al.*, 2007) and formal culling programmes (e.g. Lindeque, 1991; Cumming *et al.*, 1997; Butler, 1998; Van Aarde *et al.*, 1999) will lower individual survival. At the population level the influence of poaching on age-specific survival rates may be more profound when poachers target older individuals

(see Milner-Gulland & Mace, 1991; Ferreira *et al.*, 2008). Alternatively, providing water (e.g. Gaylard *et al.*, 2003) may lower death rates, even during droughts (Walker *et al.*, 1987). Culling of entire breeding herds plus their associated males, such as was the practice in Kruger (Whyte, 2001), may have had no or little influence on the age distribution and hence on estimates of age-specific survival rates for the population.

Droughts (e.g. Corfield, 1973; Walker *et al.*, 1987; Dudley *et al.*, 2001), disease (Berry, 1993; Lindeque, 1988; Turnbull *et al.*, 1991), and predation also affect survival. Lions target unweaned calves in the Hwange National Park, Zimbabwe (Loveridge *et al.*, 2006), and 4- to 15-year-old elephants in the Savuti Region of Botswana (Joubert, 2006). However, in most cases the incidence of predation seems low and may be relatively unimportant for survival rates at the population level.

Elephants seem sensitive to droughts, and several authors reported die-offs during dry spells (Corfield, 1973; Walker *et al.*, 1987; Dudley *et al.*, 2001). When considering that 4–6 dry spells may occur in a 50-year period (e.g. Ogotu & Owen-Smith, 2003), most elephants would be exposed to drought as a mortality agent to which they may be most sensitive when relatively young. Considering the apparent importance of rainfall for survival, the projected climate change across southern Africa, which may result in more frequent and severe droughts across much of the distributional range of elephants (IPCC, 2007) could increase elephant mortality in the coming century.

Immigration and emigration

Immigration (movement into an area) and emigration (movement out of an area) affect population growth and population size. We know that elephants do immigrate to colonise new areas or re-colonise areas they previously occupied. For instance, elephants from Mozambique colonised all of the area of Kruger within 50 years (Whyte *et al.*, 2003), at rates of 7–10 kilometres per year (Whyte, 2001). Elephants also re-colonised the Serengeti National Park in Tanzania after an absence of 40 years (Lamprey *et al.*, 1967). In some cases human actions can spur elephant movements. The provision of water certainly enabled elephants to colonise and permanently occupy areas that were relatively inhospitable, especially during the dry seasons, such as Hwange in Zimbabwe (Chamaillé-Jammes *et al.*, 2007), the Etosha National Park in Namibia (Lindeque & Lindeque, 1991) and the Khaudum Game Reserve in northern Namibia. In the case of Khaudum, civil unrest in southern Angola may have accelerated immigration (see Van Aarde & Jackson, 2007).

Based on count data, elephants apparently immigrated and emigrated in response to management in Kruger and moved into areas where densities were reduced through culling (Van Aarde *et al.*, 1999). When western park fences were removed, emigration from Kruger also gave rise to the rapid increase in elephant numbers on adjacent private land where elephant numbers were previously low (Whyte, 2001; D. Varty, Conservation Corporation, pers. comm.). Furthermore, recent movements across Kruger's eastern boundary into the Limpopo National Park in Mozambique seem to co-occur with a recent decline in elephant numbers in Kruger (H. Magome, SANParks, pers. comm.).

Published information on immigration and emigration rates for elephants is scarce, probably due to the difficulty and costs of monitoring the movements of many elephants for extended periods over vast areas. Study of the breeding herd of elephants that was observed to have colonised the Amboseli ecosystem by gradually shifting its annual home range (Moss, 1988) suggests that dispersal, immigration, and emigration events are relatively rare and hard to detect using conventional survey techniques. Genetic approaches (e.g. Spong & Creel, 2001) may facilitate the study of elephant immigration and emigration. It is likely that density, environmental factors, and physical barriers, both man-made and natural, may affect these rates. This may enhance population growth locally. For instance, preventing movements out of an area through fencing may be followed by population increase despite the limitation of resources. This happened in Kruger where elephant numbers increased at 10.4 per cent per annum prior to its complete fencing in 1976. During the period when Kruger was completely fenced, elephant numbers increased at 6.6 per cent, while numbers increased at only 1.5 per cent per year after some of the fences were removed along the western boundary in 1994 (Whyte, 2001). This may be due to elephants emigrating out of Kruger and to the surrounding areas.

Water provisioning may also influence emigration. For instance, the placing of 10–15 waterholes in Khaudum in Namibia led to the elephant population increasing from 80 in 1976 to 3 400 in 2004 (Van Aarde & Jackson, 2007). For many elephant populations in South Africa, fences that isolate conservation areas from the surrounding landscapes block dispersal, immigration and emigration. This hampers limitation of population growth through dispersal, a scenario very different to that experienced by several populations elsewhere in southern Africa. These aspects need further investigation because immigration and emigration can clearly influence population growth.

Recent literature (e.g. Bulte *et al.*, 2004; Van Aarde *et al.*, 2006; Van Aarde & Jackson, 2007) considers the stimulation and maintenance of dispersal movements of special importance to the maintenance of metapopulation

dynamics and the mitigation of impact. Such movements certainly occur, even within conservation areas (Van Aarde *et al.*, 1999). For instance, our recent analysis of landscape-specific yearly counts in Kruger suggests that population growth rates on different landscapes ranged between -20 per cent and 30 per cent annually (CERU, unpublished data). Compared to the mean annual growth rate of 4.0 per cent between 1998 and 2004 for the entire park (Young *et al.*, 2008), such extremes can be ascribed only to large-scale movements within the park. The forces responsible for these apparent large-scale movements need further investigation and are probably associated with changes in habitat conditions in response to heterogeneity in yearly rainfall across the Park.

Numbers and densities

It is difficult to count elephants. Total counts of elephants are usually based on direct censuses of all individuals that live in a study area, but usually include errors, which can be quite large, due to missed or double-counted individuals. Sample counts use statistical sampling techniques such as ground- or aerial-based line-transect surveys to get an estimate of the number of elephants in sub-areas, which are then extrapolated to the whole area (Norton-Griffiths, 1978). The sample methods and intensity of surveys affect the precision of estimates, which are statistically expressed as confidence limits of estimates. This has major implications for the validity of year-to-year comparisons of estimates to deduce trends in population growth. As a statistic, the confidence limits reflect on the precision of a population estimate - when confidence limits are high, estimates are imprecise.

When consulting the 2007 report on the status of African elephants (Blanc *et al.*, 2007) one notes 384 counts and estimates; 19 per cent of these are total counts, 34 per cent are estimates based on sample counts, and 41 per cent are estimates based on guesses. What is more, the 75 confidence limits for estimates calculated from aerial sample counts in this report (Blanc *et al.*, 2007) ranged from 10 to 376 per cent of the value of the estimate (median = 65.3 per cent). These high levels of imprecision clearly limit the value of such estimates for management and assessment of population growth rates. Wide confidence limits also may hamper the analysis of elephant population trends in South Africa where registration counts (e.g. Gough & Kerley, 2006), recapture modelling (e.g. Morley & van Aarde, 2006), and total counts (e.g. Garaï *et al.*, 2004; Whyte, 2001) may yield wide confidence limits or lack indications of the precision of estimates of the sizes of populations.

Population name	Area size (km ²)	Elephant numbers	Elephant density (number per km ²)	Year of estimate	Exponential growth rate (%±SE)	Time period (number of estimates)
Addo Elephant Park	1 250	459	2.90*	2005	1.7±0.2	1931–2005 (n=70)
Andover Game Reserve	71	11	0.15	1994	–	–
Atherstone Nature Reserve	136	60	0.44	2005	12.5±2.2	1994–2005 (n=4)
Balule Nature Reserve	400	457	1.14	2006	–	–
Borakalalo National Park	120	2	0.02	1994	–	–
Great Fish River Reserve Complex	440	2	0.01	2005	–	–
Greater Kudu Land Safaris	120	6	0.05	1995	–	–
Greater St. Lucia Wetland Park	539	45	0.08	2005	3.4±4.7	2002–2005 (n=3)
Hluhluwe-Umfolozi Game Reserve	965	346	0.36	2004	19.8±3.4	1981–2001 (n=12)
Ithala Game Reserve	297	84	0.28	2005	7.5±1.6	1990–2005 (n=5)
Kaia Ingwe	45	5	0.11	1994	–	–
Kapama Game Farm	246	36	0.15	2005	–	–
Kariega Private Game Reserve	190	11	0.06	2005	–	–
Karkloof Falls Safari Park	14	2	0.14	1990	–	–
Klaserie Private Game Reserve	628	569	0.91	2006	5.6±1.2	1978–2006 (n=10)
Kruger National Park**	19 624	12 427	0.63	2006	1.1±0.3	1964–2006 (n=38)
					4.1±0.6	1996–2006 (n=11) [#]
Kwalata Game Ranch	90	22	0.24	1994	–	–
Kwandwe Private Game Reserve	160	27	0.17	2005	–	–
Lalibela Private Game Reserve	75	11	0.15	2005	–	–
Lowhills Game Reserve	30	8	0.27	1994	–	–
Mabula Game Lodge	120	9	0.08	2004	–4.2±2.6	1989–2004 (n=4)
Madikwe Nature Reserve	700	455	0.65	2005	5.6±0.9	1995–2005 (n=4)
Mahlatini Game Reserve	15	5	0.33	1994	–	–
Makalali Private Game Reserve	140	72	0.51	2005	16.0±5.0	1994–2005 (n=4)
Makuya National Park	165	54	0.33	2006	3.3±8.1	1990–2006 (n=4)
Manyeleti Game Reserve	228	71	0.31	2006	–0.6±7.4	1990–2006 (n=3)
Marakele National Park	380	110	0.29	2005	11.5±0.6	1996–2005 (n=4)
Mkuzi Falls Safaris	22	3	0.14	1994	–	–
Mkuzi Game Reserve	380	37	0.1	2005	9.3±3.1	1994–2005 (n=4)
Mokolo River Nature Reserve	45	6	0.13	994	–	–
Mpongo Park	25	8	0.32	1990	–	–
Mthethomusha Game Reserve	80	30	0.38	2005	7.8±3.6	1990–2005 (n=3)
Mtibi Game Farm	25	6	0.24	1994	–	–
Ndzalama Game Reserve	79	8	0.1	1994	–	–
Pamula Game Lodge	21	5	0.24	1994	–	–
Paradise Game Farm	30	6	0.2	1994	–	–
Phalaborwa Mining Company	41	77	1.88	2006	8.0±6.5	1990–2006 (n=6)
Phinda Resource Reserve	150	78	0.52	2004	7.3±3.1	1990–2004 (n=4)

Population name	Area size (km ²)	Elephant numbers	Elephant density (number per km ²)	Year of estimate	Exponential growth rate (%±SE)	Time period (number of estimates)
Pilanesberg National Park	553	140	0.25	2005	11.5±1.3	1980–2005 (<i>n</i> =9)
Pongola Game Reserve	119	55	0.46	2005	10.3±5.1	1997–2005 (<i>n</i> =4)
Pongolapoort Game Reserve	80	48	0.6	2005	12.3±2.4	1997–2005 (<i>n</i> =5)
Pumulunga Game Reserve	27	3	0.11	1994	–	–
Rhinoland Safaris	70	5	0.07	1994	–	–
Rietboklaagte Game Farm	25	3	0.12	1990	–	–
Riverside Lodge	40	6	0.15	1995	–	–
Sabi Sand Game Reserve	572	857	1.5	2006	19.7±3.8	1990–2006 (<i>n</i> =6)
Selati Game Reserve	300	85	0.28	2005	–	–
Shamwari Game Reserve	150	61	0.41	2005	3.7±5.0	1994–2005 (<i>n</i> =4)
Songimvelo Game Reserve	490	60	0.12	2005	10.5±3.0	1992–2002 (<i>n</i> =4)
Sutton Game Ranch	20	4	0.2	1994	–	–
Tembe Elephant Park	300	167	0.56	2005	6.0±0.8	1974–2005 (<i>n</i> =18)
Thaba Tholo	250	17	0.07	1994	–	–
Thornybush Game Lodge	80	18	0.23	1995	–	–
Thukela Biosphere Reserve	240	9	0.04	1994	–	–
Timbavati Game Reserve	494	712	1.44	2006	12.7±1.4	1985–2006 (<i>n</i> =10)
Touchstone Game Farm	75	10	0.13	1994	–	–
Tshukudu Game Lodge	45	2	0.04	1994	–	–
Umbabat Game Reserve	144	163	1.13	2006	6.1±8.1	1994–2006 (<i>n</i> =5)
Venetia Limpopo Nature Reserve	91	61	0.67	2005	25.5±3.9	1990–2005 (<i>n</i> =6)
Vosdal Game Farm	64	3	0.05	1994	–	–
Welcome Game Reserve	21	5	0.24	1990	–	–
Welgevonden Private Game Reserve	330	100	0.3	2005	3.8±1.9	1995–2005 (<i>n</i> =4)
Zulu Nyala Safaris	7	4	0.57	1994	–	–

* Addo's population is in three separate areas each 120 km² in size. The majority of the elephants (348) lived in one of these in 2005. We present density calculated for this area.

** Estimates for Kruger do not include adjacent areas.

Estimated growth for Kruger represents the period after culling stopped.

Table 4: (previous page) A summary of the numerical status of elephant populations in South Africa. Here we provide the property sizes, population sizes, and densities for the year in which the most recent estimate was reported (data extracted from the CERU database). We also estimated exponential growth rate where the data were suitable for calculation. We used densities because in several cases areas surveyed varied from year to year for a particular locality. Exponential growth was the slope of the natural logarithm of density regressed against time ($N_t = N_0 e^{rt}$) (Caughley, 1977). We provide the time period on which the calculation of growth was based as well as the number of population estimates available in a time series for the calculation

Elephants in South Africa make up only 3.8 per cent of Africa's elephants (17 847 in South Africa and 472 269 across the continent as a whole, based on definite estimates as classified by Blanc *et al.*, 2007). Population sizes in South Africa vary considerably, with the largest in Kruger, which had 12 427 elephants in 2006 (table 4). Kruger is also the largest area in South Africa that holds elephants. Of the remaining 62 places that hold elephants, only Addo is larger than 1 000 km², of which only 360 km² is available to elephants.

Comparison of South African population sizes with those elsewhere is troublesome because the areas surveyed at a site often vary from year to year. In such cases, it is useful to calculate density to compare one locality to another or one year to another. However, this standardisation is challenging.

The ecological meaning of density may vary considerably depending on how it is calculated (Gaston *et al.*, 1999), e.g. annual ecological density = numbers per area of each vegetation type per 365 days; seasonal ecological density = numbers per area of each vegetation type per season; decadal limiting density = maximum numbers per area of each vegetation type in limiting year. Interpretation of densities may be most appropriate when measured at times when the population is limited by resources, e.g. for the dry season, when density effects may be strongest because resources then are scarce.

Based on the recent African Elephant Status Report (Blanc *et al.*, 2007) dry season elephant densities vary considerably across Africa (figure 5), probably in response to local resource availability determined by biome and rainfall; management actions such as fencing, water provisioning, and culling; natural predation; and hunting or poaching. The reality is that elephant densities, and hence numbers, vary greatly in both space and time. Densities deduced from Blanc *et al.* (2007) for South Africa ranged from 0.04 to 2.90 n.km⁻² (table 4). In addition, South Africa tends to have relatively more populations with high densities than elsewhere in Africa (figure 5). This outcome may be explained by the patterns we have noted above for birth and survival rates – in South Africa, cows have their first calf at younger ages, have subsequent calves more often, but have similar survival rates. These factors and the limitations placed on dispersal by fences could lead to higher population growth rates (see later) and result in higher densities.

Population growth

Population growth is usually expressed as a percentage value per annum. It reflects on the contribution that the individual makes to changes in population numbers. It is a summary statistic that can be compared between populations

in research on factors that limit population size. Growth rates will vary from year to year because of year-to-year variations in environmental conditions that limit population processes. In spite of this and for ease of interpretation, population ecologists often calculate growth rate from population estimates and assume that rates remain relatively constant from year to year.

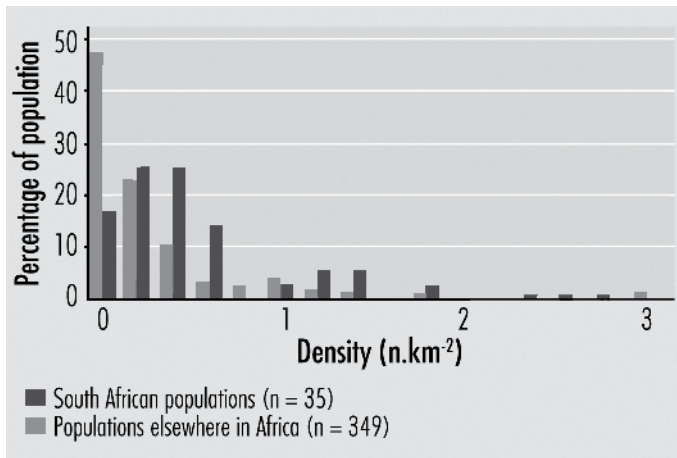


Figure 5: The distribution of elephant densities extracted from the most recent African Elephant Status Report (Blanc *et al.*, 2007). We separated estimates for South African populations from those for populations elsewhere in Africa. We counted the number of estimates falling into density classes that were 0.2 n.km² wide. The distribution for South African populations has a median (the most central value across the range of densities) of 0.31 n.km² while that for populations elsewhere in Africa was 0.11 n.km² even though 12 parks elsewhere in Africa support densities greater than those for the parks in South Africa

Population growth rates vary geographically. In eastern Africa populations are generally stable, while those in southern Africa are increasing (Blanc *et al.*, 2005). However, within southern Africa, numbers in Hwange in Zimbabwe (Chamaillé-Jammes *et al.*, 2007) and northern Botswana appear to be stabilising (Junker *et al.*, 2008). Those in some areas in Zimbabwe (Cumming *et al.*, 1997), Namibia (Lindeque, 1991), and South Africa (Van Aarde *et al.*, 1999; Gough & Kerley, 2006) are increasing, while in places in Zambia, such as the Kafue National Park (Guldmond *et al.*, 2005), the Lower Zambezi National Park and parks in the Luangwa valley, numbers are decreasing or stabilising (Ferreira *et al.*, 2008). In some instances, the estimated annual population growth exceeds the maximum theoretical growth rate. This is particularly the case for small

populations in South Africa (see table 4), where synchronised breeding and skewed age structures can cause high, short-term spurts in annual population growth rates which will not persist in the longer term.

South African populations have annual growth rates that range from -0.6 to 25.5 per cent per year (table 4). Of the 29 estimates of annual population growth rate in South Africa, only two were negative while 16 were higher than 7 per cent per annum (table 4). None of these populations were stable. Based on census data, populations elsewhere in Africa grow at annual rates ranging from -87.7 to 148.8 per cent per year (see figure 6). High apparent positive or negative population growth rates result from large-scale movements, particularly when a few elephants comprise the initial population size. Elsewhere in Africa, 70 (46 per cent) of the annual growth rates that we could estimate from population estimates were negative.

All South African populations have been exposed to some form of management that includes fencing, population control through translocations, culling or contraception, and water provision. Contrastingly, most other populations in Africa have relatively little management and are not fenced, allowing large-scale movements. The response of populations to management can best be measured by their growth rates. South Africa's intensely managed populations increased at rates that were both faster and less variable than populations elsewhere in Africa (figure 6), suggesting that conditions created by management stimulate growth. This is not surprising, since elephant populations, like those of all other species, should respond to resource supply and the protection afforded by conservation management. On the other hand, the inhibition of dispersal may also be largely responsible for higher population growth rates in fenced South African populations than for the open populations elsewhere in Africa where immigration and emigration do occur.

As indicated earlier, immigration and emigration rates are hard to determine. However, in the near future, our understanding of the influence of immigration and emigration on populations may be enhanced by comparing growth rates derived from estimated birth and death rates (see Ferreira & Van Aarde 2008) with those calculated from census data. We are aware of few field studies (e.g. Van Aarde *et al.*, 1999; Gough & Kerley, 2006; Ferreira & Van Aarde, 2008) that modelled population growth rates from birth and death rates. A few studies estimated theoretical growth rates (e.g. Hanks & McIntosh, 1973; Calef, 1988), while others used demographic predictors to evaluate population responses to contraception (e.g. Dobson, 1993; Van Aarde *et al.*, 1999) and trophy hunting (e.g. Owen, 2005).

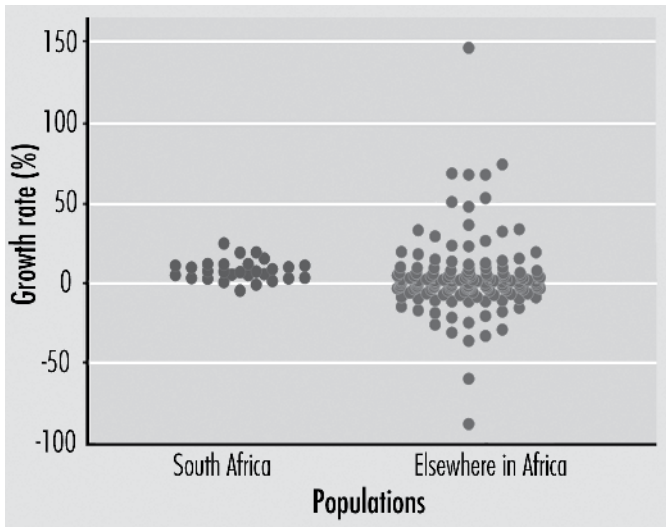


Figure 6: Exponential growth rates (Caughley, 1977) estimated from at least three population estimates in a time series for 28 South African elephant populations and 152 populations elsewhere in Africa. South African populations have a narrow distribution of growth rates (−4.2 per cent to 25.5 per cent) compared to populations elsewhere (−87.7 per cent to 148.2 per cent) and appear to centre above zero (South Africa: median = 7.7 per cent; elsewhere: median = 0.95 per cent; median refers to the most central growth rate across the range of rates)

Studies of density-dependent population growth in elephants are rare (e.g. Van Aarde *et al.*, 1999; Sinclair, 2003; Gough & Kerley, 2006; Junker *et al.*, 2008), yet they are needed to evaluate the consequences of any of the management regimes that elephant populations may be exposed to in the future.

Population limitation

Elephants are generalists and therefore utilise a variety of food resources. Even so, food availability influences vital rates. For instance, the distances that elephants need to travel between water and habitats of high nutritional value may affect energetic expenditure and influence conception and mortality of young animals. Indeed, the very low calf mortality rates found at Addo were attributed to a constant supply of food and water in comparison to other populations (Gough & Kerley, 2006). From studies elsewhere in Africa we know that conception rate varies with primary productivity as proxied by NDVI

Box 4: Individual responses to management

Elephant management techniques including culling, translocation, and contraception may have important consequences for individual elephants. Depending on the scale of action, individual responses may generate an effect at the population level.

The consequences of culling for individual elephants, especially selective culling, are poorly understood and need to be assessed (Slotow *et al.*, 2005). The trauma endured by culled orphans and those raised by inexperienced mothers puts calves at risk for developing symptoms similar to post-traumatic stress disorder in humans – abnormal startle response, depression, unpredictable asocial behaviour and hyper-aggression (Bradshaw *et al.*, 2005).

Translocation can also affect elephant behaviour. The introduction of bulls to new and strange environments occasionally results in ‘breakouts’ as bulls potentially try to return to their previous home ranges or attempt to gain access to different vegetation or reproductively active females (Garai & Carr, 2001). Additionally, adolescent males require socialisation with older bulls for normal social development (Slotow *et al.*, 2000; Bradshaw *et al.*, 2005), a requirement often neglected by translocation endeavours (e.g. Pilaanesberg and Phinda; Slotow & Van Dyk, 2001; Genis *et al.*, 2004). This problem probably holds for all South African populations that were founded through reintroduction prior to 1998 when bulls older than 25 years were not included in founder groups (Slotow & Van Dyk, 2001).

Additionally, despite early optimism that contraception was effective, safe, and reversible (Fayrer-Hosken *et al.*, 2000), it may have side-effects that influence the health and behaviour of cows (Whyte *et al.*, 1998; Pimm & Van Aarde, 2001; Van Aarde & Jackson, 2007). Hormonal treatments may cause cows to remain in sexual heat and be harassed by bulls and evicted from their social groups (Whyte & Grobler, 1997). Furthermore, as elephant society is kin-based (Archie *et al.*, 2006), artificial control of reproduction may have consequences for social hierarchies and, in turn, individual well-being (see McComb *et al.*, 2001).

(Wittemyer *et al.*, 2007b, 2007c). Conception and birth rates therefore should also vary with spatial variation in rainfall and NDVI.

Periodic droughts may also induce variation in vital rates. For instance, severe droughts synchronised both births and the length of calving intervals in Amboseli (Moss, 2001). Droughts also increase death rates in elephants and may occasionally lead to large-scale die offs (Walker *et al.*, 1987; Dudley *et al.*, 2001), as was the case in the Tsavo ecosystem in Kenya between 1975 and 1980, when many elephants died during an extended drought (Corfield, 1973; Ottichilo, 1987).

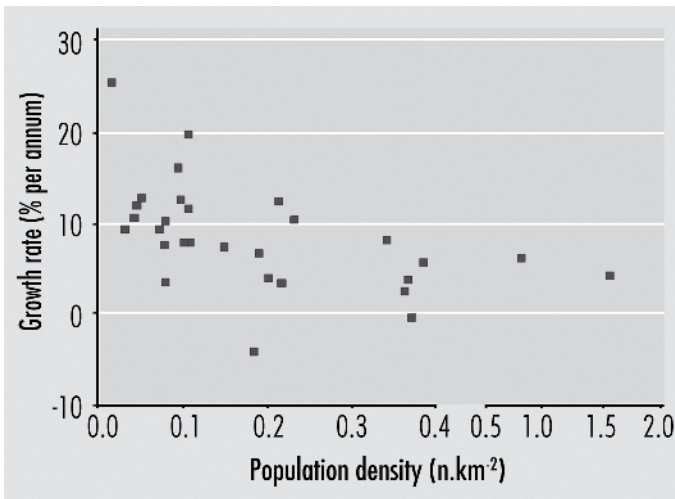


Figure 7: Exponential population growth of South African elephant populations since 1985 as a function of density. We calculated annual growth rate (expressed as percentage) from time series of density extracted for 29 places using $N_t = N_0 e^{rt}$ (Caughley, 1977) and plotted these against the density at the onset of each of the time series. Populations had higher growth rates when the starting density was low

The effect of poaching on populations can be severe (e.g. Douglas-Hamilton, 1972) and may leave demographic signals. For instance, populations in Zambia, an ivory poaching hotspot (Wasser *et al.*, 2007), continued to decline (Ferreira *et al.*, 2008) despite the ivory ban of 1989 (Stiles, 2004). Here, populations had few large and thus old elephants, herds were small (Ferreira *et al.*, 2008) and many elephants had no tusks (Steenkamp *et al.*, 2007).

Although no conclusive analysis of density dependence in African elephant populations has been carried out to date, in at least three studies equilibrium models that include density dependence, best described trends in elephant population numbers over time (Sinclair, 2003; Junker *et al.*, 2008; Chamaillé-Jammes *et al.*, 2007), while one study (Addo) found no evidence of density

dependence in population growth (Gough & Kerley, 2006). This lack of evidence for density dependence in Addo is not surprising considering the enlargement of space available to elephants there, and the high relative abundance of resources. In Kruger, Van Aarde *et al.* (1999) inferred density dependence in population growth from changes in densities after culling operations, while Van Jaarsveld *et al.* (1999) also found evidence for density dependence for Kruger and the declining Knysna population. With the exception of one population in the Timbavati, Van Jaarsveld *et al.* (1999) reported density independence in population growth for the recovering South African populations that they studied.

Exponential annual population growth rates that we calculated for South African populations since 1985 tended to be higher when densities were low at the onset of the time series on which we based calculations (figure 7). Although this is not evidence for density dependence, these observations suggest that density may explain between-population variability in population growth rates. Density therefore may be important to explain changes in population growth once densities are high enough to reduce food availability and hence reduce reproductive and survival rates as well as enhance dispersal rates, all of which will inhibit growth. The role of density dependence for the population, as well as for the impact elephants may have on other species, needs further investigation. For instance, reduced population growth at high densities may be negated if populations are artificially reduced through culling (this topic is discussed in Chapter 8). On the other hand, the numbers of elephants at levels where density reduces reproduction and survival may have unacceptable impacts on other species.

THE RESPONSES OF ELEPHANT POPULATIONS TO MANAGEMENT

Inferences on how individual elephants (see box 4) or populations of elephants will respond to management are often based on hear-say. Few measures of such responses have been published (e.g. Van Aarde *et al.*, 1999), and in general, these suffer from poor experimental design, improper replication, and *ad hoc* interpretations (Van Aarde & Jackson, 2007; Guldemond & Van Aarde 2008). For elephants in southern Africa, as for several other species elsewhere in the world, it seems that most past conservation management actions had their origins in experiential rather than experimental evidence (e.g. Pullin & Knight, 2005). For instance, the original decisions to cull elephants in several conservation areas across Africa were motivated by the apparent impact elephants may have had or were having on vegetation (e.g. Pienaar *et al.*, 1966; Laws *et al.*, 1975; Bell, 1983). However, there was little scientific evidence of such impacts, and

in the case of Kruger, supporting evidence to motivate the cull was collected after the decision to cull had been taken (e.g. Van Wyk & Fairall, 1969). We also know of no published information to illustrate that a management action such as culling had the desired outcome of reducing the impact that elephants apparently had on vegetation and other species; however, it is hard to know what might have happened in the absence of culling. Proposals to reinstate culling are founded in the so-called precautionary principle (e.g. Whyte, 2004; Mabunda, 2005). Elephant management clearly continues to be a debatable topic (Cumming & Jones, 2005; Mabunda, 2005; SANParks, 2005; Owen-Smith *et al.*, 2006; Van Aarde *et al.*, 2006). More often than not the debate seems to be founded on staunch opinion backed by advocacy, rather than scientific evidence. This is not surprising, because scientists often focus on defining and describing problems rather than on finding solutions for problems.

The response of elephant populations to both direct and indirect management actions may depend on the intensity of the actions applied. For elephant populations, direct management typically aims to reduce numbers by decreasing birth rates (e.g. through contraception), increasing death rates (e.g. through culling), or mimicking dispersal (e.g. translocation). Populations are protected and managed indirectly by erecting fences around conservation areas and by providing additional water. The underlying assumption of direct management actions is that a reduction in elephant numbers will lower the intensity of resource use and will ultimately reduce elephant impact on other species, usually vegetation. This assumption may not be valid (see Van Aarde & Jackson, 2007) because, rather than numbers alone, impact can also depend on the intensity of resource utilisation reflected by spatial use patterns (see Gordon *et al.*, 2004) and dictated by the distribution of key resources. In addition, the ultimate success of management actions to reduce impact has yet to be assessed. We therefore cannot elaborate on the effectiveness of management to reduce impact. However, we can evaluate and speculate on the responses of elephant populations to management actions such as contraception, culling, translocation, and the manipulation of resources such as water and space (e.g. restrictions through fences or providing space through transfrontier conservation areas). Here we focus on a broader comparative evaluation while later chapters focus on specific case studies.

Contraception

This topic is dealt with in detail in Chapter 6. Here we address only aspects relating to population dynamics.

The application of contraceptives to reduce fertility in wildlife is well beyond the research phase (Kirkpatrick, 2007; Perdok *et al.*, 2007). Birth rates may be reduced by treating cows with hormones and their derivatives, or with immuno-contraceptives to reduce or control fertility (e.g. Fayrer-Hosken *et al.*, 2000; Pimm & Van Aarde, 2001; see Chapter 6 for detailed methodology).

Reducing reproductive rates may also alter the age and social structures of breeding herds and possibly influence the well-being of cows and their calves (McComb *et al.*, 2001; Pimm & Van Aarde, 2001). Contraceptives may lengthen inter-calving intervals or increase the age of first calving (Perdok *et al.*, 2007). Unlike culling, contraception does not reduce numbers – instead it relies on natural mortality and reduced reproductive output to reduce population size over time.

The efforts needed to stabilise elephant numbers in large populations through birth control are both laborious and costly (Pimm & Van Aarde, 2001). At the population level, birth control is constrained by the number of females needing treatment (Whyte *et al.*, 1998). Age at first calving will only increase effectively if almost 50 per cent of pregnant cows less than 15 years old are on birth control or forced to abort (Mackey *et al.*, 2006). In Kruger, elephant population growth will only stabilise if managers treat nearly 75 per cent of adult cows continuously for 11 years (Van Aarde *et al.*, 1999). We agree with others (Bertschinger *et al.*, 2003; Delsink *et al.*, 2006; Perdok *et al.*, 2007) that immunocontraception can currently only be regarded as a proven and realistic option for reducing population growth in small, confined populations. As for the ultimate goal of management, the ability of contraception to reduce elephant impacts on vegetation still needs to be determined.

Culling

Culling is discussed in detail in Chapter 8. Culling can be directed at reducing the sizes of local populations, stabilising populations, manipulating the number of animals in distinct social groups within a population, or removing elephants from specific parts of their distributional range (e.g. from obvious zones of conflict).

Controversy aside, the 30-year elephant culling regime in Kruger provided a valuable case study. Much has been written on the topic of culling, also for species other than elephant (see Walker *et al.*, 1987; Cumming *et al.*, 1997; Proaktor *et al.*, 2007). In general, it seems that the reduction in density through culling inflates population growth rate, by releasing vital rates (age at first calving and inter-calving interval) from limitations set by density dependence

(for elephants see Whyte *et al.*, 1998; Van Aarde *et al.*, 1999). Therefore, elephant culling with the intention of maintaining populations at a level below which resources are limited is a self-perpetuating practice because populations are pushed to densities where reproductive potential and survival may be optimised. Put simply, culling can only be effective to reduce numbers in the medium term if it is maintained indefinitely and at a rate above the population's growth rate.

An interesting issue to consider is whether Kruger's elephants would have stopped increasing through density dependence should culling not have taken place. An analysis presented by Van Aarde *et al.* (1999) provides support that density dependence becomes apparent at 0.37 elephants per km⁻², and they suggested that culling was probably unnecessary unless populations remained at densities higher than that value for two or more years. However, this appeared not to be the case, and elephant density in Kruger is approaching much higher values (Blanc *et al.*, 2007).

There are two possible explanations for this discrepancy. First, perhaps the mode of density limitation during the culling era was via migration from non-culled regions at densities greater than 0.37 km⁻² to other regions in the park where the cull reduced density to relatively low levels (see Van Aarde *et al.*, 1999). In this case, it is unlikely that vital rates would change in response to reduced resource availability because elephants simply migrated to resource-rich areas rather than experiencing the limitations imposed by resource scarcity. The second explanation is that resource limitation truly limited elephant density at densities greater than 0.37 km⁻². In this case, tell-tale changes in vital rates would be expected. Unfortunately such information is not available.

The fact that the Kruger elephant population is not currently limited at the density proposed by Van Aarde *et al.* (1999) probably reflects on changes in resource availability. The assessment of Van Aarde *et al.* (1999) was based on data from a dry cycle lasting several years and including a severe drought in 1992 (see Mills *et al.*, 1995; Ogotu & Owen-Smith, 2003). Since then conditions have changed, and drought conditions may no longer limit resources, therefore explaining the lack of immediate density-dependent responses. Additionally, the relatively high densities at which elephants presently occur in Kruger could be a delayed response of reproductive output in response to culling (eruptive growth, discussed in detail in Chapter 8).

Culling apparently can effectively limit population growth only when applied continuously. For instance, following the cessation of culling in the Kruger, growth rates increased dramatically (see Whyte *et al.*, 2003). Furthermore, after the cessation of culling in 1995 in Hwange National Park

(Zimbabwe), elephant numbers almost doubled in just six years, while elsewhere in Zimbabwe, numbers grew about 28 per cent over the same period (Foggin, 2003). Even so, culling does reduce numbers, albeit temporarily.

Where selective culling may target bulls or animals of certain age classes, distorted age structures may 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 due to the release of density-dependent limitations of reproductive rate (see Sinclair, 2003). Thus, inappropriate culling may effectively increase growth rate.

A major shortcoming of past elephant culling programmes is that none of them employed an evaluation approach to assess efficiency in reducing the apparent impact that motivated the undertaking of the programmes.

Translocation

This topic is discussed in detail in Chapter 5. Initially, policy regarding the translocation of elephants was formulated to establish more elephant populations across southern Africa (Pienaar *et al.*, 1966). This was done on the premise that genetic variability of elephants could be enhanced or maintained through this process. A secondary outcome of elephant translocation developed as a more ethical solution than culling to control and/or reduce elephant numbers in a particular region. The translocation of elephants is, however, not unique to South Africa. Other African countries, such as Kenya, also have experience in shifting elephants, albeit for different reasons. There, elephants were moved from small reserves to larger parks such as the Tsavo National Park to mitigate human-elephant conflict (Njumbi *et al.*, 1996). The efficiency of these translocations still has to be assessed.

Since 1979, elephants from the Kruger have been captured, translocated, and released in other parks and reserves (Garaï *et al.*, 2004), some of them privately owned (Garaï & Carr, 2001). In some of the earlier translocation efforts, only elephant calves were moved, but due to aberrant social behaviour of young bulls (Slotow *et al.*, 2000), intact family units and adult bulls have been included in recent efforts to establish new populations or during re-introductions. Some 58 elephant populations were established in South Africa alone between 1979 and 2001 (Garaï *et al.*, 2004), with the numbers in newly founded elephant populations expected to increase (Slotow *et al.*, 2005). All of these newly established populations live in fenced reserves that are relatively small, ranging in area from 15 to 900 km² (Slotow *et al.*, 2005). One particular aspect that stands out is the high growth rates reported for these populations, some as high as

25.5 per cent (table 4). This is well beyond the maximum rate of increase that maximum birth and survival rates predict for elephants living in closed areas (Calef, 1988; Van Aarde *et al.*, 1999). This abnormally high growth rate can most likely be ascribed to synchronised calving and/or unstable population structures typical of small groups. Additionally, most of the recently established elephant populations comprise few individuals (see table 4), and estimates of their vital rates thus may suffer from statistical limitations (Akçakaya, 2002). Theoretically, the conversion of unstable age structures to stable structures will be associated with a reduction in average population growth rate to values around 5 per cent per year when populations are enclosed.

Despite aberrant population growth rates, translocations of elephants are regarded as successful to establish populations (Garaï *et al.*, 2004; Slotow *et al.*, 2005). However, its contribution to conservation needs to be questioned since many researchers warn against the effects on other species of continual increase in elephant numbers in these newly established reserves. In most of these reserves, elephants are confined to relatively small areas where space is so limited that it does not allow natural seasonal roaming. Dispersal also is impossible due to surrounding land use options. Fences that surround these areas and artificial pans and waterholes may lead to small home ranges that are intensely utilised and to high growth rates. This will intensify the impact that elephants will have on the landscape surrounding these artificial sources of water. Thus, the establishment of new populations through translocations may create more population control issues than it solved as many of these populations may soon require management to reduce impact.

More than 800 elephants were moved from the Kruger between 1979 and 2001 (Garaï *et al.*, 2004), with the main translocation efforts between 1990 and 2001 (Slotow *et al.*, 2005). On average, in those years when translocation took place, about 1 per cent of the population was removed from Kruger. Based on the trends in population numbers given by Whyte *et al.* (1998), these translocations clearly had little effect on Kruger's elephant numbers and certainly did not reduce the population's rate of increase during the 1990–2001 period.

Other aspects that may relate to the translocation of elephants, such as the demand for and availability of suitable elephant habitat, management constraints (e.g. costs of capture, care, translocation, and release of elephants), and possible effects (post-traumatic stress) on individual elephants are dealt with in Chapter 5.

Translocation may also have undesirable genetic and conservation consequences. Recent advances in genetic profiling of sub-populations as separable entities provides conservation managers with a powerful tool to locate

the sources of illegal ivory and thus to strengthen conservation efforts (see Wasser *et al.*, 2007). Mixing elephants from different regions will destroy these unique genetic signals and therefore detract rather than enhance conservation initiatives.

Translocations that mix elephants of different genetic stocks also interfere with conservation ideologies that centre on the maintenance of biodiversity, for biodiversity conservation also emphasises the maintenance of ecological processes. Of these processes, natural selection is probably the one process that gives rise to sub-population differences as an adaptation to local conditions. Interfering with this detracts from the conservation paradigm to which South Africa and several of its neighbouring countries are signatories.

The translocation of elephants is relatively easy and can give rise to the establishment of new populations, thereby recovering key ecological processes that may have been lost through earlier local exterminations of elephants. This, however, only holds when environmental conditions in areas where new populations are established meet the requirements for the development of an elephant population. This apparently is not the case for most populations established through translocations in South Africa and the conservation management benefits of translocations therefore must be questioned. Low rates of translocations may have little benefits for the donor populations, because the removal of elephants may merely re-distribute elephants in the donor populations, as has been the case when elephants were removed through culling from specific management areas in Kruger (see Van Aarde *et al.*, 1999). In conservation terms the genetic consequences of translocations when mixing individuals of different sub-populations is also not desirable. On the other hand, genetic enrichment in artificially isolated populations such as Addo may be advantageous.

Manipulation of water

Water is a primary determinant of the distribution of elephants (De Beer *et al.*, 2006; Chamailé-Jammes *et al.*, 2007; Harris *et al.*, 2008). Elephant breeding herds are especially water dependent as the young calves and lactating cows need to drink frequently (e.g. Stokke & Du Toit, 2002). It is therefore not surprising that the manipulation of surface water distribution has major consequences for the way elephants roam and forage across the land they occupy. Such water may alter seasonal movements and enable elephants to inhabit sensitive landscapes for longer periods of the year than they would have under natural conditions. This could intensify impact, especially for plants that are not predisposed to intensive utilisation. The vegetation in

such areas therefore does not have the opportunity to recover seasonally.

Water provisioning is a standard procedure many wildlife managers practise across the southern African range of elephants (see Chapter 7 for more details). Such provisioning affects movement patterns (Harris *et al.*, 2008), home range utilisation and size (Grainger *et al.*, 2005; De Beer *et al.*, 2006; De Beer, 2007) and the impact that elephants have on local vegetation (Gaylard *et al.*, 2003; De Beer *et al.*, 2006; O'Connor *et al.*, 2007). For instance, water made available in man-made waterholes could attract elephants to occupy land that they would not otherwise have occupied – habitats avoided under natural conditions may now be utilised, thus resulting in the redistribution of elephants and negating the potential for density related forces to inhibit survival and reproductive output of elephants in preferred habitats. Water provisioning therefore may boost the so-called elephant problem.

Water manipulation may also influence the demography of populations. Recent work in the Hwange National Park in Zimbabwe suggests that density tends to increase with the increase in artificial waterhole densities (Chamaillé-Jammes *et al.*, 2007). Distance to water is also a primary determinant of the densities at which elephants occur (Western, 1975; Stokke & Du Toit, 2002; Redfern *et al.*, 2003; Grainger *et al.*, 2005). Owen-Smith (1996) and Chamaillé-Jammes *et al.* (2007) suggest that the manipulation of artificial surface water can be an important tool through which to manage elephant populations. The effectiveness of water manipulation as a management tool, however, may differ between areas and between populations (Smit *et al.*, 2007b).

Water provision influences populations by enhancing survival, especially of juveniles, during droughts and/or in arid regions. Water provisioning also enhances immigration, as illustrated by our recent and ongoing assessment of population time series from several areas in northern Namibia. In northern Namibia, without exception, water provisioning in both formal and informal conservation areas was followed by an increase in population numbers locally (CERU, unpublished data). This may also explain the trends in numbers in Kruger during the 1960s and 1970s when water availability was increased artificially (Pienaar, 2005) and before a fence isolated elephants in Mozambique from those in Kruger. Therefore, the water provided in human-made structures either attracts elephants from elsewhere (as has been the case in Hwange in Zimbabwe following the establishment of additional water points (Chamaillé-Jammes *et al.*, 2007), or enhances local survival. Presently, elephants appear to be moving out of Kruger, where water sources are apparently being closed, into areas west of Kruger with an extremely high density of artificial waterholes (J. Swart, Sabi Sands Game Reserve, pers. comm.).

Surface water distribution and manipulation may cause population size to increase to artificially high numbers (Van Aarde & Jackson, 2007). Water provided in human-made structures, therefore, may be at the root of the so-called elephant problem. We are not aware of published accounts of the influence of surface water manipulation on reproductive output and survival, both of which may be implicated in the relatively high numbers at which elephants occur when water is artificially provided. This clearly needs further investigation.

Within protected areas, efforts to stabilise the availability and spread of drinking water to regions that were inaccessible during the dry season probably affected elephant survival, as young are particularly susceptible to drought conditions (Dudley *et al.*, 2001; Loveridge *et al.*, 2006). Improved survival may increase population size because survival of young is an important determinant of population growth (e.g. Gaillard *et al.*, 1998).

Surface water distribution may also determine dispersal, which influences population numbers through immigration and emigration. Artificial waterholes attract elephants and result in populations being established in areas where elephants otherwise would not occur, particularly during the dry season (Chamaillé-Jammes *et al.*, 2007; De Beer, 2007; Smit *et al.*, 2007a). This is especially true for the arid savannas where elephant populations became resident in response to water provisioning in Etosha (Lindeque, 1988), Khaudum (De Beer, 2007) and Hwange (Chamaillé-Jammes *et al.*, 2007).

Fencing

The fencing of conservation areas and the establishment of veterinary fences to control the spread of contagious diseases inhibits both seasonal movements and dispersal and thereby has consequences for the size of elephant populations (Mbaiwa & Mbaiwa, 2006; Van Aarde *et al.*, 2006; Van Aarde & Jackson, 2007; see Chapter 7 for details on fencing as a management tool).

Fences have an edge effect on the utilisation intensities of home ranges and, consequently, on the impact that elephants may have on vegetation (CERU, unpublished data). More importantly, however, at the population level, the lack of dispersal opportunities may enhance local population growth (Owen-Smith, 1988). The advent of the dropping of some of the fences surrounding Kruger is too recent for formal literature to have noted emigration events that could have resulted in a decrease in population size. Recent observations suggest a marked increase in elephant numbers in the Limpopo National Park (Mozambique) that adjoins the eastern boundary of Kruger, while at the same time, numbers in Kruger have stabilised (H. Magome, SANParks, pers. comm.). This supports our

earlier speculation that dispersal is an important determinant of local population size (Van Aarde *et al.*, 2006). This clearly needs further investigation.

Manipulation of space

The manipulation of space potentially involves the development of linkages, corridors, and/or so-called stepping stones to link sub-populations into a metapopulation structure of some kind (see Van Aarde & Jackson, 2007). The recent literature on elephant social dynamics (Archie *et al.*, 2006) and spatial use patterns of groups of elephants of differing social status (Wittemyer *et al.*, 2007a) also calls for the enhancement of space to ensure social structuring and out-breeding. Population level responses to spatial manipulation have not been recorded, except for incidences where the recent extension of the range of elephants resulted from the lifting of some of the fences of Kruger (De Villiers & Kok, 1997). This gave rise to elephants establishing themselves on vacant land in neighbouring conservation areas.

The present distributional range of elephants is patchy and extends beyond conservation areas in countries other than South Africa, though most elephants do occur in formally protected areas. Elephants do disperse readily into vacant habitats. For instance, historical records show that elephants moved from Mozambique into South Africa's Kruger, which in the early 1900s supported fewer than 10 elephants. Dispersal at annual rates of 7–10 km meant that the Park's approximate 20 000 km² was colonised within 50 years (Whyte *et al.*, 2003). Similarly, in 1955 elephants were recorded in the Serengeti after an absence of at least 40 years. Here numbers increased over a 10-year period, mainly through immigration, to some 2 000 individuals (Lamprey *et al.*, 1967).

In areas where managers manipulated water availability, elephant populations expanded rapidly and at rates that exceeded their reproductive capacity. For instance, Etosha's population comprised approximately 50 individuals in 1950 and increased to some 2 000 by 1980 (Lindeque & Lindeque, 1991). Following water supplementation in Khaudum, the population increased from around 80 in 1976 to some 3 400 in 2004 (Ben Beytell, Ministry of the Environment and Tourism, Windhoek, pers. comm.). Civil unrest in southern Angola may have contributed to this increase in Khaudum, which at ~13 per cent per year is almost triple the value that is typical for populations that increase in response to natural values of birth and deaths.

In Kruger, culling induced dispersal of elephants into areas where densities were reduced (Van Aarde *et al.*, 1999). It therefore follows that elephants do disperse when given the opportunity or when circumstances allow or force

them. This is critical to the application of landscape conservation models such as the metapopulation model to the conservation management of elephants, since the metapopulation in its true sense can only operate with dispersal (Van Aarde & Jackson, 2007).

We do not know much of the consequences that the effective increase of space would have for elephant demography. Recent arguments favour the restoration of elephant spatial dynamics, which could influence population responses and restore spatial-temporal dynamics (Van Aarde *et al.*, 2006; Van Aarde & Jackson, 2007). This may lead to local instability in elephant numbers that reduces local impact and conflict while inducing a regional stabilisation of numbers that reduces the threat to the long-term persistence of elephants. These predictions need to be evaluated and tested, but are supported by our recent analyses of differences in population growth rates for different landscape types in the Kruger.

CONCLUSIONS

The Assessment allows us to put forward a conceptual framework that can serve as a guideline for management as well as research (figure 8). The framework explicitly recognises the nature of the dilemma that pervades elephant management in South Africa where most elephants live as a single population in a large conservation area (e.g. Kruger) while the remainder live in many highly artificial and distinct populations in small and isolated reserves (see table 4).

The diverse elephant management challenges can be visualised as falling along a continuum of management intensity. Small and isolated areas invariably require intensive management and consequently will be the least natural. Such areas will contribute relatively little to elephant conservation, but they may be critical for other forms of biological diversity. In contrast, large areas require progressively less management as the integrity of natural processes increases. As a result, areas managed for elephants exist along a continuum of artificial to nearly natural, from populations as reproductive isolates to populations as connected spatial entities, and from relatively costly to relatively cost effective. Most importantly, spatial constraints of elephant-containing areas could define management responses ranging from those that focus on the symptoms, i.e. high elephant numbers (in small areas with intensive management), to those that focus on the forces that cause the symptoms, i.e. why elephant numbers are high in the first place (in large connected areas with low intensive management).

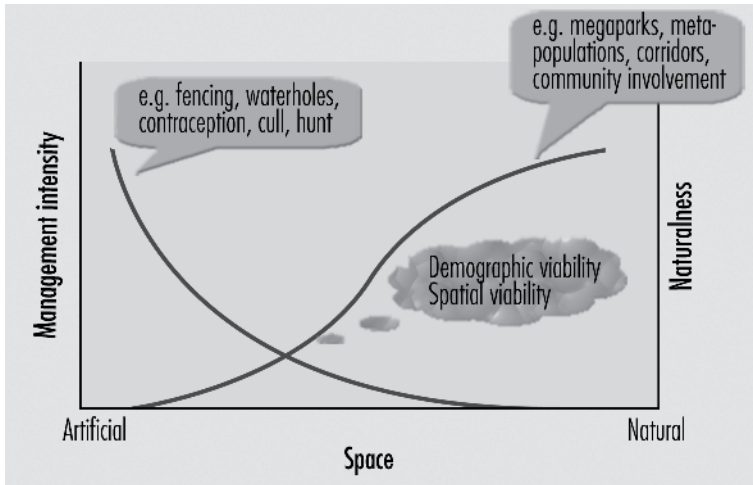


Figure 8: A conceptual model for the management of elephant populations in South Africa. Elephant populations occupy a continuum of size of habitat. Where the available area is small, intensive management is required and the level of ‘naturalness’ is low. At the other extreme, little management is needed, and the degree of naturalness is high. The aim throughout is to achieve demographic and ecological viability, given the spatial constraint. To the left of the intersection of the curves is the region of demographic and spatial limitations where populations will have to be managed. Populations to the right of the intersection increasingly may need less and less management. The point of intersection represents an approximation rather than a given point

We therefore foresee a scenario where elephants confined to small parks are managed as individuals rather than populations. In this case, the emphasis will be on limiting population size through contraception and/or translocation and protecting species sensitive to elephant impact by manipulating local range use by fencing off selected sensitive areas or trees, perhaps on a long-term rotational basis. Management methods may also include the periodic displacement of elephants from areas of these parks, either through the rotational occupation of landscapes or rotational removal of elephants themselves. Elephants here will most likely live as a breeding herd that will include only the lower tiers of social structuring known for the species (see box 1).

At the other end of the spectrum, where areas have the capacity to provide for all tiers of social organisation up to the population as a unit (see box 1), management can be more relaxed and occasional. In these more natural situations, management no longer centres on elephants, but focuses on the landscape as a spatially and temporally dynamic arena in which all

forms of biodiversity, including structural and functional diversity, have an opportunity to persist. Here, management can focus on maintaining spatial linkages for dispersal while allowing for extreme local fluctuations in elephant numbers. Creating larger areas for more effective conservation may require the internationalisation of conservation management, as foreseen in the development of transfrontier conservation initiatives presently driven by several NGOs and supported by several southern African governments.

We also need to be pragmatic. We concede that most elephant-containing areas in South Africa are likely to fall in the region of our conceptual model that proposes intense management. These areas often do not provide for seasonal movements, let alone spatial variability in demography. The managers of such areas cannot aim to achieve demographic viability through natural limiting mechanisms such as density-dependent birth reductions, drought-related mortalities and local dispersal. They will have to resort to active intervention to reduce impact, probably by manipulating population sizes in sensitive places and varying spatial occupation to ameliorate impacts on other species.

REFERENCES

- Akçakaya, H.R. 2002. Estimating the variance of survival rates and fecundities. *Animal Conservation* 5, 333–336.
- Alexander, K.A., C. Gibbons, M. Ramotadima, M.E.J. Vandewalle, J. Mucheka, I.M. Cattadori & N. Drake 2006. Long-term changes in elephant distribution and seasonal factors: Influence on conflict incidence and impacts on gender specific rural livelihoods. In: L.E.O. Braak & R. Smuts (eds) Towards rationalizing transboundary elephant management and human needs in the Kavango/mid-Zambezi region. Unpublished proceedings of a workshop presented on 23 and 24 May 2006 in Gaborone, Botswana, by Conservation International (Southern Africa Wilderness and Transfrontier Conservation Programme), Cape Town, 36–44.
- Archie, E.A., C.J. Moss & S.C. Alberts 2006. The ties that bind: genetic relatedness predicts the fission and fusion of social groups in wild African elephants. *Proceedings of the Royal Society B* 273, 513–522.
- Bates, L.A., K.N. Sayaliel, N.W. Njiraini, C.J. Moss, J.H. Poole & R.W. Byrne 2007. Elephants classify human ethnic groups by odor and garment color. *Current Biology* 17, 1–6.
- Bell, R.H.V. 1983. Decision making in wildlife management with reference to problems of overpopulation. In: R. Owen-Smith (ed.) *Management of large*

- mammals in African conservation areas*. HAUM Educational Publishers, Pretoria, 145–171.
- Bengis, R.G. 1996. Elephant population control in African national parks. *Pachyderm* 22, 83–86.
- Berry, H.H. 1993. Surveillance and control of anthrax and rabies in wild herbivores and carnivores in Namibia. *Revue Scientifique et Technique – Office International Des Epizooties*, 137–146.
- Bertschinger, H.J., J.F. Kirkpatrick, R.A. Fayrer-Hosken, R.A. Grobler & J.J. van Altena 2003. Immunocontraception of African elephants using porcine zona pellucida vaccine. In: B. Colenbrander, J. de Gooijer, R. Paling, S.S. Stout; T. Stout & W.R. Allen (eds) *Managing African elephant populations: act or let die?* Proceedings of an expert consultation on the Control of Wild Elephant Populations, Faculty of Veterinary Medicine, Utrecht University, Netherlands, 45–47, <http://elephantpopulationcontrol.library.uu.nl/paginas/frames.html> (accessed 5 April 2006).
- Blanc, J.J., R.F.W. Barnes, C.G. Craig, I. Douglas-Hamilton, H.T. Dublin, J.A. Hart & C.R. Thouless 2005. Changes in elephant numbers in major savanna populations in eastern and southern Africa. *Pachyderm* 38, 19–28.
- Blanc, J.J., R.F.W. Barnes, G.C. Craig, H.T. Dublin, C.R. Thouless, I. Douglas-Hamilton & J.A. Hart 2007. *African elephant status report: An update from the African Elephant Database*. IUCN, Gland.
- Bradshaw, G.A., A.N. Schore, L.B. Brown, J.H. Poole & C.J. Moss 2005. Elephant breakdown. *Nature* 433, 807.
- Bulte, E., R. Damania, L. Gillson & K. Lindsay 2004. Space – the final frontier for economists and elephants. *Science* 306, 420–421.
- Buss, I.O. & N.S. Smith 1966. Observations on reproduction and breeding behaviour of the African elephant. *Journal of Wildlife Management* 30, 375–388.
- Butler, V. 1998. Elephants: trimming the herd. *BioScience* 48, 76–81.
- Calef, G.W. 1988. Maximum rate of increase in the African elephant. *African Journal of Ecology* 26, 323–327.
- Case, T.J. 2000. *An illustrated guide to theoretical ecology*. Oxford University Press, Oxford.
- Caughley, G. 1977. *Analysis of vertebrate populations*. John Wiley & Sons, New York.
- Chamaillé-Jammes, S., M. Valeix, & H. Fritz 2007. Managing heterogeneity in elephant distribution: between elephant population density and surface-water availability. *Journal of Applied Ecology* 44, 625–633.

- Coe, M.J., D.H. Cumming & J. Phillipson 1976. Biomass and production of large herbivores in relation to rainfall and primary productivity. *Oecologia* 22, 341–354.
- Corfield, T.F. 1973. Elephant mortality in Tsavo National Park, Kenya. *African Journal of Ecology* 11, 339–368.
- Coulson, T., F. Guinness, J. Pemberton & T. Clutton-Brock 2004. The demographic consequences of releasing a population of red deer. *Ecology* 85, 411–422.
- Couzin, I.D. 2006. Behavioral ecology: Social organization in fission-fusion societies. *Current Biology* 16, 169–171.
- Cozzi, B., S. Spagnoli & L. Bruno 2001. An overview of the central nervous system of the elephant through a critical appraisal of the literature published in the XIX and XX centuries. *Brain Research Bulletin* 54, 219–227.
- Cröze, H. 1972. A modified photogrammetric technique for assessing age structure of elephant populations and its use in Kidepo National Park. *East African Wildlife Journal* 10, 91–115.
- Cumming, D.H.M., M.B. Fenton, I.L. Rautenbach, R.D. Taylor, G.S. Cumming, M.S. Cumming, J.M. Dunlop, A.G. Ford, M.D. Hovorka, D.S. Johnston, M. Kalcounis, Z. Mahlangu & C.V.R. Portfors 1997. Elephants, woodlands and biodiversity in southern Africa. *South African Journal of Science* 93, 231–236.
- Cumming, D.H.M. & B. Jones 2005. *Elephants in southern Africa: Management issues and options*. WWF SARPO, Harare.
- Dai, X., G. Shannon, R. Slotow, B. Page & J. Duffy 2007. Short-duration daytime movements of a cow herd of African elephants. *Journal of Mammalogy* 88, 151–157.
- De Beer, Y. 2007. Determinants and consequences of elephant spatial use in Southern Africa's arid savannas. MSc thesis, University of Pretoria, Pretoria.
- De Beer, Y., W. Kilian, W. Versveld & R.J. van Aarde 2006. Elephants and low rainfall alter woody vegetation in Etosha National Park, Namibia. *Journal of Arid Environments* 64, 412–421.
- Delsink, A.K., J.J. van Altena, D. Grobler, H. Bertschinger, J. Kirkpatrick & R. Slotow 2006. Regulation of a small, discrete African elephant population through immunocontraception in the Makalali Conservancy, Limpopo, South Africa. *South African Journal of Science* 102, 403–405.
- De Villiers, P.A. & O.B. Kok 1988. Eto-ekologiese aspekte van olifante in die Nasionale Etoshawildtuin. *Madoqua* 15, 319–338.

- De Villiers, P.A. & O.B. Kok 1997. Home range, association and related aspects of elephants in the eastern Transvaal Lowveld. *African Journal of Ecology* 35, 224–236.
- Dobson, A.P. 1993. Effect of fertility control on elephant population dynamics. *Journal of Reproduction and Fertility Supplement* 90, 293–298.
- Douglas-Hamilton, I. 1972. On the ecology of the African elephant. Ph.D. thesis, Oxford University, Oxford.
- Douglas-Hamilton, I., T. Krink & F. Vollrath 2005. Movements and corridors of African elephants in relation to protected areas. *Naturwissenschaften* 92, 158–163.
- Dudley, J.P., G.C. Craig, D.S. Gibson, G. Haynes & J. Klimowicz 2001. Drought mortality of bush elephants in Hwange National Park, Zimbabwe. *African Journal of Ecology* 39, 187–194.
- Dunham, K.M. 1988. Demographic changes in the Zambezi Valley elephants (*Loxodonta africana*). *Journal of Zoology* 56, 382–388.
- Fatti, L.P., G.L. Smuts, A.M. Starfield & A.A. Spurdle 1980. Age determination in African elephants. *Journal of Mammalogy* 61, 547–551.
- Fayrer-Hosken, R.A., D. Grobler, J.J. van Altena, H.J. Bertschinger & J.F. Kirkpatrick 2000. Immunocontraception of African elephants. *Nature* 407, 149.
- Ferreira, S.M. & R.J. van Aarde 2008. A rapid method to estimate some of the population variables for African elephants. *Journal of Wildlife Management* 72, 822–899.
- Ferreira, S.M., R.J. van Aarde & J. Junker 2008. Ivory poaching disrupts Zambian savanna elephant population structures (in review).
- Foggin, C. 2003. The elephant problem in Zimbabwe: can there be an alternative to culling? In: B. Colenbrander, J. de Gooijer, R. Paling, S.S. Stout; T. Stout & W.R. Allen (eds) *Managing African elephant populations: act or let die?* Proceedings of an expert consultation on the Control of Wild Elephant Populations, Faculty of Veterinary Medicine, Utrecht University, Netherlands, 17–21, <http://elephantpopulationcontrol.library.uu.nl/paginas/frames.html> (accessed 5 April 2006).
- Foley, C.A.H. 2002. *The effects of poaching on elephant social systems*. Princeton University, Princeton.
- Forman, R.T.T. & M. Godron. 1986. *Landscape Ecology*. John Wiley & Sons, New York.
- Gaillard, J.-M., M. Festa-Bianchet & N.G. Yoccoz 1998. Population dynamics of large herbivores: Variable recruitment with constant adult survival. *Trends in Ecology and Evolution* 13, 58–63.

- Garai, M.E. & R.D. Carr 2001. Unsuccessful introductions of adult elephant bulls to confined areas in South Africa. *Pachyderm* 31, 52–57.
- Garai, M.E., R. Slotow, R.D. Carr & B. Reilly 2004. Elephant reintroductions to small fenced reserves in South Africa. *Pachyderm* 37, 28–36.
- Gaston, K.J., T.M. Blackburn & R.D. Gregory 1999. Does variation in census area confound density comparisons? *Journal of Applied Ecology* 36, 191–204.
- Gaylard, A., N. Owen-Smith & J.V. Redfearn. 2003. Surface water availability: Implications for heterogeneity and ecosystem processes. In: J. du Toit, K.H. Rogers & H.C. Biggs (eds) *The Kruger experience: Ecology and management of savanna heterogeneity*. Island Press, Washington, 171–188.
- Genis, H., R. Slotow & K. Pretorius 2004. The effect of mature elephant bull introduction on resident bull population ranging patterns and musth periods: Phinda Private Game Reserve. *Ecological Journal* 6, 14–19.
- Gibbs, J.P. 2000. Monitoring populations. In: L. Boitani & T.K. Fuller (eds) *Research techniques in animal ecology – controversies and consequences*. Columbia University Press, New York.
- Gillson, L. & K. Lindsay 2003. Ivory and ecology – changing perspectives on elephant management and the international trade in ivory. *Environmental Science & Policy* 6, 411–419.
- Gordon, I.J., A.J. Hester & M. Festa-Bianchet 2004. The management of wild large herbivores to meet economic, conservation and environmental objectives. *Journal of Applied Ecology* 41, 1021–1031.
- Gough, K. & G.I.H. Kerley 2006. Demography and population dynamics in the elephants *Loxodonta africana* of Addo Elephant National Park, South Africa: is there evidence of density dependent regulation? *Oryx* 40, 434–441.
- Grainger, M., R. van Aarde & I. Whyte 2005. Landscape heterogeneity and the use of space by elephants in Kruger National Park, South Africa. *African Journal of Ecology* 43, 369–375.
- Guldmond, R.A.R. 2006. The influence of savannah elephants on vegetation: A case study in the Tembe Elephant Park, South Africa. Ph.D. thesis, University of Pretoria, Pretoria.
- Guldmond, R. & R. van Aarde 2008. A meta-analysis of the impact of African elephants on savanna vegetation. *Journal of Wildlife Management* 72 (4), 892–899.
- Guldmond, R., E. Lehman, S. Ferreira & R. van Aarde 2005. Elephant numbers in Kafue National Park, Zambia. *Pachyderm* 39, 50–56.
- Hakeem, A.Y., P.R. Hof, C.C. Sherwood, R.C. Switzer, L.E.L. Rasmussen & J.N. Ellman 2005. Brain of the African elephant (*Loxodonta africana*):

- Neuroanatomy from magnetic resonance images. *Anatomical Record Part A* 287A, 1117–1127.
- Hall-Martin, A.J. 1992. Distribution and status of the African elephant *Loxodonta africana* in South Africa, 1652–1992. *Koedoe* 35, 65–80.
- Hanks, J. 1971. Reproduction of the elephant (*Loxodonta africana*) in the Luangwa Valley, Zambia. *Journal of Reproduction and Fertility* 30, 13–26.
- Hanks, J. 1972. Growth of the African elephant (*Loxodonta africana*). *East African Wildlife Journal* 10, 251–272.
- Hanks, J. 1979. *A Struggle for Survival: The Elephant Problem*. C. Struik, Cape Town.
- Hanks, J. & J.E.A. McIntosh 1973. Population dynamics of the African elephant (*Loxodonta africana*). *Journal of Zoology* 169, 29–38.
- Harestad, A.S. & F.L. Bunnell 1979. Home range and body weight: a re-evaluation. *Ecology* 60, 389–402.
- Harris, G.M., G.J. Russel, R.J. van Aarde & S.L. Pimm 2008. Habitat use of savanna elephants in southern Africa. *Oryx* 42, 66–75.
- Hart, B.L., L.A. Hart & N. Pinter-Wollman 2007. Large brains and cognition: where do elephants fit in? *Neuroscience and Biobehavioural Reviews* doi:10.1016/j.neubiorev.2007.05.012.
- Hoare, R.E. 1999. Determinants of human-elephant conflict in a land-use mosaic. *Journal of Applied Ecology* 36, 689–700.
- Hoare, R.E. & J. du Toit 1999. Coexistence between people and elephants in African savannas. *Conservation Biology* 13, 633–639.
- Hodges, J.K., R.J. van Aarde, M. Heistermann and H.O. Hoppen 1994. Progesterone content and biosynthetic potential of the corpus luteum of the African elephant (*Loxodonta africana*). *Journal of Reproduction and Fertility* 102, 163–168.
- Hunter, N. & T. Milliken 2004. Clarifying MIKE and ETIS. *Pachyderm* 36, 129–132.
- Illius, A.W. 2006. Foraging and population dynamics. In: K. Danell, R. Bergström, P. Duncan & J. Pastor (eds) *Large herbivore ecology, ecosystem dynamics and conservation*. Cambridge University Press, Cambridge.
- IPCC 2007. *Climate change 2007*. The IPCC Fourth Assessment Report AR4. Available at <http://www.ipcc.ch/>
- Jachmann, H. 1980. Population dynamics of the elephants in the Kasungu National Park, Malawi. *Netherlands Journal of Zoology* 30, 622–634.
- Jachmann, H. 1984. The ecology of the elephants in Kasungu National Park, Malawi, with specific reference to management of elephant populations in

- the Brachystegia biome of South Central Africa. Ph.D. thesis, University of Groningen, Groningen.
- Jachmann, H. 1986. Notes on the population dynamics of the Kasungu elephants. *African Journal of Ecology* 24, 215–226.
- Jachmann, H. 1988. Estimating age in African elephants: A revision of Laws' molar evaluation technique. *African Journal of Ecology* 26, 51–56.
- Jackson, T.P., S. Mosojane, S. Ferreira & R.J. van Aarde 2008. Solutions for elephant crop raiding in northern Botswana: moving away from symptomatic approaches. *Oryx* 42, 83–91.
- Joubert, D. 2006. Hunting behaviour of lions (*Panthera leo*) on elephants (*Loxodonta africana*) in the Chobe National Park, Botswana. *African Journal of Ecology* 44, 279–281.
- Junker, J., R.J. van Aarde & S.M. Ferreira 2008. Temporal trends in elephant *Loxodonta africana* numbers and densities in northern Botswana: is the population really increasing? *Oryx* 42, 58–65.
- Kinahan, A.A., S.L. Pimm & R.J. van Aarde 2007. Ambient temperature and landscape use in the savanna elephant (*Loxodonta africana*). *Journal of Thermal Biology* 32, 47–58.
- Kirkpatrick, J.F. 2007. Measuring the effects of wildlife contraception: The argument for comparing apples with oranges. *Reproduction, Fertility and Development* 19, 548–552.
- Lamprey, H.F., P.E. Glover, H.I.M. Turner & R.H.V. Bell 1967. Invasion of the Serengeti National Park by elephants. *African Journal of Ecology* 5, 151–166.
- Laws, R.M. 1966. Age criteria for the African elephant *Loxodonta a. africana*. *East African Wildlife Journal* 4, 1–37.
- Laws, R.M. 1969. The Tsavo research project. *Journal of Reproduction and Fertility Supplements* 6, 495–531.
- Laws, R.M., I.S.C. Parker & R.C.B. Johnstone 1975. *Elephants and their habitats: The ecology of elephants in North Bunyoro, Uganda*. Clarendon Press, Oxford.
- Lee, P.C. 1987. Allomothering among African elephants. *Animal Behaviour* 35, 278–291.
- Lee, P.C. & C.J. Moss. 1995. Statural growth in the African elephant (*Loxodonta africana*). *Journal of Zoology London* 236, 29–41.
- Leggett, K. 2006a. Home range and seasonal movement of elephants in the Kunene Region, northwestern Namibia. *African Zoology* 41, 17–36.

- Leggett, K. 2006b. Effect of artificial water points on the movement and behaviour of desert-dwelling elephants of north-western Namibia. *Pachyderm* 40, 40–51.
- Leuthold, W. 1977. Spatial organisation and strategy of habitat utilization of elephants in Tsavo National Park, Kenya. *Zeitschrift fur Saugetierkunde* 42, 358–379.
- Lewis, D.M. 1984. Demographic changes in the Luangwa Valley elephants. *Biological Conservation* 29, 7–14.
- Li, H. & J.F. Reynolds 1994. A simulation experiment to quantify spatial heterogeneity in categorical maps. *Ecology* 75, 2446–2455.
- Lindeque, M. 1988. Population dynamics of elephants in Etosha National Park, S.W.A./Namibia. Ph.D. thesis, University of Stellenbosch, Stellenbosch.
- Lindeque, M. 1991. Age structure of the elephant population in the Etosha National Park, Namibia. *Madoqua* 18, 27–32.
- Lindeque, M. & P.M. Lindeque 1991. Satellite tracking of elephants in northern Namibia. *African Journal of Ecology* 29, 196–206.
- Loveridge, A.J., J.E. Hunt, F. Murindagomo & D.W. Macdonald 2006. Influence of drought on predation of elephant (*Loxodonta africana*) calves by lions (*Panthera leo*) in an African wooded savannah. *Journal of Zoology* 270, 523–530.
- Mabunda, D. 2005. *Report to the Minister: Environmental Affairs and Tourism on developing elephant management plans for national parks with recommendations on the process to be followed*. SANParks, Pretoria. Available online at <http://www.sanparks.org/events/elephants/>.
- Mackey, R.L., B.R. Page, D. Duffy & R. Slotow 2006. Modelling elephant population growth in small, fenced, South African reserves. *South African Journal of Wildlife Research* 36, 33–43.
- Mbaiwa, J.E. & O.I. Mbaiwa 2006. The effects of veterinary fences on wildlife populations in Okavango Delta, Botswana. *International Journal of Wilderness* 13, 17–41.
- McComb, K., C. Moss, S. Sayaille & L. Baker 2000. Unusually extensive networks of vocal recognition in African elephants. *Animal Behaviour* 59, 1103–1109.
- McComb, K., C.J. Moss, S.M. Durant, L. Baker & S. Sayialel 2001. Matriarchs as repositories of social knowledge in African elephants. *Science* 292, 491–494.
- McComb, K., D. Reby, L. Baker, C. Moss & S. Sayaille 2003. Long distance communication of acoustic cues to social identity in African elephants. *Animal Behaviour* 65, 317–329.

- McComb, K., L. Baker & C. Moss 2006. African elephants show high level of interest in the skulls and ivory of their own species. *Biology Letters* 2, 26–28.
- McKnight, B. 2000. Changes in elephant demography, reproduction and group structure in Tsavo East National Park (1966–1994). *Pachyderm* 29, 15–24.
- Mills, M.G.L., H.C. Biggs & I.J. Whyte 1995. The relation between rainfall, lion predation and population trends in African herbivores. *Wildlife Research* 22, 75–88.
- Milner-Gulland, E.J. & R. Mace 1991. The impact of the ivory trade on the African elephant *Loxodonta africana* population as assessed by data from the trade. *Biological Conservation* 55, 215–229.
- Morley, R.C. 2005. The demography of a fragmented population of the savanna elephant (*Loxodonta africana* Blumenbach) in Maputaland. Ph.D. thesis, University of Pretoria, Pretoria.
- Morley, R.C. & R.J. van Aarde 2006. Estimating abundance for a savanna elephant population using mark-resight methods: A case study for the Tembe Elephant Park, South Africa. *Journal of Zoology, London* 271, 418–427.
- Morrison, T.A., P.I. Chiyo, C.J. Moss & S.C. Alberts 2005. Measures of dung bolus size for known-age African elephants (*Loxodonta africana*): Implications for age estimation. *Journal of Zoology, London* 266, 89–94.
- Moss, C.J. 1988. *Elephant memories: Thirteen years in the life of an elephant family*. William Morrow, New York.
- Moss, C.J. 2001. The demography of an African elephant (*Loxodonta africana*) population in Amboseli, Kenya. *Journal of Zoology, London* 255, 145–156.
- Moss, C.J. & J.H. Poole. 1983. Relationships and social structure of African elephants. In: R.A. Hinde (ed) *Primate Social Relations: An integrated approach*. Sinauer, New York, 315–325.
- Murwira, A. & A.K. Skidmore 2005. The response of elephants to the spatial heterogeneity of vegetation in a Southern African agricultural landscape. *Landscape Ecology* 20, 217–234.
- Nellemann, C., S.R. Moe & L.P. Rutina 2002. Links between terrain characteristics and forage patterns of elephants (*Loxodonta africana*) in northern Botswana. *Journal of Tropical Ecology* 18, 835–844.
- Njumbi, S., J. Waithaka, S. Gachago, J. Sakwa, K. Mwathe, P. Mungai, M. Mulama, H. Mutinda, P. Omondi & M. Litoroh 1996. Translocation of elephants: The Kenyan experience. *Pachyderm* 22, 61–65.
- Norton-Griffiths, M. 1978. *Counting animals*. AWLF, London.
- Ntumi, C.P., R.J. van Aarde, N. Fairall & W.F. de Boer 2005. Use of space and habitat use by elephants (*Loxodonta africana*) in the Maputo Elephant

- Reserve, Mozambique. *South African Journal of Wildlife Research* 35, 139–146.
- O'Connor, T.G., P.S. Goodman & B. Clegg 2007. A functional hypothesis of the threat of local extirpation of woody plant species by elephant in Africa. *Biological Conservation* 136, 329–345.
- Ogutu, J.O. & N. Owen-Smith 2003. ENSO, rainfall and temperature influences on extreme population declines among African savanna ungulates. *Ecology Letters* 6, 412–419.
- Osborn, F.V. 2004. The concept of home range in relation to elephants in Africa. *Pachyderm* 37, 37–44.
- Osborn, F.V. & G.E. Parker 2003. Towards an integrated approach for reducing the conflict between elephants and people: A review of current research. *Oryx* 37, 80–84.
- Ott, T. 2007. Landscape heterogeneity is a determinant of range utilization by African elephant (*Loxodonta africana*) in mesic savannas. MSc thesis, University of Pretoria, Pretoria.
- Ottichilo, W.K. 1987. The causes of the recent heavy elephant mortality in the Tsavo ecosystem, Kenya, 1975–80. *Biological Conservation* 41, 279–289.
- Owen, C-S. 2005. Is the supply of trophy elephants to the Botswana hunting market sustainable? MSc thesis, University of Cape Town, Cape Town.
- Owen-Smith, N. 1983. *Management of large mammals in African conservation areas*. Proceedings of a symposium held in Pretoria, South Africa, April 1982. Haum, Pretoria.
- Owen-Smith, R.N. 1988. *Mega herbivores: the influence of very large body size on ecology*. Cambridge University Press, Cambridge.
- Owen-Smith, N. 1990. Demography of a large herbivore, the Greater Kudu *Tragelaphus strepsiceros*, in relation to rainfall. *Journal of Animal Ecology* 59, 893–913.
- Owen-Smith, N. 1996. Ecological guidelines for waterpoints in extensive protected areas. *South African Journal of Wildlife Research* 26, 107–112.
- Owen-Smith, N., G.I.H. Kerley, B. Page, R. Slotow & R.J. van Aarde 2006. A scientific perspective on the management of elephants in the Kruger National Park and elsewhere. *South African Journal of Science* 102, 389–394.
- Parker, G.E. & F.V. Osborne 2001. Dual-season crop damage by elephants in eastern Zambezi Valley, Zimbabwe. *Pachyderm* 30, 49–56.
- Payne, K. 2003. Sources of social complexity in the three elephant species. In: F.B.M. de Waal & P.L. Tyack (eds) *Animal social complexity*. Harvard University Press, Cambridge, 57–85.

- Perdok, A.A., W.F. de Boer & T.A.E. Stout 2007. Prospects for managing African elephant population growth by immuno-contraception: a review. *Pachyderm* 42, 1–11.
- Pettorelli, N., J.O. Vik, A. Mysterud, J. Gaillard, C.J. Tucker & N.C. Stenseth 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology and Evolution* 20, 503–510.
- Pimm, S.L. & R.J. van Aarde. 2001. African elephants and contraception. *Nature* 411, 766.
- Pienaar, D. 2005. Water provision in the Kruger National Park. In: K.H. Rogers (ed.) *Elephants and biodiversity – a synthesis of current understanding of the role and management of elephants in savanna ecosystems*. SANParks, Skukuza, 227–234.
- Pienaar, U. de V., P. van Wyk & N. Fairall 1966. An aerial census of elephant and buffalo in Kruger National Park, and the implications thereof on intended management schemes. *Koedoe* 9, 40–107.
- Poole, J.H. & C.J. Moss 1989. Elephant mate searching: group dynamics and vocal and olfactory communication. In: P. Jewell & G. Maloiy (eds) *The biology of large African mammals in their environment: Symposia of the Zoological Society of London* Vol. 61, Clarendon, 111–125.
- Proaktor, G., T. Coulson & E.J. Milner-Gulland 2007. Evolutionary responses to harvesting in ungulates. *Journal of Animal Ecology* 76, 669–678.
- Pullin, A.S. & T.M. Knight 2005. Assessing conservation management evidence base: A survey of management-plan compilers in the United Kingdom and Australia. *Conservation Biology* 19, 1989–1996.
- Redfern, J.V., R. Grant, H. Biggs & W.M. Getz 2003. Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology* 84, 2092–2107.
- Reeve, R. 2006. Wildlife trade, sanctions and compliance: Lessons from the CITES regime. *International Affairs* 82, 881–897.
- Reilly, J. 2002. Growth in the Sumatran elephant (*Elephas maximus sumatranus*) and age estimation based on dung diameter. *Journal of Zoology, London* 258, 205–213.
- Said, S. & S. Servanty 2005. The influence of landscape structure on female roe deer home-range size. *Landscape Ecology* 20, 1003–1012.
- SANParks. 2005. *The great elephant indaba: finding an African solution to an African problem*. South African National Parks, Pretoria.
- Sankaran, M., N.P. Hanan, R.J. Scholes, J. Ratnam, D.J. Augustine, B.S. Cade, J. Gignoux, S.I. Higgins, X. le Roux, F. Ludwig, J. Ardo, F. Banyikwa, A. Bronn, G. Bucini, K.K. Caylor, M.B. Coughenour, A. Diouf, W. Ekaya,

- C.J. Feral, E.C. February, P.G.H. Frost, P. Hiernaux, H. Hrabar, K.L. Metzger, H.H.T. Prins, S. Ringrose, W. Seas, J. Tews, J. Worden & N. Zambatis 2005. Determinants of woody cover in African savannas. *Nature* 438, 846–849.
- Scoone, I. 1995. Exploiting heterogeneity: Habitat use by cattle in dryland Zimbabwe. *Journal of Arid Environments* 29, 221–237.
- Shrader, A.M., S.M. Ferreira, M.E. McElveen, P.C. Lee, C.J. Moss & R.J. van Aarde 2006a. Growth and age determination of African savanna elephants. *Journal of Zoology, London* 270, 40–48.
- Shrader, A.M. S.M. Ferreira & R.J. van Aarde 2006b. Digital photogrammetry and laser rangefinder techniques to measure African elephants. *South African Journal of Wildlife Research* 36, 1–7.
- Sikes, S.K. 1966. The African elephant, *Loxodonta africana*: A field method for the estimation of age. *Journal of Zoology, London* 150, 279–295.
- Sinclair, A.R.E. 2003. Mammal population regulation, keystone processes and ecosystem dynamics. *Philosophical Transactions of the Royal Society London* 358, 1729–1740.
- Sitati, N.W., M.J. Walpole, R.J. Smith & N. Leader-Williams 2003. Predicting spatial aspects of human-elephant conflict. *Journal of Applied Ecology* 40, 667–677.
- Slotow, R. & G. van Dyk 2001. Role of delinquent young 'orphan' male elephants in high mortality of white rhinos in Pilanesberg National Park, South Africa. *Koedoe* 44, 85–94.
- Slotow R. & G. van Dyk 2004. Ranging of older male elephants introduced to an existing small population without older males: Pilanesberg National Park. *Koedoe* 47, 91–104.
- Slotow, R., G. van Dyk, J. Poole, B. Page & A. Klocke 2000. Older bull elephants control young males. *Nature* 408, 425–426.
- Slotow, R., M.E. Garaï, B. Reilly, B. Page & R.D. Carr 2005. Population dynamics of elephants re-introduced to small fenced reserves in South Africa. *South African Journal of Wildlife Research* 35, 23–32.
- Smit, I.P.J., C.C. Grant & B.J. Devereux 2007a. Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park. *Biological Conservation* 136, 85–99.
- Smit, I.P.J., C.C. Grant & I.J. Whyte 2007b. Elephants and water provision: What are the management links? *Diversity and Distributions* 13, 666–669.
- Smuts, G.L. 1975. Reproduction and population characteristics of elephants in the Kruger National Park South Africa. *Journal of the Southern African Wildlife Management Association* 5, 1–10.

- Spong, G. & S. Creel. 2001. Deriving dispersal distances from genetic data. *Proceedings of the Royal Society London B* 268, 2571–2574.
- Steenkamp, G., S.M. Ferreira & M.N. Bester 2007. Tusklessness and tusk fractures in free-ranging African savanna elephants (*Loxodonta africana*). *Journal of the South African Veterinary Association* 78, 75–80.
- Stiles, D. 2004. The ivory trade and elephant conservation. *Environmental Conservation* 31, 309–321.
- Stokke, S. & J.T. du Toit 2002. Sexual segregation in habitat use by elephants in Chobe National Park, Botswana. *African Journal of Ecology* 40, 360–371.
- Sukumar, R., N.V. Joshi & V. Krisnamurthy 1988. Growth in the Asian elephant. *Proceedings of the Indian Academy of Sciences* 97, 561–571.
- Thouless, C.R. 1995. Long distance movements of elephants in northern Kenya. *African Journal of Ecology* 33, 321–334.
- Tufto, J., R. Anderson & J. Linnell 1996. Habitat use and ecological correlates of home range size in a small cervid: the roe deer. *Journal of Animal Ecology* 65, 715–724.
- Turnbull, P.C., R.H. Bell, K. Saigawa, F.E. Munyenyembe, C.K. Mulenga & L.H. Makala 1991. Anthrax in wildlife in the Luangwa Valley, Zambia. *The Veterinary Record* 128, 399–403.
- Van Aarde, R., I. Whyte & S. Pimm 1999. Culling and dynamics of the Kruger National Park African elephant population. *Animal Conservation* 2, 287–294.
- Van Aarde, R.J., T. Jackson & D.G. Erasmus 2005. Assessment of seasonal home-range use by elephants across southern Africa's seven elephant clusters. Unpublished Report. Conservation Ecology Research Unit, Peace Parks Foundation, University of Pretoria. Available on <http://www.up.ac.za/academic/zoology/ceru/Home.htm>.
- Van Aarde, R.J., T.P. Jackson & S.M. Ferreira 2006. Conservation science and elephant management in southern Africa. *South African Journal of Science* 102, 385–388.
- Van Aarde, R.J. & T. Jackson 2007. Megaparks for metapopulations: Addressing the causes of locally high elephant numbers in South Africa. *Biological Conservation* 134, 289–297.
- Van Jaarsveld, A.S., A.O. Nicholls & M.H. Knight 1999. Modelling and assessment of South African elephant *Loxodonta africana* population persistence. *Environmental Modelling and Assessment* 4, 155–163.
- Van Wyk, P. & N. Fairall 1969. The influence of the African elephant on the vegetation of the Kruger National Park. *Koedoe* 12, 57–89.

- Verlinden, A. & I.K.N. Gavor 1998. Satellite tracking of elephants in northern Botswana. *African Journal of Ecology* 36, 105–116.
- Viljoen, 1988. The ecology of the desert-dwelling elephants *Loxodonta africana* (Blumenbach, 1797) of Western Damaraland and Kaokoland. Ph.D. thesis (Wildlife Management), University of Pretoria, Pretoria.
- Walker, B.H., R.H. Emslie, R.N. Owen-Smith & R.J. Scholes 1987. To cull or not cull: Lessons from a southern African drought. *Journal of Applied Ecology* 24, 381–401.
- Wall, J., I. Douglas-Hamilton, & F. Vollrath 2006. Elephants avoid costly mountaineering. *Current Biology* 16, 527–529.
- Wasser, S.K.C., R. Mailand, B. Booth, E. Mutayoba, B. Kisamo, B. Clark & M. Stephens 2007. Using DNA to track the origin of the largest ivory seizure since the 1989 trade ban. *Proceedings of the National Academy of Science, U.S.A.* 104, 4228–4233.
- Western, D. 1975. Water availability and its influence on the structure and dynamics of a large mammal community. *East African Wildlife Journal* 13, 265–286.
- Western, D., C. Moss & N. Georgiadis 1983. Age estimation and population age structure of elephants from footprint dimensions. *Journal of Wildlife Management* 47, 1192–1197.
- Western, D. & W.K. Lindsay 1984. Seasonal herd dynamics of a savanna elephant population. *African Journal of Ecology* 22, 229–244.
- Whitehouse, A.M. & A.J. Hall-Martin 2000. Elephants in Addo Elephant National Park, South Africa: Reconstruction of the population's history. *Oryx* 34, 46–55.
- Whyte, I.J. 2001. Conservation management of the Kruger National Park elephant population. Ph.D. thesis, University of Pretoria, Pretoria.
- Whyte, I.J. 2004. Ecological basis of the new elephant management policy for Kruger National Park and expected outcomes. *Pachyderm* 36, 99–108.
- Whyte, I.J. & D. Grobler 1997. *The current status of contraception research in the Kruger National Park*. Scientific report 13/97. National Parks Board, Skukuza.
- Whyte, I. J., R.J. van Aarde, R.J. & S.L. Pimm 1998. Managing the elephants of Kruger National Park. *Animal Conservation* 1, 77–83.
- Whyte, I.J., R.J. van Aarde & S.L. Pimm 2003. Kruger elephant population: its size and consequences for ecosystem heterogeneity. In: J.T. du Toit, K.H. Rogers & H.C. Biggs (eds) *The Kruger experience: Ecology and management of savanna heterogeneity*. Island Press, Washington, 332–348.

- Wittemyer, G., I. Douglas-Hamilton & W.M. Getz 2005a. The socioecology of elephants: Analysis of the processes creating multitiered social structures. *Animal Behaviour* 69, 1357–1371.
- Wittemyer, G., D. Daballen, H. Rasmussen, O. Kahindi & I. Douglas-Hamilton 2005b. Demographic status of elephants in the Samburu and Buffalo Springs National Reserves, Kenya. *African Journal of Ecology* 43, 1365–2028.
- Wittemyer, G. & W.M. Getz 2007. Hierarchical dominance structure and social organization in African elephants, *Loxodonta africana*. *Animal Behaviour* 73, 671–681.
- Wittemyer, G., W.M. Getz, F. Vollrath & I. Douglas-Hamilton 2007a. Social dominance, seasonal movements, and spatial segregation in African elephants: A contribution to conservation behavior. *Behavioral Ecology and Sociobiology* 61, 1919–1931.
- Wittemyer, G., A. Ganswindt & K. Hodges 2007b. The impact of ecological variability on the reproductive endocrinology of wild female African elephants. *Hormones and Behaviour* 51, 346–354.
- Wittemyer, G., H.B. Rasmussen & I. Douglas-Hamilton 2007c. Breeding phenology in relation to NDVI variability in free-ranging African elephant. *Ecography* 30, 42–50.
- Woodd, A.M. 1999. A demographic model to predict future growth of the Addo elephant population. *Koedoe* 42, 97–100.
- Young, E. 1970. Water as faktor in die ekologie van wild in die Nasionale Krugerwildtuin. Ph.D. thesis, University of Pretoria, Pretoria.
- Young, K.D., S.M. Ferreira & R.J. van Aarde 2008. The influence of increasing population size and vegetation productivity on elephant distribution in the Kruger National Park. *Austral Ecology* (accepted).