

Environmental stochasticity and African elephant population dynamics: investigating limitation through juvenile mortality

By

Leigh-Ann Woolley

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ABSTRACT

The successful conservation management of African elephants depends largely on understanding the fundamental processes driving the population regulation of this species. Southern Africa's increasing populations have raised concern over the impact of high elephant densities on the system, in stark contrast against the elephant's more precarious position in other parts of Africa. As we search for solutions from the processes of historical elephant regulation, we realise that there is a decided lack of empirical evidence to explicitly direct our efforts. In this PhD, I attempt to investigate the application of the classic pattern of large herbivore population limitation, which mainly involves high juvenile mortality in response to stochastic environmental events, to African elephant population dynamics. Firstly, I evaluated the magnitude and frequency of mortality events that would be required to prevent elephant population growth. The death of 85 % of infants and weaned calves would need to occur twice a generation, while a single severe mortality event (causing the death of all infants and weaned calves and 10 % of the rest of the population) once a generation would be sufficient. However, the severity of these events is not matched in natural occurrence in Africa today and only a single recorded event in Tsavo National Park, Kenya, in the 1970's has come close when more than 7 000 died during a very severe drought. Secondly, I evaluated the potential role of fire as a stochastic, mass-mortality event limiting elephant populations. I found that fire functions in a similar manner to other environmental catastrophes and primarily causes high juvenile mortality. However, this catastrophic event also highlighted the extreme behavioural and physiological impacts experienced by the elephant population involved. The potential role of these types of events on long-term female fecundity needs further investigation. In isolation, this type of mortality event would need to occur with high frequency to prevent population growth. However, in combination with a decrease in female fecundity, these stochastic events may have a much greater impact on population demography than first thought. Thirdly, I investigated a potential mechanistic link between stochastic mortality events and juvenile susceptibility to resource limitation. Allometric relationships dictate that juveniles select a diet of higher quality than adult elephants. We found that this was achieved by weaned calf selection of higher quality plant parts, although use of plant types and plant species was similar to that of adult females, who they move across the landscape with. The strong sexual dimorphism exhibited by this species was reflected in adult male use of lower quality

forage than adult females (or juveniles) in both dry and wet seasons. Diet quality scaled negatively with body size, but adult females consistently selected a higher quality diet than adult males, irrespective of body size. The nutritional and reproductive demands placed on an individual during different life-history stages therefore influence foraging strategies, together with nutrient requirements, e.g. phosphorus for pregnancy/lactation selected consistently by females when unrestricted in the wet season, protein for growth selected consistently by weaned calves. Competitive displacement of adult females to feed at higher levels in the canopy by calves also influenced feeding behaviour. Therefore intraspecific body size, nutritional requirements (in terms of nutrients and energy) and competition had a strong influence on foraging strategy employed by age-sex classes of elephants in response to seasonal environmental change. More selective juvenile foraging requirements means that juveniles are most susceptible to resource limitation, for example during stochastic environmental events such as droughts. In small, closed systems, juvenile mortality is likely to have a strong influence on elephant population regulation, with a slight, temporary decrease in female fecundity possibly acting in conjunction with juvenile mortality effects. Therefore, stochastic environmental events such as drought and fire may be the only natural incidence of population regulation to occur in these systems, where populations continue to grow exponentially and there is no evidence of density-dependence (as in the case of many small, fenced reserves in South Africa). In large, open, high-density systems in other parts of southern Africa, density dependence acts strongly on female fecundity and causes low levels of juvenile mortality in areas of local population aggregation. Therefore, in isolation, natural juvenile mortality is unlikely to regulate African elephant populations, but in conjunction with decreased female fecundity in response to density-dependent feedbacks and stochastic environmental events, population regulation may occur. The management of long-lived megaherbivore species with similar demographic drivers must include an appreciation of the complexity of population response to manipulation of mortality or fecundity effects. Small changes can potentially result in large shifts in population dynamics. Further insight into the mechanisms driving these processes will allow sound scientific support of megaherbivore management decisions to be made throughout Africa.

PREFACE

The dissertation includes four paper manuscripts, prepared for submission to different scientific peer-reviewed journals (as indicated on the title page of each chapter). Styles and formatting of these chapters follow the respective journal requirements. This results in some duplication in study site description and methods between chapters. A single reference list was compiled for the general introduction (Chapter 1) and synthesis (Chapter 6) and follows after Chapter 6.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any tertiary institution. Where use has been made of the work of others it is duly acknowledged in the text.

All fieldwork was carried out in Pilanesberg National Park in the North West Province of South Africa, through the School of Biological and Conservation Sciences, University of KwaZulu-Natal, Westville from September 2003 to March 2006.

This work was performed under the supervision of Prof. Rob Slotow and the co-supervision of Mr. Bruce Page.

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DECLARATION 1 - PLAGIARISM

I, Leigh-Ann Woolley, declare that:

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. This thesis has not been submitted for any degree or examination at any other university.
3. This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.
4. This thesis does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:
 - a. Their words have been re-written but the general information attributed to them has been referenced
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DECLARATION 2 - PUBLICATIONS

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis (include publications in preparation, submitted, *in press* and published and give details of the contributions of each author to the experimental work and writing of each publication) .

Publication 1

Woolley, L.-A., Mackey, R.L., Page, B.R., Slotow, R. 2008a. Modelling the effect of age-specific mortality on African elephant population dynamics: can natural mortality provide regulation? *Oryx* 42: 49–57.

Author contributions:

LAW constructed simulations, processed and analyzed data, designed and wrote paper. RLM contributed to model and simulation design, and provided valuable manuscript comments. BRP created population model, and provided valuable comments to manuscript. RS contributed to design of paper and provided valuable comments to manuscript.

Publication 2

Woolley, L.-A., Millsaugh, J.J., Woods, R.J., Janse van Rensburg, S., Mackey, R.L., Page, B.R. & Slotow, R. 2008b. Population and individual elephant response to a catastrophic fire in Pilanesberg National Park. *PLoS ONE* 3: e3233. doi:10.1371/journal.pone.0003233

Author contributions:

LAW conceived and designed paper, collected and analyzed data, and wrote paper. JJM and RJW processed faecal samples for glucocorticoid metabolites and contributed valuable comments to the manuscript. SJvR assisted in field collection of data. RLM contributed to statistical analysis of data and manuscript comments. BRP contributed valuable comments to the manuscript. RS contributed to paper conception and design, and added valuable comments to manuscript.

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Author contributions:

LAW conceived and designed paper, collected and analyzed data, and wrote paper. JJM and RJW processed faecal samples for glucocorticoid metabolites and contributed valuable comments to the manuscript. SJvR assisted in field collection of data. BRP and RS contributed valuable comments to the manuscript.

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Woolley, L.-A., Page, B.R. & Slotow, R. (Submitted manuscript). Foraging strategy within African elephant family units: why body size matters.

Prepared for submission to *Ecosystems*.

Author contributions:

LAW conceived and designed paper, collected and analyzed data, and wrote paper. BRP and RS contributed to study design, methods of data analysis and added valuable comments to the manuscript.

Signed:

Leigh-Ann Woolley

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Chapter 1

General Introduction

Historically, the African elephant (*Loxodonta africana*) occurred throughout sub-Saharan Africa (Blanc *et al.*, 2007). However, at the turn of the twentieth century, elephants were in decline throughout their former range, primarily due to human impact (e.g. ivory hunting (Parker, 2004), and loss of habitat to agriculture (Milner-Gulland & Beddington, 1993)). Currently elephants are distributed across the continent ranging from small, fragmented populations in West Africa, to large, relatively undisturbed free-ranging populations in eastern, central and southern Africa (Blanc *et al.*, 2007; Carruthers *et al.*, 2008).

Southern Africa has the highest number of elephants and accounts for the largest extent of elephant range in Africa, making up 39% of total range area (Blanc *et al.*, 2007). Most of southern Africa's elephants survive within national parks, the majority being unfenced (typical for Botswana, Namibia, Zambia, Zimbabwe and Mozambique), but South Africa has many small ($< 1000 \text{ km}^2$), fenced reserves containing elephants (Slotow *et al.*, 2005). The Kruger National Park in South Africa is home to most ($\sim 15\,000$) of the country's elephants (Carruthers *et al.*, 2008).

Elephant numbers have increased steadily in southern Africa to the point that conservation authorities are concerned with the impact of high numbers of elephant (Kerley *et al.*, 2008), motivating the debate over the control of elephant population size in some places (Mabunda, 2005; Owen-Smith *et al.*, 2006; Biggs *et al.*, 2008). Here the impact of high elephant densities lies in stark contrast against the elephant's more precarious status beyond southern Africa (IUCN status Low Concern in southern Africa, Vulnerable rest of Africa (Blanc *et al.*, 2008); Baxter & Getz, 2005; Owen-Smith *et al.*, 2006). The debate centres on the complexity and uncertainty surrounding long-term elephant population dynamics, the recovery-impact cycles between elephants and their forage resources, the impact of elephants on other species and the appropriate methods of elephant management (Mabunda, 2005; Owen-Smith *et al.*,

2006; Biggs *et al.*, 2008; Kerley *et al.*, 2008). The ‘elephant problem’ has arisen in conjunction with the expansion of human activity and settlements across the landscape and there is concern that the ecosystems containing elephants, and the people that live adjacent to elephant populations, are becoming increasingly threatened by possibly irreversible elephant impact on the system (Caughley, 1976; Biggs *et al.*, 2008; Carruthers *et al.*, 2008; Kerley *et al.*, 2008; Twine & Magome, 2008). There is thus an urgency about the need for scientific consensus and ultimately a future course of action for the management of elephants in the southern African region (Biggs *et al.*, 2008; Kerley *et al.*, 2008).

The African elephant is the largest extant terrestrial mammal and classified as a megaherbivore of body size in excess of 1 ton (Owen-Smith, 1988). Their large body size makes the scale of their impact on the ecosystem large and may result in changes to vegetation and biodiversity (Kerley *et al.*, 2008). Elephants can thus be considered as a keystone species (Power *et al.*, 1996; Sinclair, 2003), a term that is often extended to ‘ecological engineers’ (Jones *et al.*, 1994). This implies that their removal or significant increase in a system may have consequences for other components (Mills *et al.*, 1993). Elephants have the potential to significantly alter their environment which can have far-reaching consequences, for example their contributions can range from plant seed dispersal (Kerley & Landman, 2006) to tree mortality (Landman *et al.*, 2008), as well as increased availability of forage for other species (Smallie & O’Connor, 2000; Skarpe *et al.*, 2004; Makhabu *et al.*, 2006), the excavation of waterholes in dry riverbeds (Conybeare & Haynes, 1984), and the creation of refugia for invertebrates under toppled tree trunks (Govender, 2005). An increase in elephant population size can amplify these impacts, especially in closed systems where spatial and temporal variation in impacts is reduced (Kerley *et al.*, 2008). Therefore any management decisions must take all possible ecosystem impacts into account.

In South Africa, elephant management philosophies have changed over time from an initial focus on species preservation to the stabilization of animal numbers (carrying-capacity paradigm), which involved the manipulation of artificial waterpoints and elephant culling practices (e.g. van Wyk & Fairall, 1969; Whyte *et al.*, 1998, Biggs *et al.*, 2008). Scientific consensus shifted thereafter to recognize heterogeneity and variability as an integral part of ecosystem dynamics and focus shifted from managing population numbers to the consideration of entire ecosystems (Bradshaw & Bekoff, 2001; Meffe *et al.*, 2002; Biggs &

Rogers, 2003; Biggs *et al.*, 2008). The control of elephant populations by culling has been under moratorium since the mid-1990's (Slotow *et al.*, 2008). However, scientific uncertainty persists as there is no long-term empirical evidence of the consequences of high elephant densities (Owen-Smith *et al.*, 2006; Kerley *et al.*, 2008; Biggs *et al.*, 2008).

A key uncertainty that emerges is what limits populations naturally, and whether this limitation will occur at the same levels in human modified systems (e.g. with fences or artificial water) compared to natural systems (Owen-Smith *et al.*, 2006). The regulation of elephant populations living in variable environments governed by climate-driven environmental stochasticity remains poorly understood. Therefore it is difficult to predict when and how elephant populations may self-regulate if resources are limited (Owen-Smith *et al.*, 2006; van Aarde *et al.*, 2008; Slotow *et al.*, 2008). The processes driving elephant population dynamics would provide valuable insight upon which management decisions could be based. Inferences can be drawn, however, from the consequences of past management practices (e.g. culling, translocation) on elephant population dynamics, as well as scientific knowledge of the processes active in the regulation of other large herbivore populations.

All South African elephant populations have been managed in some way due to their containment within fences (Bertshinger *et al.*, 2008; Grant *et al.*, 2008; Grobler *et al.*, 2008; Slotow *et al.*, 2008; van Aarde *et al.*, 2008), while other unfenced populations in Africa have had relatively little management interference (Carruthers *et al.*, 2008). South Africa has seen a faster increase in elephant populations (i.e. higher growth rates), with less variability in growth rates, than that of populations elsewhere in Africa (van Jaarsveld *et al.*, 1999; Slotow *et al.*, 2005; Mackey *et al.*, 2006; van Aarde *et al.*, 2008). Therefore, management efforts seem to have created conditions promoting high elephant population growth, possibly due to high resource (e.g. water) supply, protection from poaching and the prevention of dispersal which forces locally high elephant densities (Slotow *et al.*, 2005; Mackey *et al.*, 2006; Grant *et al.*, 2008; van Aarde *et al.*, 2008).

Original decisions taken throughout Africa to cull elephants were made according to the perceived impact of high elephant numbers on the vegetation of an area (e.g. Pienaar *et al.*, 1966; van Wyk & Fairall, 1969; Laws *et al.*, 1975; Bell, 1983). However, culled populations

generally show a trend of maximum population growth post-culling (van Aarde & Jackson, 2007; Slotow *et al.*, 2008). The reduction in density seems to increase population growth rate by releasing vital rates from density-dependent limitations, thereby maximising reproductive potential (Whyte *et al.*, 1998; van Aarde *et al.*, 1999; Slotow *et al.*, 2008). However, high growth rates in post-cull populations could also be ascribed to these populations still being far from the ecological carrying capacity set by resource limitation levels (Fowler, 1981; Owen-Smith *et al.*, 2006). The growth phase post-cull inevitably leads to a population bias towards young individuals (e.g. Coulson *et al.*, 2004; White *et al.*, 2007; Mackey *et al.*, in press). These skewed population age structures can result in high growth rates (Mackey *et al.*, 2006). It has also been suggested that the skewed population age structure of many of the South African populations, either as founder-effects or as a result of culling operations, holds the population in a state of eruptive growth where populations overshoot their natural limits due to population response inertia (Caughley, 1970; Forsyth & Caley, 2006; Slotow *et al.*, 2008; Mackey *et al.*, in press). Where stable age structure is present, density dependence acts to constrain population growth over the long-term where a decline in key limiting resources causes a subsequent decline in the population through limit cycles (Caughley, 1970).

Similarly, newly established populations from translocation operations also show extremely high growth rates (Slotow *et al.*, 2005; Mackey *et al.*, 2006), well beyond the maximum rate of increase predicted by birth and death rates for confined elephant populations (Calef, 1988; van Aarde *et al.*, 1999). A population comprised of many young fecund females can result in abnormally high growth rates through synchronised calving and very low mortality rates ascribed to unstable population structures, where mortality from old age is not initially present and juvenile mortality is prevented due to high resource availability (Mackey *et al.*, 2006; van Aarde *et al.*, 2008). Theoretically, as these populations age and stable structures are established, population growth rates would decline (Mackey *et al.*, 2006; Mackey *et al.*, in press). Therefore the manipulation of elephant population structure can have a profound effect on the mechanisms of natural limitation. Past management actions highlight the complexity of the processes involved in elephant population dynamics and, in fact, the sensitivity of the mechanisms of natural limitation to perturbation (Owen-Smith *et al.*, 2006; Slotow *et al.*, 2008; van Aarde *et al.*, 2008).

The population dynamics of herbivore populations is dictated by the difference between births, deaths, emigration and immigration, with the vital rates of the population (e.g. age at sexual maturity, conception rate, gestation period, inter-birthing interval) influencing its fecundity, growth potential and turnover or generation time (Fowler, 1981; Gaillard *et al.*, 2000). Some species may be resource limited, displaying density-dependent responses (Coulson *et al.*, 2001). Others may be top-down limited by predators (Owen-Smith *et al.*, 2005). Long-lived species may also be limited by stochastic environmental events (e.g. drought, flood, fire, disease) which can cause sudden and significant shifts in population size and dynamics over a very short time, if the effects of such impacts on the demographics of the population are of sufficient frequency and intensity (Mangel & Tier, 1994; Clutton-Brock *et al.*, 1997; Saether, 1997; Gaillard *et al.*, 1998; Turner & Vale, 1998; Saether *et al.*, 2002; Bull & Bonsall, 2008). In large, predator-free herbivore systems, population growth is most sensitive to adult survivorship, but high temporal variation in juvenile survival typically drives variability in population growth rates both during stochastic environmental events and density-dependent situations (Gaillard *et al.*, 1998, 2000; Owen-Smith & Mason 2005). In long-lived vertebrates, density-dependent feedbacks affect juvenile survival first, then age at first breeding, adult fecundity and adult survival (Eberhardt, 1977, 2002; Gaillard *et al.*, 1998). Typically, environmental variability affects juvenile survival most considerably (Saether, 1997; Gaillard *et al.*, 1999, 2000; Owen-Smith *et al.*, 2005). Therefore, general patterns identified for large mammalian herbivores suggest that juvenile survival is the key factor responsible for fluctuations in population size.

As in other large herbivore populations, elephant population dynamics seems closely tied to resource limitation (e.g. Fritz *et al.*, 2002) and variation in recruitment is driven by a combination of environmental stochasticity and population density effects (Wittemyer *et al.*, 2007; Chamaillé-Jammes *et al.*, 2008; van Aarde *et al.*, 2008). The mechanisms of population regulation are thought to involve both female fecundity and juvenile mortality in response to temporal variation in resource availability and quality, with seasonal variation affecting female reproductive outputs such as ovulation and conception (Wittemyer *et al.*, 2007), and severe environmental perturbation (e.g. drought) resulting in high juvenile mortality (Dudley *et al.*, 2001; Moss, 2001; Foley *et al.*, 2008) and decreased female fecundity (*cf* Leggatt, 2003). Although mortality rates are very important in determining population persistence, resource availability dictated by stochastic environmental events (e.g. drought) or population

density also affect vital rates (van Aarde *et al.*, 2008), for example female elephant conception rates varied with primary productivity in Kenya (Wittemyer *et al.*, 2007).

The natural limitation of elephant populations is therefore likely to be driven by processes affecting vital rates (Wittemyer *et al.*, 2007), and/or resulting in mortalities (Moss, 2001; Dudley *et al.*, 2001; Wittemyer *et al.*, 2005; Foley *et al.*, 2008), as well as temporal and spatial factors affecting emigration and immigration (Junker *et al.*, 2008; Chamaillé-Jammes *et al.*, 2008). In the fenced reserves of South Africa, natural emigration and immigration are removed, emphasising the role of mortality and fecundity in the potential growth of these populations (Slotow *et al.*, 2005; Mackey *et al.*, 2006).

Although density influences on population growth are ultimately inevitable (Sinclair, 2003), there is a lack of evidence to dispel the uncertainty surrounding the exact stage at which elephant populations will respond in systems differing in rainfall and habitat conditions (Gough & Kerley, 2006; Junker *et al.*, 2008; Chamaillé-Jammes *et al.*, 2008). Large-bodied herbivore populations seem to maintain near-maximal growth rates even when very near to the limits set by forage resources (Fowler & Smith, 1973; Fowler, 1981). Therefore, it is difficult to predict when and how density-dependent feedbacks will occur in elephant populations.

Most evidence suggests that some South African populations may be showing slight reproductive impacts in response to high elephant densities (van Aarde *et al.*, 1999; van Jaarsveld *et al.*, 1999), but others show no evidence of density dependence (van Jaarsveld *et al.*, 1999; Gough & Kerley, 2006). It has been suggested that the free-ranging populations in Botswana and Zimbabwe may be showing signs of density dependence (Junker *et al.*, 2008; Chamaillé-Jammes *et al.*, 2008), but in these regions high elephant densities are either countered by dispersal (Junker *et al.*, 2008) or density-dependent feedbacks act at elephant densities exceeding 2 km^{-2} (Chamaillé-Jammes *et al.*, 2008), suggesting that natural limitation through density dependence may only occur at very high elephant densities. This is possibly due to the lag in population level response in vital rates to the resource restriction imposed by high densities of elephants, due to the characteristic life history traits of this species, i.e. long generation times, low annual fecundity, high survival rates (Laws *et al.*, 1975; Moss, 2001; Wittemyer *et al.*, 2007).

In contrast to changes in vital rates, mortality responses to stochastic environmental events are immediate (Dudley *et al.*, 2001; Moss, 2001; Wittemyer *et al.*, 2005; Foley *et al.*, 2008; Valeix *et al.*, 2008; Woolley *et al.*, 2008b). However, as a single mechanism acting alone on the population, the levels of mortality and the frequency of these events required to prevent population growth may need to be very high and/or very frequent to facilitate population regulation (Woolley *et al.*, 2008a). Population fluctuations in large herbivore systems are closely tied to climatic variation which influences resource availability (Saether, 1997; Post & Stenseth, 1999; Gaillard *et al.*, 2000). In particular, variability in dry season rainfall has an underlying influence on the population dynamics of large herbivores in semi-arid savannas (Mduma *et al.*, 1999; Dudley *et al.*, 2001; Ogutu & Owen-Smith, 2003; Dunham *et al.*, 2004; Foley *et al.*, 2008; Valeix *et al.*, 2008). Although historical evidence is lacking, it is known that environmental events such as drought increase elephant mortality rates (Corfield, 1973; Moss, 2001; Dudley *et al.*, 2001; Wittemyer *et al.*, 2005; Foley *et al.*, 2008), although large-scale die-offs are rare (e.g. Corfield, 1973). Lower levels of drought mortality may occur approximately once a generation and mainly involves juveniles (e.g. Moss, 2001; Dudley *et al.*, 2001; Foley *et al.*, 2008). In other large herbivore populations, predation on the adult segment can cause dramatic shifts in population dynamics (e.g. Owen-Smith & Mason, 2005), and in combination with stochastic environmental events such as disease outbreaks (e.g. Gasaway *et al.*, 1996) or drought (e.g. Walker *et al.*, 1987; Owen-Smith & Mason, 2005) can result in population regulation or decline. Large herbivore population dynamics can be strongly influenced by single mortality events, but the strength of impact depends on where mortality acts, i.e. the age-sex classes most affected, with adult female mortality having the greatest effect (Gaillard *et al.*, 1998, 2000; Saether, 1997; Ogutu & Owen-Smith, 2005; Owen-Smith & Mason, 2005; Owen-Smith *et al.*, 2005).

As in other large herbivore populations, natural mortality in large, well-established, free-ranging elephant populations is age-dependent, with the youngest being most susceptible to dry season impacts (Moss, 2001; Dudley *et al.*, 2001; Foley *et al.*, 2008). For example, in Tarangire National Park, Tanzania, 20 % of calves died within a nine month period in a severe drought in 1993 (Foley *et al.*, 2008). In this case, the sex of the calf had an important influence on survival, with highest occurrence of male calf mortality, while the experience of mothers also influenced calf mortality (Foley *et al.*, 2008). In the lowveld of Zimbabwe, all

calves under eight years of age died during a drought between 1991 and 1993 (Leggatt, 2003), and a drought in 1994 killed 5 – 9 % of the elephant population of Hwange National Park, Zimbabwe, with the highest frequency of mortality occurring in the youngest age class (Dudley *et al.*, 2001). Elephants in some parts of the Kalahari Sands region of Hwange National Park dig craters to reach water during the dry season and droughts (Weir, 1971). Mortality in the youngest age-classes in 1994 was also influenced by whether elephants could reach this water (Dudley *et al.*, 2001). Whereas nursing calves can rely on milk for hydration, juvenile weaned calves died from dehydration when the water table dropped below the level reachable by their trunks (Conybeare & Haynes, 1984). High juvenile mortality during resource restriction can cause discriminate age-group mortalities and subsequent gaps in age distribution (Moss, 2001; Dudley *et al.*, 2001; Foley *et al.*, 2008). The exact mechanisms driving juvenile elephant mortality have not been investigated, but it could be linked to body size influences on resource (food and water) requirements. The physiological mechanisms triggering the increased susceptibility of juvenile red kangaroos (*Macropus rufus*) to resource limitation during drought have been linked to relative energy requirements and the allometric scaling of diet quality (Munn & Dawson, 2006; Munn *et al.*, 2006).

Temporal variation in resource availability due to seasonal environmental change limits the quantity and quality of resources available to elephants (Owen-Smith, 1988). Free-ranging African elephants in deciduous semi-arid savannas respond to temporal heterogeneity in food availability and quality by switching the composition of their diet from predominantly grass in the wet, summer season to browse in the dry, winter season (Owen-Smith, 1988; Cerling *et al.*, 2006; Kos *et al.*, in press). Protein and energy gains are maximised through ingestion of forage at the first flush of new growth (van Soest, 1996; Scholes, 2003).

The ability of different age and sex classes to cope with this type of environmental stochasticity varies mainly due to body size influences on physiology. The higher tolerance of large-bodied herbivores to lower quality diets has been used to explain differences between species of different body size (e.g. Demment & van Soest, 1985; du Toit & Owen-Smith, 1989; Clauss & Lechner-Doll, 2001), as well as sexual dimorphism in ungulates (e.g. Beier, 1987; du Toit, 1995) and the African elephant (Stokke & du Toit, 2000), where it was shown that smaller-bodied adult females selected a diet of higher quality than large-bodied adult males. Increased nutritional demands imposed on adult females by pregnancy and/or lactation

means that adult male and female elephants of similar body size are likely to have differing nutritional requirements (van Soest, 1996).

As a megaherbivore species, the African elephant provides us with a model of population regulation applicable to other megaherbivores (e.g. white rhino (*Ceratotherium simum*), black rhino (*Diceros bicornis*), hippopotamus (*Hippopotamus amphibious*), giraffe (*Giraffa camelopardalis*)) operating in similar systems where extrinsic factors, such as the effects of resource limitation on survival and fecundity, act to regulate populations (Owen-Smith, 1988). In these large, long-lived species similar population processes function to regulate populations, with wide fluctuation in juvenile survival in response to both stochastic environmental variation and changes in population density, and displays of cyclic variability associated with environmental conditions and predation effects (Owen-Smith, 1988; Ogotu & Owen-Smith, 2005; Owen-Smith & Mason, 2005; Owen-Smith *et al.*, 2005). Predation may play a greater role in the dynamics of smaller species (e.g. giraffe), where mortality from predation, especially by lions (*Panthera leo*), features more strongly than it does for elephants (e.g. Ogotu & Owen-Smith, 2005).

Aims and objectives

This dissertation attempts to fill some of the gaps in our empirical knowledge of the mechanisms and consequences of elephant population regulation driven by stochastic environmental events.

Specifically I investigate:

- (1) where mortality needs to act to regulate elephant populations (i.e. magnitude and frequency of age-specific mortality);
- (2) the potential role of fire as a stochastic, mass-mortality event; and
- (3) why juveniles (especially weaned calves) are more susceptible to stochastic environmental restriction, given body size influences on diet quality requirements.

Where appropriate, the behaviour and physiology of individual elephants and the population as a whole were integrated into assessments of population dynamics and intraspecific responses to temporal variation in resource availability.

Findings will attempt to extend our broader knowledge base beyond known generalizations of demographic processes driving large herbivore population dynamics to reveal the potential role of stochastic environmental events, together with possible causes of juvenile mortality. The successful conservation management of the African elephant, as well as other megaherbivore species with similar demographic drivers, hinges on understanding these types of fundamental population processes and their particular contribution to natural population regulation. Management decisions can be taken to augment these natural processes, in that way ensuring species survival within a system in accordance with specific conservation objectives.

The four chapters hereafter are constructed as paper manuscripts, submitted to scientific, peer-reviewed journals. Each addresses the main aims outlined above. In Chapter 2 (published *Oryx* 42(1): 49-57) I used a population model to simulate mortality events for the evaluation of the magnitude and frequency of age-specific mortalities required to prevent elephant population growth. In Chapter 3 (published *PLoS ONE* 3(9): e3233. doi: 10.1371/journal.pone.0003233), elephant response to a catastrophic fire is assessed on a behavioural, physiological and demographic basis. In Chapter 4 (in press *Journal of Wildlife Management*) elephant diet quality differences are investigated according to sex and body size, to assess disparities in age-specific susceptibility to forage quality restriction. In Chapter 5 (prepared for submission to *Ecosystems*) I compare the seasonal foraging strategies employed by adult females and weaned calves within the elephant family unit to evaluate potential impacts on juveniles during times of nutritional stress. Chapter 6 is a general discussion of the findings and implications of Chapters 2 – 5.

Chapter 2

Modelling the effect of age-specific mortality on African elephant

***Loxodonta africana* populations: can natural mortality provide regulation?**

Leigh-Ann Woolley *, Robin L. Mackey, Bruce R. Page and Rob Slotow

*School of Biological and Conservation Sciences, University of KwaZulu-Natal, Howard
College Campus, Durban 4041, South Africa*

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Abstract

The historical regulation of African elephant *Loxodonta africana* populations could provide guidelines for management efforts and decisions in areas where elephant numbers are now increasing. However, there are few detailed records of the natural mortality processes of the past. Therefore, we modelled elephant population growth to evaluate possible effects of age-specific mortality. Model projections indicated that an annual mortality of 17.1% of juveniles or 10.5% of adults would be sufficient to prevent population growth. For age classes below or just at sexual maturity (i.e. 0-3, 4-7, 8-11) 37.5% annual mortality of one of these classes was required to achieve 0% population growth. These mortality levels are much higher than those reported in southern Africa today. Simulations of episodic mortality events (e.g. droughts) indicated that such events would need to occur every 16 years at a severity that would cause the mortality of all infants and weaned calves (0 - 7 year old), as well as 10% of adults and subadults (8 - 60 year old) to prevent long-term population growth. An 8-year frequency required the mortality of 84.7% of infants and weaned calves. Historically, it is possible that high drought mortality and frequency, and high predation levels, may have reduced population growth significantly but current mortality rates and frequencies are insufficient to constrain long-term average population growth at 0%. The natural limitation of existent elephant populations through mortality is therefore unlikely, indicating a need for active management of the increasing elephant populations in southern Africa today.

Keywords

Demography, elephant management, growth rates, *Loxodonta africana*, mortality, population model, southern Africa.

Introduction

There is concern over the current rate of increase of African elephant *Loxodonta africana* populations in southern Africa. Past maximum annual elephant growth rates have been estimated at up to 7% (Hanks & McIntosh, 1973; Calef, 1988) but more recent studies indicate that short-term rates of growth can be much higher. Van Jaarsveld *et al.* (1999) calculated average annual growth rates of up to 15%, and Mackey *et al.* (2006) showed that annual growth rates of 10 - 15% were not uncommon in nature reserves in South Africa.

Up to the mid 1990s culling was promoted as a management tool for elephant populations confined to conservation areas in southern Africa (Buechner *et al.*, 1963; Glover, 1963; van Wyk & Fairall, 1969). However, there is now again debate over the impact of high numbers of elephants and the possible need to further reduce populations. This creates a conservation dilemma, with the impact of high elephant densities on biodiversity being in contrast with the elephant's more precarious status beyond southern Africa (Baxter & Getz, 2005; Mabunda, 2005; Owen-Smith *et al.*, 2006). The lack of evidence for density dependent responses in elephant populations (Gough & Kerley, 2006) suggests the current high rates of population growth may not slow down under natural conditions. Although density feedbacks must inevitably influence population growth, it is uncertain at which stage this occurs in different elephant systems (Owen-Smith *et al.*, 2006). Maximum population growth rate can be maintained in large-bodied mammals until the point when forage resources can no longer support the population (Fowler & Smith, 1973; Fowler, 1981). However, because of their long generation times elephant populations can lag in their response to changing forage availability, theoretically causing oscillations in the numbers of elephants and forage rather than the achievement of an equilibrium (Caughley, 1976).

The direct study of long-term mortality is difficult in a long-lived mammal and few studies have documented elephant populations over a long timescale (Whitehouse & Hall-Martin, 2000; Moss, 2001; Wittemyer, 2001; Wittemyer *et al.*, 2005). Natural mortality in large, well-established, free-ranging elephant populations is age-dependent, with the youngest being most susceptible to dry season impacts (Moss, 2001; Dudley *et al.*, 2001). For example, all calves <8 years of age died during a drought over 1991 - 1993 in the lowveld of Zimbabwe (Leggatt, 2003), and a drought in 1994 killed 5-9% of the elephant population of Hwange National Park, Zimbabwe, with the highest frequency of mortality occurring in the youngest

age class (Dudley *et al.*, 2001). Elephants in some parts of the Kalahari Sands region of Hwange National Park may be entirely dependent on sub-surface drinking water during the dry season and droughts (Weir, 1971), digging craters to reach water, and mortality in the youngest age-class in 1994 was also influenced by whether elephants could reach this water. Whereas nursing calves can rely on milk for hydration, juvenile weaned calves die from dehydration when the water table drops below the level reachable by their trunks (Conybeare & Haynes, 1984).

In addition to drought and senescence other, less common, causes of elephant mortality include disease, injury, and predation by lions and humans (Corfield, 1973; Laws *et al.*, 1975; Walker *et al.*, 1987; Moss 2001; Dudley *et al.*, 2001; Wittemyer *et al.*, 2005). Generally, little mortality can be attributed to disease, except in Etosha where endemic anthrax causes mortality in all age classes (Lindeque & Turnbull, 1994). Predation by lions most commonly involves juvenile elephants (Ruggiero, 1991; Wittemyer *et al.*, 2005). Injury and human predation mainly affect adults, with poaching for ivory having reduced numbers of large adult elephants in the 1970s and 1980s, especially in East Africa (Ottichillo *et al.*, 1987; Moss, 2001; Wittemyer *et al.*, 2005).

Because any long-term consequences of high elephant densities have not yet been observed there are scientific uncertainties surrounding elephant management. Nevertheless, decision-makers are again looking for ways to manage the overpopulation of elephants in southern African nature reserves, with the need to evaluate the long-term effects of mortality on population growth being of particular importance. In the absence of direct evidence of the long-term effects of mortality we therefore used a mathematical population model with various scenarios to gauge the magnitude of mortality required to bring about a zero population growth rate. This enabled us to (1) examine the age-specific mortality levels required to prevent long-term population growth, and (2) simulate age-specific mortality resulting from drought events.

Methods

The model

We used a probabilistic age and state model, based on the model of Wu & Botkin (1980), incorporating aspects of elephant life history and the following demographic parameters:

maximum expected lifespan, female age at sexual maturity, average calving interval for the population, age at menopause, sex ratio of newborns, and age-specific probabilities of survival. The number of individuals of different ages and biological states were transitioned through a matrix in which the number of individuals of each age was recorded in the rows and states in the columns, i.e. males (first column); sexually immature females (second column); sexually mature but not pregnant females (third column); pregnant females in the first or second year of pregnancy (next two columns), females in the first, second, third or fourth year post-parturition anoestrus (next four columns). Males aged and died, but were not transitioned through specific states as it was assumed that sexually mature males were always present in the population and thus conception was not limited by the presence of mature males. All parameters other than the maximum expected lifespan and average period of anoestrus were input as probabilities for each age and state (i.e. probability of sexual maturity, probability of conception, probability of survival, and the sex ratio or probability of being born female). Menopause was included as a probability of conception in older individuals, and variations in mortality as the probability of survival in different ages and states. For this simulation the state of the individual was assumed not to influence mortality. The number of individuals dying and/or conceiving in each cell of the matrix was determined by comparing the input probability value with a value obtained from a random number generator that produced a normal distribution of values between 0 and 1. The model was thus stochastic in nature but input probabilities were kept constant over the period of simulation. The population was recorded at the end of each year of a simulation. The statistical variation introduced by the probabilistic approach was determined by repeating each simulation 500 times and the means and standard deviations calculated from these replicate simulations.

Population parameters

A lifespan of 60 years was used in all simulations (Hanks & McIntosh, 1973; Wu & Botkin, 1980; Whyte *et al.*, 1998), along with a moderate estimate of menopause at 50 years of age (Hanks & McIntosh, 1973; Wu & Botkin, 1980; Owen-Smith, 1988; Woodd, 1999; Moss, 2001). Female age at sexual maturity was set to 10 years (Smuts, 1975; Moss, 2001; Mackey *et al.*, 2006) and a mean calving interval, or period of time between consecutive births for females averaged over all females in the population, of 4 years was used (Eltringham, 1982; Owen-Smith, 1988; Whyte *et al.*, 1998; Whitehouse & Hall-Martin, 2000; Moss, 2001). A birth sex ratio of 1:1 was used (Laws *et al.*, 1975; Calef, 1988; Whitehouse & Hall-Martin,

2000; Moss, 2001). The probability of female conception has been found to vary with age, with lowest conception in the youngest and oldest individuals (Wu & Botkin 1980, Dominy *et al.* 1998). However, Mackey *et al.* (2006) concluded that variation in the age-specific probability of conception had little effect on model projections of population growth; we therefore chose to simplify our model by using a probability of conception of 1 for all of breeding age.

Simulations

A hypothetical initial population was created by running two females each of 6, 7 and 8 years old (i.e. a total of six females) through the model using the population parameters above. When the population age structure was constant with time (i.e. population size was increasing at a constant rate, and survivorship and fecundity rates were constant), this population size and structure was selected as the initial population, which consisted of 759 individuals, with juveniles (0-9 years old) comprising 54% and adults (10-60 years old) 46% of the total population.

Using the initial population, simulations were run over 300 years, so as to include at least 10 generations and allow enough time to evaluate long-term trends. To examine the potential effects of different age-specific mortality regimes several mortality schedules were simulated, with mortality occurring from year 21 onwards after allowing 20 years for the initial effects of the population parameters to occur. Mortality scenarios were run until the population reached a 0% population growth rate over the 280 year time period after mortality was initiated. The percentage annual mortality of the following age classes, required to achieve 0% total population growth over 280 years, was examined: overall population mortality; adult (10 - 60 years old) mortality; juvenile (0 - 9 years old) mortality; mortality in 10-year age classes; and mortality in 4-year age classes. The grouping of individuals into 10-year age classes was to separate the juvenile (0 to 9 years old) from the adult age classes. Further division into 4-year age classes added more biological relevance to age divisions, as it divided the young portion of the population into infants (0 - 3 years), weaned calves (4 - 7 years) and subadults (8 - 11 years). The weaned calf class was set at 4 years because calving interval (in this case 4 years) usually determines the average age at which a calf is weaned, with almost all calves suckling until the birth of the next calf, or just a few months thereafter (Lee & Moss, 1986).

To evaluate the measure of dispersion of results due to the probabilistic nature of the model, 95% confidence limits of the mean population growth rate were calculated from the means and standard deviations obtained from replicate simulations (Zar, 1974). Population growth rate was calculated using the standard equation for exponential population growth (Begon & Mortimer, 1986): % population growth = $(e^r - 1) * 100$, where $r = (\ln N_{t2} - \ln N_{t1}) / t$, N_{t1} and N_{t2} are population size at the beginning and end of the time interval in question, respectively, and t is the length of the time span in years.

We examined the frequency of episodic mortality events required to prevent population growth when 100% mortality occurred in each age class. The same age classes used in the annual mortality scenarios above were used in the evaluation of episodic mortality. A drought event was then simulated at a frequency of 16 years (the average cyclic frequency of rainfall occurring in southern Africa; Tyson *et al.* 1975; Louw 1982; Reason & Rouault 2002). The levels of mortality required in infant and weaned calf (0 - 7 years), as well as sub-adult and adult (8 - 60 years) age classes, to give a long-term population growth rate of 0%, were examined. The mortality levels required with a drought frequency of 8 years were also assessed. Age at sexual maturity was then adjusted to 14 years of age and calving interval to 5 years to examine the effect of these reproductive delays on the mortality required to prevent long-term population growth at a frequency of 16 years.

Drought events were simulated as single year occurrences of high mortality, as an alternative to multiple year occurrences of low mortality. The intensity and duration of drought affects the levels of drought-related mortality experienced by elephant populations (Dudley *et al.*, 2001) and the frequency of elephant drought mortality occurs most prolifically after some years of drought-related resource restriction, resulting in a mortality event (Moss, 2001). The longevity of the elephant, the low mortality among adults even under poor conditions, the ability to effectively exploit browse when necessary and a unique combination of life history traits affect the elephant's ability to respond immediately to temporal variability in environmental conditions (Fowler & Smith, 1973; Moss, 2001; Wittemyer *et al.*, 2007).

The sensitivity of model projections to adjustments in mean calving interval, female age at sexual maturity, initial population size and structure was assessed by varying each of these

parameters separately whilst keeping all else constant. Mean calving interval was adjusted to 3, 5 and 6 years, female age at sexual maturity was adjusted to 12 and 14 years, and initial population structure was adjusted to be adult biased by taking 349 individuals (46% of baseline initial population size) from the juvenile age class and adding it to the adult age class with an even spread of individuals in each year, and vice versa for a juvenile biased initial population size.

Results

The achievement of 0% population growth is the focus of all mortality scenarios. The levels of mortality giving this growth rate are sectioned into annual and episodic mortality events, as well as different age classes. The frequencies of specific episodic events, and the level of mortality of different age classes during these episodic events, are central to the results presented.

Annual age-specific mortality

The mortality of the age classes (i.e. entire population, adults, and juveniles, and 10-year and 4-year age classes) required to give 0% population growth are given in Fig. 1. The percentage age-specific mortality required to produce the curves in Fig. 1 are presented in Table 1 and outlined below.

It was projected that 5.9% annual mortality of the entire population across all ages was required to achieve 0% population growth, whereas the annual mortality of 10.5% of adults (10-60 years old) or 17.1% of juveniles (0-9 years old) was required to achieve the same result. The effectiveness of mortality in 10-year age classes for controlling population growth differed amongst age classes. The annual mortality of 19.3% of 10 - 19 year olds would result in 0% population growth. However, 100% annual mortality of individuals in the 20 - 29 year age class was required to level off population size. For 10-year age classes above this (i.e. 30 - 39; 40 - 49 etc.) 100% annual mortality of individuals was insufficient to reduce population growth to 0%.

Within individual 4-year age classes below and just at sexual maturity (i.e. 0 - 3; 4 - 7; 8 - 11 years), 37.5% annual mortality was required to achieve 0% population growth. An annual mortality of 41.4% of 12 - 15 year olds, or 53.1% of 16 - 19 year olds, or 97.1% of 20 - 23

year olds resulted in a levelling off of population size. Annual mortality of 100% of individuals in age classes >30 years (i.e. 30 - 39; 40 - 49, etc.) was insufficient to reduce population growth to 0%.

Mortality of age classes >20 years achieved 0% growth more quickly than that of age groups <20 years. However, the percentage mortality required to achieve 0% growth in age classes > 20 years, as well as the average population size attained, and the variability of this population size, was higher than in classes below 20 years.

The variability of results due to the stochastic nature of the model is indicated by the 95% confidence limits of mean population size and growth rates (Table 1, Fig. 2). The mortality of 5.9% of the entire population resulted in a population growth rate confidence interval of ± 0.04 (Table 1). Population growth rate confidence limits from age-specific mortality scenarios were < 0.04 (Table 1). The 95% confidence limit of the mean population size, calculated from 500 replicate simulations of 5.9% annual mortality of the entire population, did not coincide with 95% confidence limits calculated similarly from 5.8 or 6.0% annual mortality of the entire population (Fig. 2a). Confidence limits showed slight overlap for adult and juvenile mortality scenarios but this disappeared with increasing simulation time, as well as a 0.1% change in percentage mortality either side of that required to give 0% population growth (Fig. 2b,c). Therefore, results can be considered statistically reliable, although few replications at slightly lower or higher levels of mortality may result in 0% population growth.

Episodic mortality

When mortality occurred from discrete events on an episodic, rather than annual, basis, it was found that 100% mortality of the adult age class was required at a frequency of 18 - 19 years to produce 0% long-term population growth (Fig. 3a) and 100% juvenile mortality was required at a frequency of 13 years (Fig. 3b). The episodic mortality of 10-year age classes could not be examined for classes >20 years, as a mortality rate of 100% was required on an annual basis to prevent growth of the population. A frequency of 11 years was sufficient to prevent long-term population growth if 100% of the 10 - 19 year age class occurred (Fig. 3b), while 100% mortality in 4-year age classes at a frequency of 4 - 5 years was required (Fig. 3a).

Episodic mortality at a frequency of 16 years resulted in 0% long-term population growth if there was 100% mortality of infants and weaned calves (0 - 7 years) and 10% of the rest of the population (Fig. 4). An 8-year frequency required the mortality of 84.6% of infants and weaned calves (0 - 7 years old) to give an overall 0% population growth and cycling about a constant mean population size of 2,743 (± 455). If age at sexual maturity was adjusted to 14 years of age and calving interval to 5 years, the mortality of 100% of infants and weaned calves every 16 years, or 78% of infants and weaned calves every 8 years, was sufficient to prevent long-term population growth.

Model robustness

Model projections of age-specific mortality were most sensitive to a change in mean calving interval and, to a lesser extent, age at sexual maturity (Table 2). Model projections were not sensitive to population age structure. In age classes with individuals >20 years, mortality requirements for 0% growth tended towards 100%.

Discussion

With the recent trend of increasing elephant populations across southern Africa, decision makers are attempting to take past population patterns into account when implementing elephant management plans (Mabunda, 2005). The historical limitation of free-ranging elephant populations may have been driven by a combination of factors. It is not known whether predation by large cats or prehistoric predators may have influenced elephant population dynamics in the past but human predation has had a significant impact on elephant population size since prehistoric times (Kay, 2002; Surovell *et al.*, 2005). Episodic events, such as drought, have influenced both past and present elephant mortality patterns (Walker *et al.*, 1987; McKnight, 2000; Dudley *et al.*, 2001).

Senescence and predation are forms of mortality that could occur throughout any year. Model projections from this study indicate that an annual mortality of 5.9% of the entire elephant population would be required to reduce the long-term population growth to 0%. In contrast to this, a mean annual mortality rate of just 0.4% was found in small fenced reserves in South Africa (Slotow *et al.*, 2005), 3.2% in the Kruger National Park (Whyte, 2001) and *c.* 3% in Amboseli National Park, Kenya, which was averaged over 27 years that included both

drought and high human impacts (Moss, 2001). The average annual mortality rate over 1998 - 2003 for Samburu and Buffalo Springs National Reserves, Kenya, was 2.6% (Wittemyer *et al.*, 2005). If predation were historically common it may have been a limiting factor for elephant population growth in the past. However, in southern Africa today predation on elephants occurs rarely and accounts are generally anecdotal, with known accounts of predation on elephants by lions mainly involving juveniles (Ruggiero, 1991). In the Samburu and Buffalo Springs National Reserves 23.8% of calf mortalities recorded over 1998 - 2003 were attributed to lion and these mortalities accounted for only 4% of total population mortality (Wittemyer *et al.*, 2005). These levels of predation on juvenile elephants do not reach the projected 17% annual mortality rate of this age class required to achieve 0% population growth. Therefore, the current elephant mortality rate due to senescence and predation is unlikely to control elephant population size.

In southern Africa there is considerable decadal variability in drought events, with a 16 - 20 year cycle in total rainfall (Tyson *et al.*, 1975; Louw, 1982; Reason & Rouault, 2002; Rouault & Richard, 2005). The realization of modelled projections of mortality of all adults every 18 years, or all juveniles every 13 years, is therefore very unlikely. Adult mortality at such a high level is unrealistic, while a very severe drought causing the mortality of all juveniles would be uncommon at a frequency of 13 years. Very little natural adult elephant mortality has been recorded during drought events but juvenile mortality is usually high (Haynes, 1987; Dudley *et al.*, 2001; Moss, 2001). A drought frequency of 16 years, in accordance with the rainfall cycle of the southern African region, was projected to require the death of all infants and weaned calves, as well as 10% of adults and subadults. These levels of mortality would perhaps be possible in an extremely severe drought event, such as that which led to the notorious die-off of at least 7,000 elephants (15% of the Tsavo East elephant population) during an extreme drought in 1970 - 1971 (Corfield, 1973). However, severe droughts do not occur with any regularity, or at frequencies less than, or equal to, 16 years (Rouault & Richard, 2005).

Separately, predation and drought mortality are unlikely to have historically controlled elephant population growth but if, in combination, the resulting mortality occurred at high levels and frequencies (i.e. regular, severe droughts effecting the death of juveniles and adults, together with high predation levels) this may have contributed significantly to

historical control of elephant populations. In southern Africa today, however, reported rates of mortality due to senescence, predation and drought are not high enough to control elephant population size.

There are few options left for decision-makers to take in areas with high elephant densities and population growth rates. In general, either higher mortality rates can be introduced via culling, or simulated by live removal of elephants, or populations can be left to increase at current rates, with the expectation that density feedbacks will eventually reduce the population growth rate to zero. However, it has been recommended that any measures be applied through differential management of the specific situation, with each assessed independently and suitable measures taken according to what is possible, e.g. removal of elephants from sensitive areas, restriction of surface water in sensitive areas, biochemical contraception of elephant populations in small, or fenced reserves (Owen-Smith *et al.*, 2006).

The matriarchal social system of the elephant must be considered if culling or removals occur, with the possibility that sex- and age-specific mortality would be better options. An adult female has an extremely strong bond with her suckling calf, whereas weaned calves have looser bonds with their mothers and other members of the family group (Moss & Poole, 1983). Predation of weaned elephant calves by lion is common because of these weakened bonds (Ruggiero, 1991; Wittemyer *et al.*, 2005). Mortality of weaned calves is also common during drought periods (Dudley *et al.*, 2001; Moss, 2001). Thus the mortality of weaned calves may have a significant role in the natural mortality pattern.

High temporal variation in juvenile survival typically drives population growth rates in predator-free systems, although growth rates are more sensitive to changes in adult survival (Saether, 1997; Gaillard *et al.*, 1998, 2000). In systems where large predators are present adult, as well as juvenile, survival responds to environmental variability due to interactions between resource availability, population size and predation pressure (Owen-Smith *et al.*, 2005). Our model projections indicated that adult mortality was very important in the short-term achievement of 0% growth but a higher percentage of individuals were required to die in these age classes (>20 years) than in juvenile age classes (<20 years) to achieve the same result. The mortality of 100% of individuals >30 years old was insufficient to reduce population growth to 0%. This is easily understandable if the mean generation time is *c.* 15-

20 years, with animals >30 years old having a low influence on the growth rate of the population. Juvenile mortality was important in maintaining population size at a lower average level, as well as causing less fluctuation in population size about this average than that obtained from the mortality of adult age classes. Therefore, while it is more common to find high juvenile mortality in elephant populations (Laws, 1969; Corfield, 1973), adult mortality can cause a significant shift in bringing about a more immediate reduction of population growth.

Mortality impacts can be significant during times of resource limitation but female fecundity and reproductive limitations can also play a significant role. Wittemyer *et al.* (2007) suggest that demographic fluctuations in African elephant populations are not driven by the classic juvenile mortality pattern observed in many ungulate populations but by the relationship between female fecundity and ecological stochasticity. Density feedbacks are expected to affect elephant population growth through possible influences on female fecundity and reproductive delays caused by competition for available resources at high elephant densities (Dobson, 1993; Sinclair, 2003; Owen-Smith *et al.*, 2006). Reproductive delays are evident in some populations that live in extreme conditions, such as that of Namibia, where a mean calving interval of 5 years and age at first calving of 11 - 20 years seems to be sufficient to curb population increase (Leggatt, 2003). Our model projections indicated that an increase in mean calving interval and female age at sexual maturity caused a decrease in mortality requirements to prevent elephant population growth. Therefore, in combination with density-dependence, stochastic environmental events can have a significant impact on the limitation of elephant populations.

The effects of episodic mortality events require long-term assessment over hundreds of years, as elephant population sizes may historically have varied significantly in the short-term, with mean population size evident only on assessment of many episodic mortality events. Model projections indicated that while long-term average population growth may be constrained at 0%, oscillations of population size about an overall mean may have high amplitude, resulting in high short-term variability in population size. In the case of episodic mortality events, modelled populations varied by >1,000 elephants (mean \pm 500), which totalled *c.* 40% of mean population size. Annual mortality rates reported over short periods will therefore not reliably indicate the real mortality losses over extended periods.

Historically, it may have been possible that a combination of high drought mortality and predation kept elephant population growth in check. Today, however, artificial waterholes minimize the effects of resource limitation and dehydration due to drought, elephants are well protected from human predation, and reserves are resource-rich, resulting in rapidly increasing populations. Our modelled projections of elephant population growth suggest that the current level and frequency of natural mortality in southern Africa is insufficient to prevent long-term growth of the elephant populations of the region. Therefore, interventions to increase mortality or introduce reproductive delays are needed if population growth is to be prevented.

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Table 1 Percentage mortality required of each age class, mean population size obtained and the time, since mortality was implemented, required to achieve 0% mean population growth rate, and the 95% confidence limits of the mean population growth rate.

Age class (years)	Mortality required (%)	Mean population size (\pm SD)	Time (years)	95% CL
0-60 (entire population)	5.9	2,226 \pm 26	5	0.04
10-60 (adults)	10.5	2,238 \pm 29	5	0.03
10-year age classes				
0-9 (juveniles)	17.1	2,848 \pm 142	150	0.02
10-19	19.3	2,915 \pm 112	150	0.01
20-29	100	3,128 \pm 167	60	0.02
4-year age classes				
0-3	37.5	3,030 \pm 177	150	0.02
4-7	37.5	3,161 \pm 162	150	0.02
8-11	37.4	3,022 \pm 131	150	0.01
12-15	41.4	3,080 \pm 125	150	0.01
16-19	53.1	3,664 \pm 210	100	0.01
20-23	97.1	4,200 \pm 339	100	0.02

Table 2 The sensitivity of the model to changes in mean calving interval and age at sexual maturity as the percentage change from baseline mortality requirements.

Age class (years)	Baseline (%) ¹	Sensitivities ² (% change from baseline)				
		Calving interval (years)			Age at sexual maturity (years)	
		3	5	6	12	14
0-60 (entire population)	5.9	+1.3	-0.9	-1.4	-0.4	-0.8
10-60 (adult)	10.5	+3.7	-2.2	-3.1	-1.5	-2.6
10-year age classes						
0-9 (juvenile)	17.1	+2.3	-2.7	-3.2	-0.6	-0.6
10-19	19.3	+3.7	-2.8	-3.8	-1.8	-2.4
20-29	100	*	0.0	-14.2	0.0	-67.4
30-39	*	*	*	*	*	*
4-year age classes						
0-3	37.5	+4.0	-4.3	-6.0	-1.3	-1.4
4-7	37.5	+4.0	-4.3	-6.0	-1.3	-1.3
8-11	37.4	+4.1	-4.2	-5.9	-1.2	-1.2
12-15	41.4	+9.4	-6.2	-7.9	-4.6	-5.2
16-19	53.1	+43.8	-9.8	-12.6	-7.0	-12.9
20-23	97.1	*	-6.1	-48.5	-9.5	-61.7
24-27	*	*	*	96.4	*	*
28-31	*	*	*	*	*	*

¹Projected percentage mortality required to achieve 0% population growth using the baseline population parameters of a 4-year calving interval and 10-year age at sexual maturity.

²+, an increase from the baseline; -, a decrease; *, 100% mortality in a particular age class was not sufficient to cause a zero population growth. If baseline percentage of 100% was insufficient and a result was obtained after adjustment of sensitivity parameters, neither + nor - is shown.

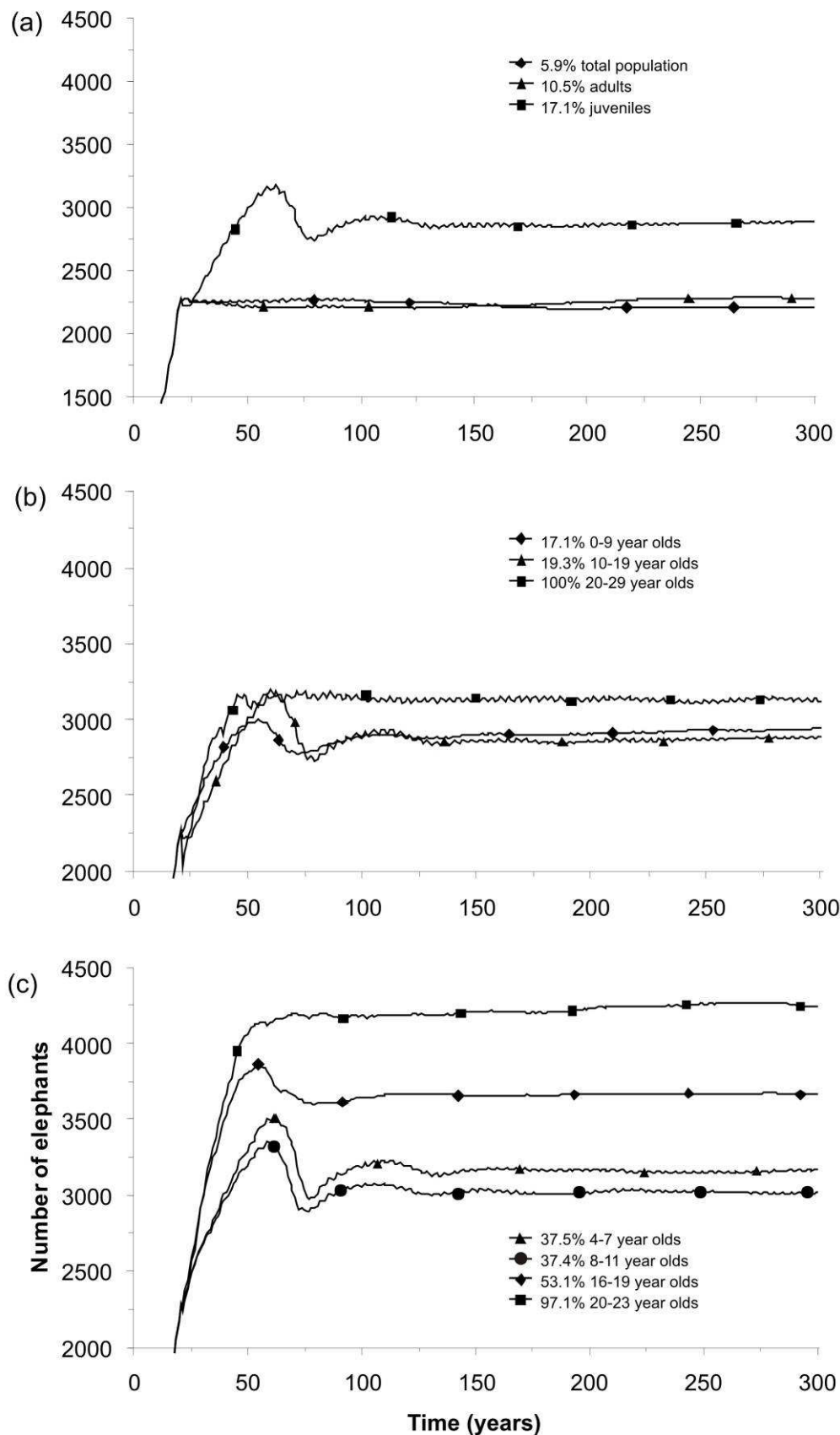


Fig. 1 Change in projected elephant population size over a 300 year duration under the following annual age-specific mortality scenarios: (a) total population mortality, adult (10-60 year olds) mortality, and juvenile (0-9years) mortality; (b) 10-year age classes; (c) 4-year age classes. Population size (at 37.5% mortality) of 0-3 and 12-15 year olds fell between the 4-7 and 8-11 year age projections and therefore, to reduce clutter, were not included in this figure.

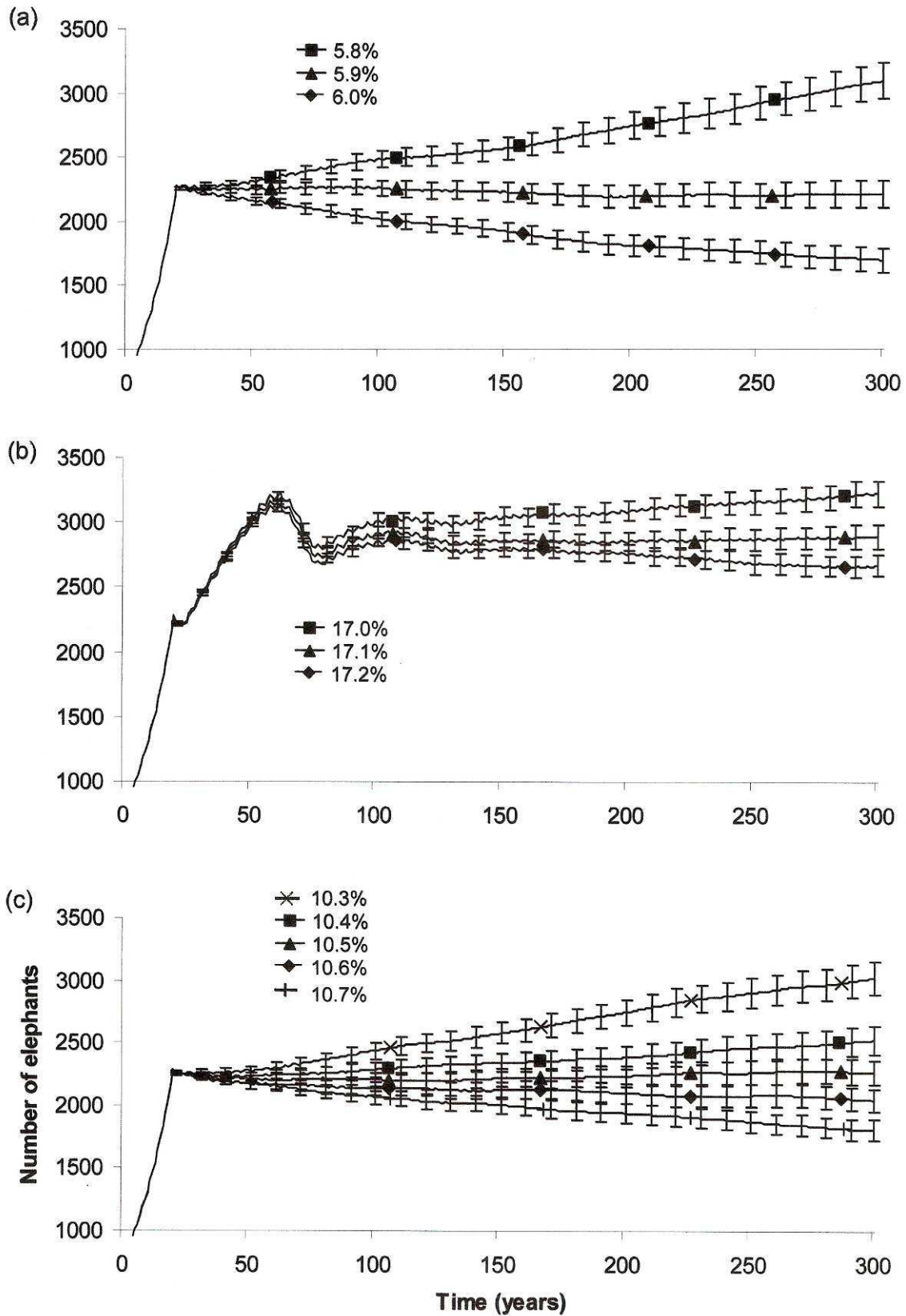


Fig. 2 The mean population size \pm 95% confidence limits resulting from: (a) annual total population mortality, (b) annual juvenile mortality, and (c) annual adult mortality.

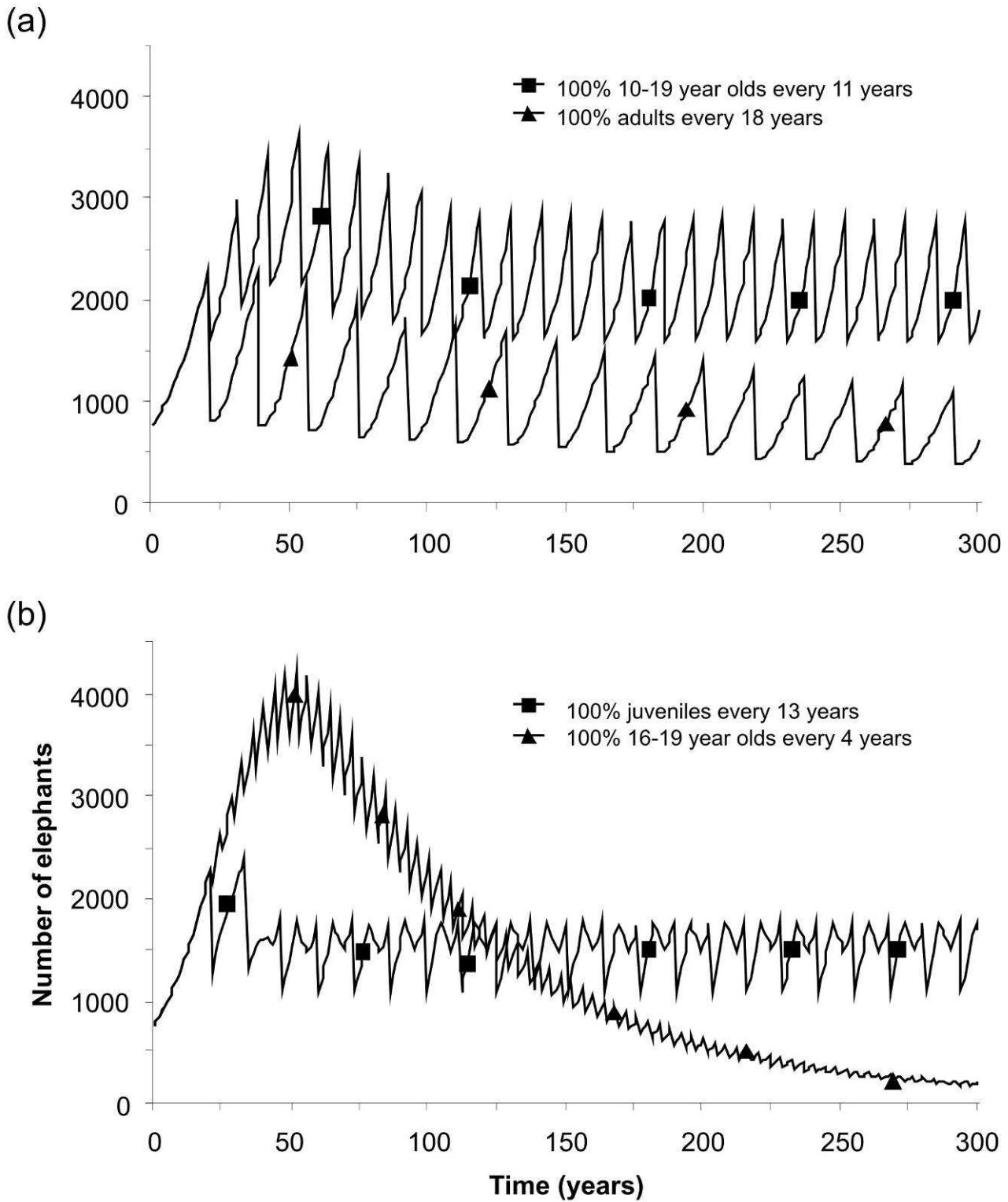


Fig. 3 The change in projected elephant population size over 300 years when the following episodic mortality events occur: (a) adult mortality at a frequency of 18 years giving a mean population size of 956 (± 422), or mortality of 10-19 year olds every 11 years giving a mean population size of 2,153 (± 509); and (b) juvenile mortality every 13 years giving a mean population size of 1,532 (± 245), or mortality of 16-19 year olds every 4 years.

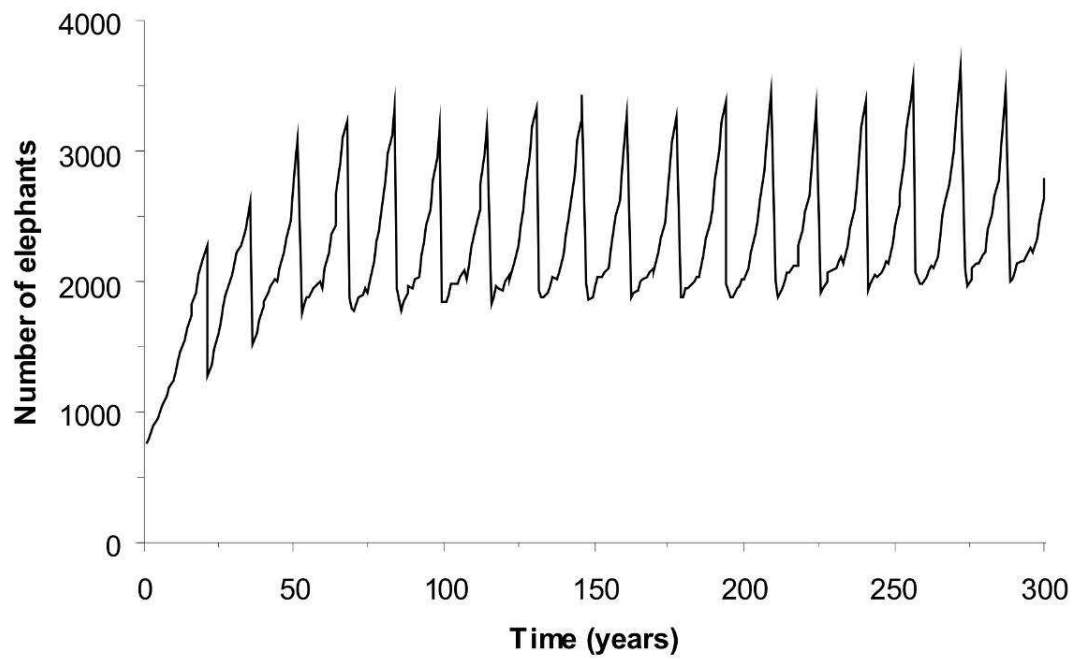


Fig. 4 The change in projected elephant population size over 300 years with 100% mortality of infants and weaned calves (0-7 year olds) and 10% of the rest of the population at a 16 year frequency, giving a mean population size of 2,253 (± 528).

Chapter 3

Population and individual elephant response to a catastrophic fire in Pilanesberg National Park

Leigh-Ann Woolley^{1*}, Joshua J. Millspaugh², Rami J. Woods², Samantha Janse van
Rensburg¹, Robin L. Mackey¹, Bruce Page¹, Rob Slotow¹

¹ *Amarula Elephant Research Programme, School of Biological and Conservation
Sciences, Westville Campus, University of KwaZulu-Natal, Private Bag X54001, Durban
4000, South Africa.*

² *Department of Fisheries and Wildlife Sciences, 302 Natural Resources Building,
University of Missouri, Columbia, Missouri 65211, USA.*

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Abstract

In predator-free large herbivore populations, where density-dependent feedbacks occur at the limit where forage resources can no longer support the population, environmental catastrophes may play a significant role in population regulation. The potential role of fire as a stochastic mass-mortality event limiting these populations is poorly understood, so too the behavioural and physiological responses of the affected animals to this type of large disturbance event. During September 2005, a wildfire resulted in mortality of 29 (18% population mortality) and injury to 18, African elephants in Pilanesberg National Park, South Africa. We examined movement and herd association patterns of six GPS-collared breeding herds, and evaluated population physiological response through faecal glucocorticoid metabolite (stress) levels. We investigated population size, structure and projected growth rates using a simulation model. After an initial flight response post-fire, severely injured breeding herds reduced daily displacement with increased daily variability, reduced home range size, spent more time in non-tourist areas and associated less with other herds. Uninjured, or less severely injured, breeding herds also shifted into non-tourist areas post-fire, but in contrast, increased displacement rate (both mean and variability), did not adjust home range size and formed larger herds post-fire. Adult cow stress hormone levels increased significantly post-fire, whereas juvenile and adult bull stress levels did not change significantly. Most mortality occurred to the juvenile age class causing a change in post-fire population age structure. Projected population growth rate remained unchanged at 6.5% p.a., and at current fecundity levels, the population would reach its previous level three to four years post-fire. The natural mortality patterns seen in elephant populations during stochastic events, such as droughts, follows that of the classic mortality pattern seen in predator-free large ungulate populations, i.e. mainly involving juveniles. Fire therefore functions in a similar manner to other environmental catastrophes and may be a natural mechanism contributing to population limitation. Welfare concerns of arson fires, burning during “hot-fire” conditions and the conservation implications of fire suppression (i.e. removal of a potential contributing factor to natural population regulation) should be integrated into fire management strategies for conservation areas.

Introduction

Successful conservation management of large mammals has the ironic consequence of problems associated with overpopulation [1]. This is particularly so with fragmented, small populations or with keystone species that, at high population densities, can impose negative impacts on the system [2]. A key uncertainty that emerges is what limits such populations naturally, and whether such limitation will occur at the same levels in human modified systems (e.g. with fences or artificial water) compared to natural systems [1]. Some species may be resource limited, displaying density dependent responses [3]. Others may be top-down limited by predators [4]. Long-lived species may also be limited by environmental catastrophes, such as drought, flood, fire or disease, which can cause sudden and, at times, significant shifts in population size and dynamics over a very short time, if the effects of such catastrophic impacts on demographics are of sufficient frequency and intensity [5]. Although there is some theoretical and empirical evidence that drought may limit elephant populations [6], there has been no evaluation of the role that fire may play. Due to their rare occurrence, evaluation of the impacts of such events on population dynamics and individual responses is also rare.

Fire is commonly applied for ecosystem management in savannas and arson fires occur regularly [7]. Whilst the impact of fire on plant mortality has been extensively researched, there is little research that has assessed the influence of fire on mortality in animals or the welfare issues associated with fire in savanna systems. Given elephants are highly intelligent and social mammals, fire, or other severe disturbances, may also precipitate behavioural or physiological responses. For example, high elephant poaching caused heavily stressed elephants to form larger groups than unstressed elephants [8].

The extremely hot, dry, windy (“hot-fire”) conditions experienced towards the end of the dry season in Pilanesberg National Park (PNP), a small (570km²), fenced reserve in South Africa facilitated the spread of an uncontrolled wild fire. The area had a 1 – 2 year fuel load, with the last pre-fire rains falling in May 2005. Below average (~ 630 mm p.a.) annual rainfall of 554 mm was recorded during the 2004/5 wet season, while 824 mm fell in 2003/4 and 411 mm in 2002/3. On 21 September 2005, ambient midday air

temperature was 34°C, while wind speed was generally strong but variable in direction. The fire entered the western boundary of the Park near Tlatlaganyane village on 20 September 2005 and within two days had moved across an area of approximately 61 km². This catastrophic fire resulted in the mortality of 29 and injury to 18 elephants, unprecedented in PNP, where few natural elephant mortalities had occurred prior to this event [9,10]. This event provided us with the opportunity to assess the potential influence of severe fires in which animals become trapped on the behavioural, physiological and demographic responses of the elephant population. We provide an assessment of (1) the behavioural and physiological responses of the elephants to this large disturbance event, and (2) the potential for rare, stochastic mass-mortality events to limit population size. We examined movement and herd association patterns of six GPS-collared breeding herds, and evaluated physiological response through faecal glucocorticoid metabolite (stress) levels [11,12]. We investigated population size, structure and projected growth rates.

Results

Behavioural response

Daily displacement

There was no significant difference in mean daily displacement over four days before versus after the fire for all cows ($t_5 = -1.238$, $P = 0.271$). However, injured herds (CE03, CE88) and a herd in close proximity to the fire at time of injury (CE32) moved significantly further per day after the fire than before ($t_2 = -6.915$, $P = 0.020$), while there was no significant difference in mean daily displacement of uninjured herds (CE13, CE61, CE81) over four days before versus after the fire (Figure 1).

There was no significant difference in daily displacement among collared cows over a ten-day period before the fire ($F_{5, 54} = 0.305$, $P = 0.908$). However, there was a significant difference in daily displacement among collared cows over the ten-day period, post-flight, after the fire ($F_{5, 54} = 9.346$, $P < 0.0005$). Injured cows (CE03 and CE88) moved at a significantly slower rate in the ten days after the fire ($t_9 = 4.486$, $P = 0.002$; $t_9 = 2.756$, $P = 0.022$ respectively), compared with ten-day daily displacement before the fire (Figure

1). Uninjured cows CE61, CE81, CE32 and CE13, did not show a significant change in daily displacement in the ten day period before versus after the fire ($t_9 = -0.450$, $P = 0.663$; $t_9 = -0.930$, $P = 0.928$; $t_9 = 1.084$, $P = 0.307$; $t_9 = 0.745$, $P = 0.476$ respectively) (Figure 1). There was no significant difference in the coefficients of variation (CV) of daily displacement for the ten-day periods pre- and post-fire ($t_9 = -2.064$, $P = 0.094$), but a general trend of increased variability is evident for those herds involved in the fire (CE03, CE88) or those close to the fire when injuries occurred (CE32) (Figure 1).

There was no significant difference in daily displacement among collared cows over a three-month period before the fire ($F_{5, 540} = 1.709$, $P = 0.131$). However, there was a significant difference in daily displacement among collared cows over a three-month period post-fire ($F_{5, 540} = 5.720$, $P < 0.001$). The daily displacement over three months for injured cows CE03 and CE88, as well as CE88's new matriarch CE13, were not statistically different, while daily displacement for CE88 and CE13 was not statistically different from uninjured cows (CE81, CE61 and CE32) (Figure 1). Uninjured cows CE81 and CE61 showed significant increase in their daily displacement during three months post-fire ($t_{90} = -3.664$, $P < 0.001$; $t_{90} = -3.830$, $P < 0.001$) (Figure 1). Severely injured cow CE03 showed a significant decrease in three-month daily displacement post-fire ($t_{90} = -3.240$, $P < 0.0005$) (Figure 1). Less severely injured cow CE88, matriarch CE13 and uninjured cow CE32 showed no significant difference in three month daily displacement before versus after the fire ($t_{90} = -1.337$, $P = 0.185$; $t_{90} = -0.747$, $P = 0.457$; $t_{90} = -1.641$, $P = 0.104$ respectively) (Figure 1). There was a significant difference between pre- and post-fire CV in daily displacement over three months ($t_9 = -2.984$, $P = 0.031$), with a general trend of increase in variability post-fire (Figure 1).

Home range

There was no significant difference in home range size before and after the fire among all cows (50% kernel size, $t_5 = 0.505$, $P = 0.635$; 95% kernel home range, $t_5 = -0.024$, $P = 0.982$). Only severely injured cow CE03 reduced the size of her core home range (36.1 km² to 6.3 km²) and 95% home range (305.9 km² to 71.6 km²) dramatically after the fire

and her home range shifted from the central areas of the Park to the south-eastern wilderness area (Figure 2).

Cows spent significantly more time in the wilderness areas of the Park in the three months after than in the three months before the fire ($t_5 = -4.510$, $P = 0.006$). Percentage overlap of home ranges indicated a shift in home range location post-fire (Figure 2).

There was no significant difference in core (50% kernel) range size over the 44 day period before versus after the fire ($t_5 = -1.290$, $P = 0.267$). However, the size of 95% kernel home range differed significantly over this time period ($t_5 = -3.753$, $P = 0.020$), with most cows having a larger 95% home range after the fire. Home range size for the 44 day period after the first spring rains was not significantly different to home range size before the rain (50%: $t_5 = 0.096$, $P = 0.928$; 95%: $t_5 = 0.654$, $P = 0.542$). Percentage overlap of before rain 95% home range and after rain 95% home range was 47.2%, 80.5%, 73.2%, 90.7%, 64.8% and 78.1% for CE03, CE13, CE32, CE61, CE81 and CE88 respectively. Therefore, all except severely injured cow CE03 had similar 95% home range location before versus after the rain. This suggests that the change in season post-fire was not the reason for the change in 95% home range we observed.

Herd fission/fusion

The time spent associating with other herds pre- and post-fire was significantly different for uninjured versus injured cows ($t_4 = -3.675$, $P = 0.021$). For the first two months post-fire, fission behaviour was exhibited by injured cows, with CE03 and CE88 spending only 10.3 % and 34.7 % of their time associating with other herds respectively, compared with 91.2 % and 62.2 % respectively before the fire. In the third month post-fire, CE03 exhibited increased fusion behaviour, with association time increasing from 10.3 % to 43.8 % and CE88 joined uninjured collared cow CE13 (permanent association to August 2008). Uninjured cows generally exhibited greater fusion behaviour after the fire.

Physiological stress response

While pre- versus post-fire measurement, in general, had no significant effect on stress hormone levels ($F_{1, 133} = 0.261, P = 0.610$), there was a significant difference among elephant age-sex classes (i.e. juvenile, adult bull, adult cow) ($F_{2, 133} = 16.155, P < 0.001$). There was also a significant interaction between pre- versus post-fire and elephant age-sex class ($F_{2, 133} = 4.240, P = 0.016$). Before the fire, adult cow and juvenile stress levels were not significantly different, but were both significantly lower than adult bull stress levels (Figure 3). Cow stress levels increased significantly post-fire but juvenile and bull stress levels were unchanged by the fire (Figure 3).

Evaluation of stress hormone levels before versus after the first Spring rain fell showed that there was no significant change in stress hormone levels between wet and dry 44 day periods ($F_{1, 98} = 0.015, P = 0.902$).

Demography

Five family units and six independent adult bulls suffered burn injuries (47 individuals), of which 29 mortalities occurred (17.6% of pre-fire population total) (Table 1). Five juveniles between six and ten years of age, 11 adult females and two adult males recovered from their burn injuries (Table 1). Fifteen infants (≤ 3 years old), seven weaned calves (4 to 10 years old), four adult females and three adult males died, either as a direct result of their burn injuries, or from euthanasia implemented by Park authorities due to the severity of their injuries (Table 1). Initial post-fire assessment resulted in the euthanasia of two of the four adult females and all three adult males, with veterinarians deciding on strict euthanasia criteria which included $> 50\%$ burns to total body surface area, marked oedema, eschars, severe suppurative oozing and severe impairment of mobility due to burn lesions. Seventeen of the injured juveniles were taken to a holding facility off-site and their wounds treated. Only two of these elephants survived and were released back into the Park. Of the fifteen juveniles that died, ten were euthanized, with euthanasia criteria including $> 50\%$ burns to total body surface area, large skin surface area with open tissue, comparative behavioural records indicating severe pain and distress, collapse without recovery after revival, as well as low blood protein and

calcium. Euthanasia was only considered in cases where recovery was impossible (criteria for recovery see [13]) and thus mortality can be considered representative of natural fire mortality.

Age structure, classified according to 10-year and 4-year age classes, was significantly different after the fire than before (10-year age classes: $G_3 = 70.637$, $P < 0.001$; 4-year age classes: $G_3 = 71.598$, $P < 0.001$). Model projections over 30 years showed no change in projected population growth rates achieved using demographic data before the fire, as well as demographic data after fire mortalities were accounted for (6.5% p.a.). It took four years for the projected population to recover to the pre-fire population size of 165 individuals (Figure 4). In the absence of fire, the population was projected to grow to 303, 577, and 1079 individuals in 10, 20, and 30 years respectively (Figure 4). Taking into account the effects of fire on the population structure, the population was projected to reach 255, 485, and 903 individuals in the same timeframes (Figure 4). For this type of mortality event to reduce long-term population growth rate to 0%, it would be required at a frequency of every three to four years (Figure 4).

Discussion

A large disturbance event causing catastrophic injury and mortality has consequences that can significantly affect the functioning and behaviour of an elephant population. In response to a catastrophic fire in PNP, injured elephant cows showed an initial short-term (lasting about four days) flight response post-fire, a longer-term (over about ten days to three months) decrease in daily displacement, a shift in home range, social withdrawal, seclusion to non-tourist areas, and significantly higher stress levels. However, behavioural responses were not limited to injured individuals alone. Uninjured cows also showed altered physiological and behavioural responses post-fire. These cows had significantly raised stress levels, a general increase in daily displacement, more variability in daily distance moved, withdrawal to non-tourist areas and a herd fusion response. Injured herds therefore may have signalled their distress to uninjured herds. Elephant family groups that show a high frequency of association have been known to act in a co-coordinated manner, due to the complex social behaviour and long-range

communication used by elephants [14,15]. The stress of injury, together with social disruption due to the loss of and injury to family members is likely to have affected the behaviour of injured breeding herds. This is additional to the increased vulnerability of injured juveniles to predation, or the compromised ability of injured adult cows to protect their young, which would have increased stress levels. The incidence of elephant calf predation has been found to increase during times of drought when nutritional stress and dehydration facilitates the circumstances where calves can lag behind the herd and become vulnerable to predators [16]. Injured calves were seen alone in PNP after the fire (pers. obs.), increasing their vulnerability to predation.

The physiological and behavioural responses apparent in the PNP population post-fire are consistent with elephant reactions to stressful conditions. Breeding herds showed raised stress levels and a fusion response to cow immobilizations and high-volume tourist activity in PNP [9]. Working elephants in a safari operation had high stress hormone levels associated with transportation and episodic loud noises, such as lightning and thunderstorms and human-induced activities, with baseline levels of faecal glucocorticoid metabolites for adult elephants in PNP of approximately 25ng.g^{-1} [12]. Heavily stressed elephants, responding to high levels of poaching, formed larger groups than unstressed elephants [8]. Stress responses to culling in Kruger National Park were initial flight, taking elephants outside of home ranges [17], as well as the movement of elephants into and out of culling regions in response to culling events [18,19]. As these studies indicate, elephants are stressed by human-induced and natural disturbances. Stressed animals alter their behaviour in an attempt to eliminate the stressor. Thus, shifts in home range and seclusion to non-tourist areas are predictable, adaptable responses to disturbance. Therefore, a fire event resulting in elephant mortality has the potential to induce severe behavioural and physiological stress responses (see [20] for review of trauma effects on neuroendocrinological development of elephants, and subsequent non-normative behaviour). Whereas drought may cause elephant mortalities over an extended period of time [21], fire mortality occurs within a short time period after the event. Long-term elephant behavioural response to fire mortality may therefore persist, due the dramatic and traumatic nature of the event [20].

The demographic impact of fire on the PNP elephant population predominantly involved the mortality of juveniles (76% of total mortality). Among large herbivore populations where predators are absent, high temporal variation in juvenile survival is often seen, with fairly constant adult survival [22-24]. In systems where large predators are present, both adult and juvenile survival responds to environmental variability, due to interactions between resource availability, population size and predation pressure [4]. Without constant predation pressure, the natural mortality patterns often seen in African elephant populations during stochastic events, such as droughts, follows that of the classic mortality pattern seen in predator-free large ungulate populations, which mainly involves juveniles [21,25,26]. Fire therefore functions in a similar manner to other environmental catastrophes.

Population structure prior to the fire was significantly different post-mortality, due to predominant mortality in the juvenile age-class. In effect, the loss of a high proportion of juveniles serves not only to lower population size, but also to increase calving interval where the lost calf creates a gap between siblings. However, among large herbivore populations, population growth is most sensitive to adult mortality, especially that of prime-aged females [22-24,29]. The mortality of only four adult females from the PNP population as a result of the fire meant that projected population growth rate remained unchanged. Therefore, the ability of this type of stochastic, catastrophic mortality exhibited in the PNP fire to limit population size or growth would require higher or more frequent mortality, would need to include a higher proportion of adult females [19,29], or cause demographic delays such as a decline in conception rates, increased inter-calving interval, or increased age at sexual maturity [10,30].

In order to reduce the PNP elephant population growth rate to zero, this type and level of mortality event would be required at a frequency of approximately three to four years. This gives an indication of the resilience of elephant populations to environmental perturbation. The demographic response of populations to episodic mortality is influenced by the life-history characteristics of the species. Elephant life-history is typical

of large-bodied ungulates in that these mammals have long generation times, low fecundity and high adult survival [30,31]. In elephant populations, a unique combination of life-history traits prolong demographic response to environmental disturbance [30] and maximum population growth rate tends to be maintained until the very limit where forage resources can no longer support the population before density dependent feedbacks occur [1,32,33]. Therefore, stochastic mortality alone has the potential to limit short-term population size, but is unlikely to affect population growth over the long-term. However, in combination with density-dependent effects, elephant populations may be limited by environmental catastrophes and the stochasticity brought about by temporal variation in resources. Thus when populations are close to carrying capacity, and background mortalities are higher and fecundities lower than observed here, less intense mortality would be required to achieve a stabilizing effect, and longer intervals between periodic catastrophes could still result in fire-induced mortalities influencing demographics substantially. Catastrophic fires are likely to be rare events with expected return in the order of decades [27]. Therefore in isolation these events will not provide population regulation, but in combination with other stochastic environmental events and density-dependent feedbacks, they may play a role in population limitation. Thus removal of fire from the system in some actively managed nature reserves may not only be detrimental to the vegetation [7,28], but also the dynamics of herbivore populations where fire mortality may be avoided. These fire events should not be considered as negative catastrophes but instead as integral to the savanna system, with the potential to make infrequent but positive contributions to the regulation of abundant herbivore populations.

Burning during the late dry season, under “hot-fire” conditions when fires can be very intense, can result in catastrophic mortality of large mammal species. Arson fires during these times have the potential to impact not only the vegetation of the area, but also raise welfare concerns over any animals affected by the fire due to the significant stress responses and behavioural changes which may occur. The conservation status and abundance of species will influence fire management requirements. The contribution of fire mortality to abundant game species (e.g. blue wildebeest (*Connochaetes taurinus*), impala (*Aepyceros melampus*)) population dynamics may be less problematic than to that

of threatened species such as the black rhino (*Diceros bicornis*), which would conversely require extreme awareness of the need to prevent potentially intense catastrophic fires to ensure minimum mortality impacts. If herbivore populations are fairly stable, even a rare catastrophic fire could cause a shift in population dynamics that, in combination with the current factors causing regulation, may cause a population decline. Therefore, the integration of the conservation implications of intense, hot-fire suppression (i.e. removal of a potential contributing factor to natural population regulation), the welfare concerns of arson fires and burning during “hot-fire” conditions into fire management strategies for conservation areas is important.

Materials and methods

Study site

Pilanesberg National Park (PNP; 25°24'S, 27°08'E; 570 km²), North West Province, South Africa, is located within the transition zone of Kalahari Thornveld in the west and Bushveld in the east [34]. The habitat consists mainly of savanna ranging from broadleaf/*Acacia* thickets to open grassland. There are several dams within the Park, one major perennial river system and many ephemeral tributaries and streams. The region has summer rainfall of approximately 630 mm p.a. Geologically, PNP is an extinct volcanic crater formed over 1 200 million years ago and is an example of an alkaline ring complex [35]. The weathering of this complex has created a rugged, hilly landscape, with steep slopes and deep valleys (Figure 5). PNP is open to tourists, but has large “wilderness” areas where there is no tourist access, limited management tracks, and is rarely traversed by people (Figure 5). This wilderness zone comprises approximately half of the total area of PNP. Elephant were introduced to PNP between 1981 and 1998 [36]. As of early September 2005, the PNP population totalled 165 individually identified elephants, of which 37 were independent adult bulls and 128 were part of 18 relatively stable matriarchal family groups. All individuals in the population were known from unique ear notches and tusk configuration. Pre-fire, the population was made up of 86 juveniles under 10 years of age (56 males, 30 females), 23 10-20 year old adults (10 males, 13 females), as well as 29 adult females and 27 adult males between the ages of 20 and 42

(oldest elephants in population). There had been no mortality from old age, with the first expected to occur in around 15 years time [37].

Behavioural response

We investigated both short-term and long-term responses of the elephants to a fire event that caused elephant injury on the afternoon of 21 September 2005. Short-term responses were investigated over a four and ten-day period pre- and post-fire. Longer-term responses were assessed over three months pre- and post-fire. Prior to the fire, GPS-collars had been fitted to six elephant cows, belonging to different breeding herds within the PNP population. The movement of these elephants (CE03, CE13, CE32, CE61, CE81 and CE88) was assumed to depict the movement behaviour of the breeding herd to which they belonged [14]. Location points were taken at similar times of the afternoon for each cow every day. Members of two of these breeding herds were injured in the fire (CE03 and CE88). CE03 was severely injured, with more than 45% total body surface area (TBSA) burned and CE88 was less severely injured, sustaining burn injuries to approximately 20% TBSA [13]. Analyses pre-fire included data before fire injury occurred, while post-fire analyses included data post-injury.

All statistical analyses in this paper were performed in SPSS 15.0 (SPSS Inc., Chicago, Illinois, USA) with $\alpha = 0.05$. In the case of parametric tests, assumptions were tested and satisfied. The work was approved by the Animal Ethics Committee of the University of KwaZulu-Natal.

Daily displacement

The distance moved by the collared elephants each day (24 hour fixes) was calculated using polylines in the Animal Movement Extension [38] to ArcView 3.2 (ESRI Inc., Redlands, California, USA). We considered this shortest line between the two readings as an index of daily displacement, and refer to this value as daily displacement hereafter.

To test whether there was an initial flight directly after the fire, mean daily displacement of all cows over four days before and after the fire was compared using a paired samples

t-test. Four day mean daily displacement of injured cows (CE03, CE88) as well as uninjured cow in close proximity to fire during injury (CE32) was tested with a paired-samples t-test and the same was done for four day mean daily displacement of uninjured cows (CE13, CE61, CE81).

The mean daily displacement during a ten day period before the fire was compared among cows using one-way ANOVA, and the same was done for mean daily displacement for a ten day period, post-flight, after the fire (i.e. day 5 – 14). A paired-samples t-test was performed on each cow's daily displacement ten days before and post-flight, after the fire. Variability in displacement was assessed using coefficient of variation (CV) for each cow's daily displacement over ten days, pre- and after flight, post-fire; these were contrasted using a paired-samples t-test. We performed the same contrasts of daily displacement from a three month period directly before the fire (21 June 2005 – 21 September 2005) and after the fire (22 September 2005 – 22 December 2005).

Home range

Each cow's 24-hourly locations for a period of three months pre- and post-fire were mapped in ArcView 3.2. We calculated Kernel home ranges (core home range enclosed by the 50% probability contour and 95% home range enclosed by the 95% probability contour) in animal movement extension SA 2.1 [38], using least-squares cross-validation (LSCV) smoothing. Both 50% core and 95% home ranges were compared before versus after the fire using paired-samples t-tests. Percentage of overlap between the 95% home range before the fire and after the fire was calculated for each cow according to the following equation [39]:

$$\% \text{ overlap} = [(A_{ab}/A_b \times A_{ab}/A_a)]^{1/2} \times 100,$$

where A_{ab} is the area of overlap between home range before the fire (A_b) and home range after the fire (A_a). Percentage overlap data, together with the percentage of locations of each cow in either the wilderness or tourist zones of PNP for three months pre- and post-

fire, were used to establish whether a shift in home range had occurred subsequent to the fire and to ascertain if the elephants avoided the tourist zone after the disturbance. A paired-samples t-test was used to compare the percentage location of collared cows in the wilderness zone pre- and post-fire.

An increase in home range size has been reported for elephants in semi-arid environments during the wet season, due to increased access to areas with ephemeral water sources in the wet season [40,41]. The first spring rains fell in PNP on 4 November, 2005. In order to examine whether there was a change in home range size and location after the rain (and therefore establish whether any change could be attributed to a seasonal shift in home range alone), kernel home range was calculated for 44 day periods before the fire (9 August – 21 September 2005), after the fire but before the rain (22 September – 4 November 2005), as well as after the rain (5 November – 18 December 2005). Areas of 50% and 95% home ranges for each collared cow over these time periods were compared (paired-samples t-test).

Approximately 70% of PNP was burnt during the 2005 dry season. Thus during the late dry season (post-fire and before the rains), the availability of forage was similar throughout the Park in terms of fire-impacted vegetation. We therefore did not consider the post-burn condition of the vegetation as a bias to elephant movement decisions over the study period.

Herd fission/fusion

To determine whether the breeding herds showed a ‘fission’ or ‘fusion’ response (i.e. whether breeding herds came together or dispersed, respectively) following the fire, we compared the number of matriarchs (where one matriarch indicates the presence of one herd) seen together in the three-month period pre- and post-fire. A herd’s grouping tendency was represented by the percentage fusion, calculated as the number of sightings of a particular herd with other breeding herds, as a percentage of the total number of sightings of that herd. For each herd, percentage fusion was calculated before the fire and after the fire. Because injured and uninjured herds showed opposite fusion trends, a t-test

on the difference between pre- and post-fire percentage fusion was used to compare injured and uninjured collared herds. Injured cow fusion response over three months post-fire was further broken down into the first two months post-fire, and the month following that, to examine any change in association pattern on partial recovery from injury.

Physiological stress response

Severe, persistent stress can cause glucocorticoid levels to increase and remain elevated [42]. The measurement of glucocorticoid metabolite levels in elephant faeces has proven a useful non-invasive way of investigating stress levels in African elephants [12,43,44]. A total of 171 fresh (i.e. < 6 hours since deposition) elephant faecal samples were collected randomly from the PNP population in the three-month periods before and after the fire. Some samples were collected from known individuals at the time of deposition. Those that were not, were classified according to the approximate age of the elephant from which they came [45], where age was estimated from dung bolus size. Average dung bolus diameter greater than 16 cm was considered to belong to adult bulls; all adult cows in the PNP population, with the exception of one, were below 30 years of age at the time of sample collection, corresponding to dung bolus diameters of approximately 14 cm. For anonymous samples with a bolus > 16 cm in diameter, the sample was considered to originate from an adult bull if it was from a site where a single track indicated the presence of a large, solitary elephant. Samples were assigned to cows if they were collected from a site where tracks indicated breeding herd activity and if bolus diameters were between 10 - 14 cm. Samples with a dung bolus diameter < 10 cm were considered to belong to juveniles.

Faecal glucocorticoid metabolite levels were measured using methods involving the use of a corticosterone I¹²⁵ radioimmunoassay (RIA) kit (MP Biomedicals, Costa Mesa, California, USA) [46,47]. This assay has been validated and used for elephants [12,47].

Differences in glucocorticoid levels among adult males, adult females and juveniles, pre- and post-fire, were compared using two-way ANOVA. Repeated measures ANOVA was

not used because samples before and after the fire were not necessarily, and likely improbably, from the same individuals.

The effect of season on stress levels was examined to establish whether any change in stress hormone level after the fire was consistent with the onset of the first spring rains and thus a seasonal change in stress hormone level. An analysis (two-way ANOVA) of stress hormone levels was carried out over 44 day periods post-fire (i.e. before the rain 22 September – 4 November 2005 and after the rain 5 November – 18 December 2005). Wet and dry season stress levels for different elephant states (juveniles, adult cows and adult bulls) were compared.

Demography

The effect of the fire on PNP elephant population size and age structure was assessed by accounting for all mortalities (categorized according to age and sex) and comparing population size and age structure before the fire with that after the fire. A G-test was used to assess if age structure was different, by separating total count data into 10-year and 4-year age classes and comparing the number of elephants in each age class pre- and post-fire.

The potential for fire to limit the population was considered using a probabilistic age and state model [48]. The model was used to calculate population size over 30 years, a time-period relevant for conservation management decision-making, using population data (1) before the fire, and (2) after the fire. The model was also used to determine how often a fire of this nature would need to occur for long-term population growth rate to be reduced to zero over a period of 300 years, to allow for ample reproductive generations and growth. Population growth rate was calculated using projected population size from demographic data before the fire and after the fire, according to the following standard equation for exponential population growth:

$$\% \text{ population growth} = (e^r - 1) \times 100,$$

where $r = (\ln N_{t_2} - \ln N_{t_1}) / t$ and N_{t_1} and N_{t_2} are population size at the beginning and end of the time interval in question, respectively; and t is the length of the time span in years.

The model incorporated aspects of the life history of individuals and the following important demographic parameters according to acceptable values from the literature: maximum expected lifespan of 60 years [18,37], female age at sexual maturity of ten years [10,31], average calving interval for the population of four years [31,49], age at menopause of 50 years [37,50] and a 1:1 sex ratio of newborns [31,49]. These parameters were a slightly conservative estimate of those estimated from past elephant demographic patterns in PNP [10].

The model used was a probabilistic matrix model, where numbers of individuals of different ages were transitioned through specific biological states, i.e. males; sexually immature females; sexually mature, non-pregnant females; pregnant females (in first or second year of pregnancy); females in the first, second, third or fourth year post-parturition. Males were aged but not transitioned through specific states. All parameters other than average calving interval were input as probabilities for each age and state, determined by comparison of input probability value with one obtained from a random number generator that produced a normal distribution of values between 0 and 1. The statistical variation introduced by the probabilistic approach was determined by repeating each simulation 500 times and the means and standard deviations were calculated from these replicate simulations. The population was recorded at the end of each year of a simulation.

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Table 1. Demographic response to fire: elephant mortality and survival recorded after a fire in Pilanesberg National Park on 21 September 2005, giving the herd of origin and an estimate of elephant age are given (as of December 2005).

Herd	Collared cow	Age of individuals in different categories *	
		Injured and died	Injured and survived
Gold	CE 57	1, 2 , 3 , 4, 8	4 , 8 , 8, 10 , 25 , 30 , 35
Monica	CE 98	1, 2 , 4	10 , 12 , 30
Red	CE 07	2 , 2, 3, 35	8, 12
Sheena	CE 88	2, 2, 3 , 4, 4, 6, 30 , 30	8, 20
Yellow	CE 03	1, 1 , 2 , 4, 5, 30	15 , 42
Adult bulls		12, 15, 20	12, 15

* Females are indicated in bold.

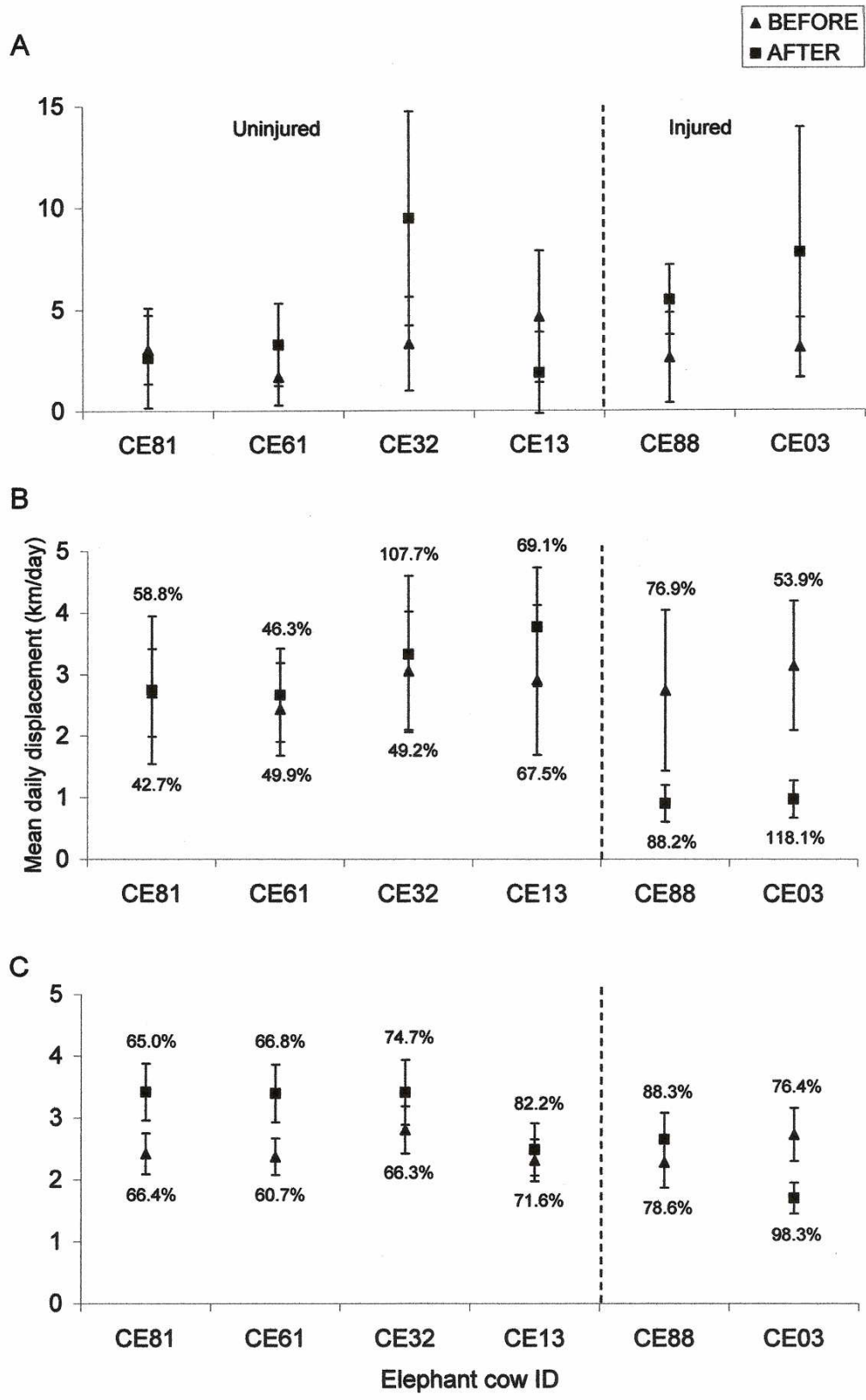


Figure 1. Behavioural response to fire giving mean daily displacement ($\pm 95\%$ CL) of each collared cow over: (A) 4 days, (B) 10 days and (C) 3 months, before and after the fire. Coefficients of variation (CV (%)) of daily displacement before or after the fire are given above or below the upper or lower limit of CL bars. Pre-fire CV's are located above if the value of pre-fire mean $\pm 95\%$ CL is located above (i.e. is greater than) post-fire mean $\pm 95\%$ CL. Where mean $\pm 95\%$ CL pre- and post-fire are equal, pre-fire CV's are located below CL bar.

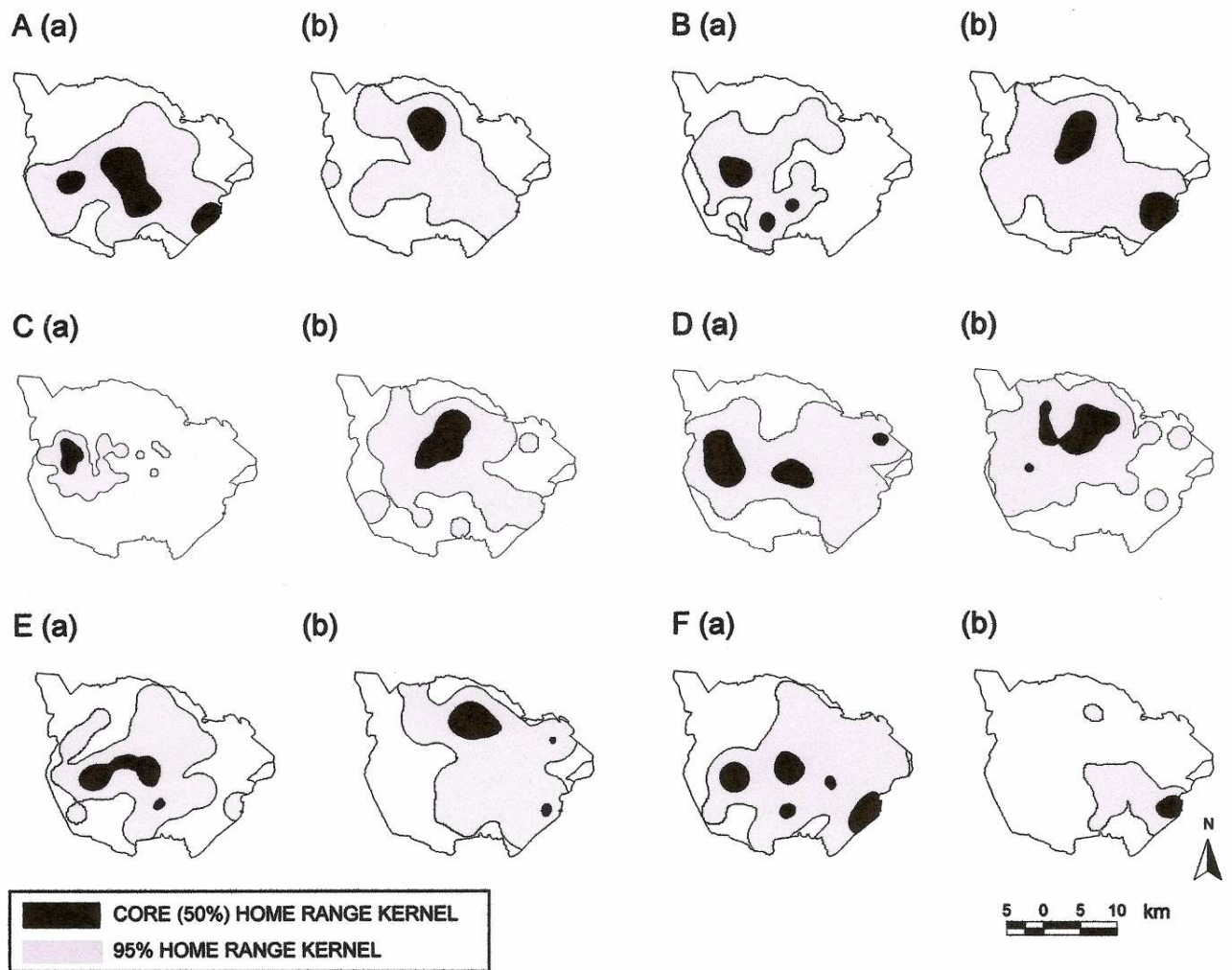


Figure 2. Behavioural response to fire showing core home range and 95% home range kernels for: uninjured adult cows (A) CE13, (B) CE81, (C) CE61, (D) CE32 and injured adult cows (E) CE88 and (F) CE03 three months (a) before and (b) after injury in a fire on 21 September 2005 in Pilanesberg National Park. The percentage overlap between 95% home ranges before and after the fire was: (A) 80.5, (B) 72.7, (C) 49.7, (D) 86.0, (E) 74.1 and (F) 52.5 respectively.

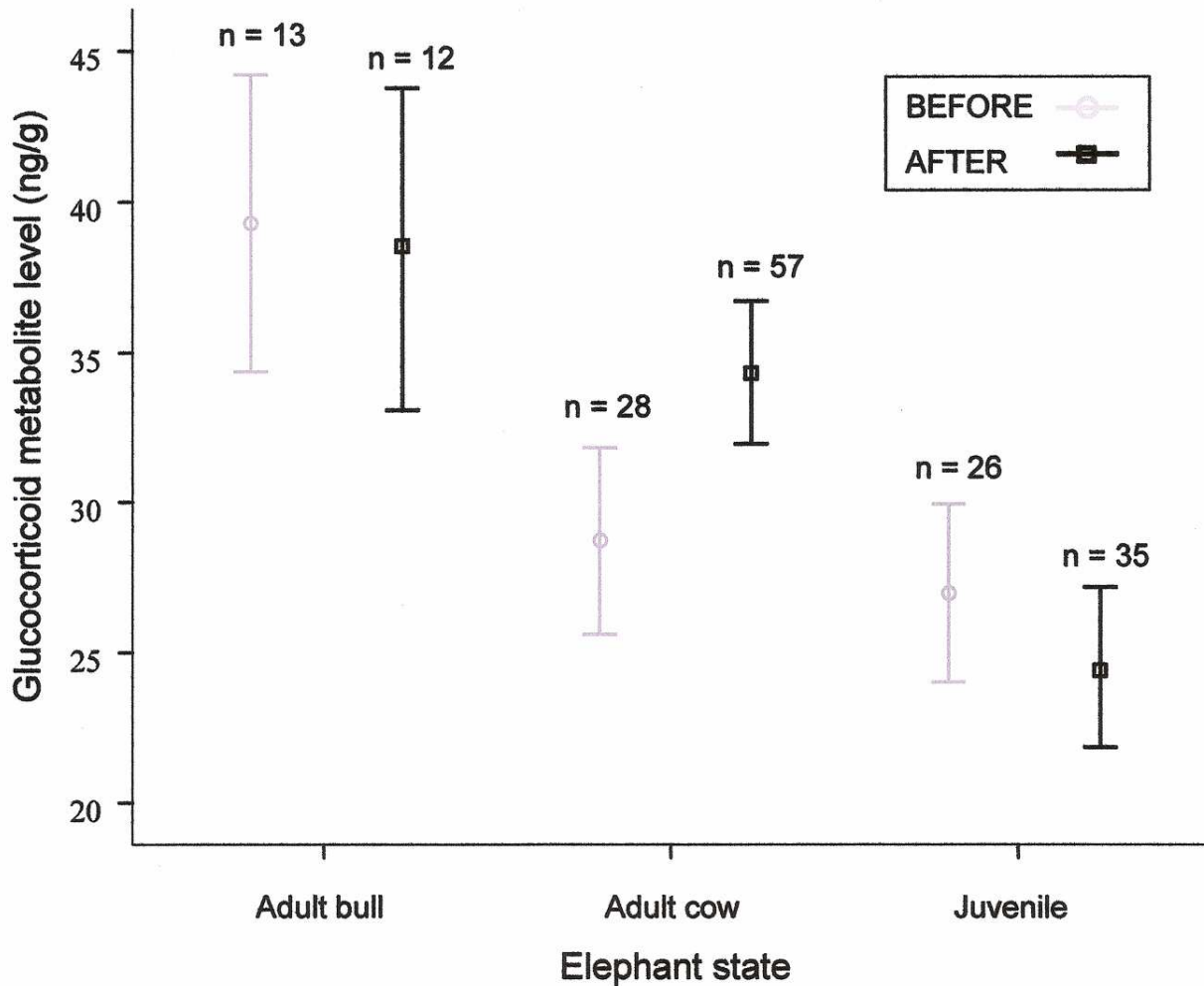


Figure 3. Physiological response to fire indicated by glucocorticoid metabolite (stress) levels (mean \pm 95% CL) for adult bulls, adult cows and juveniles before and after the fire. Sample size (n) is shown above each category.

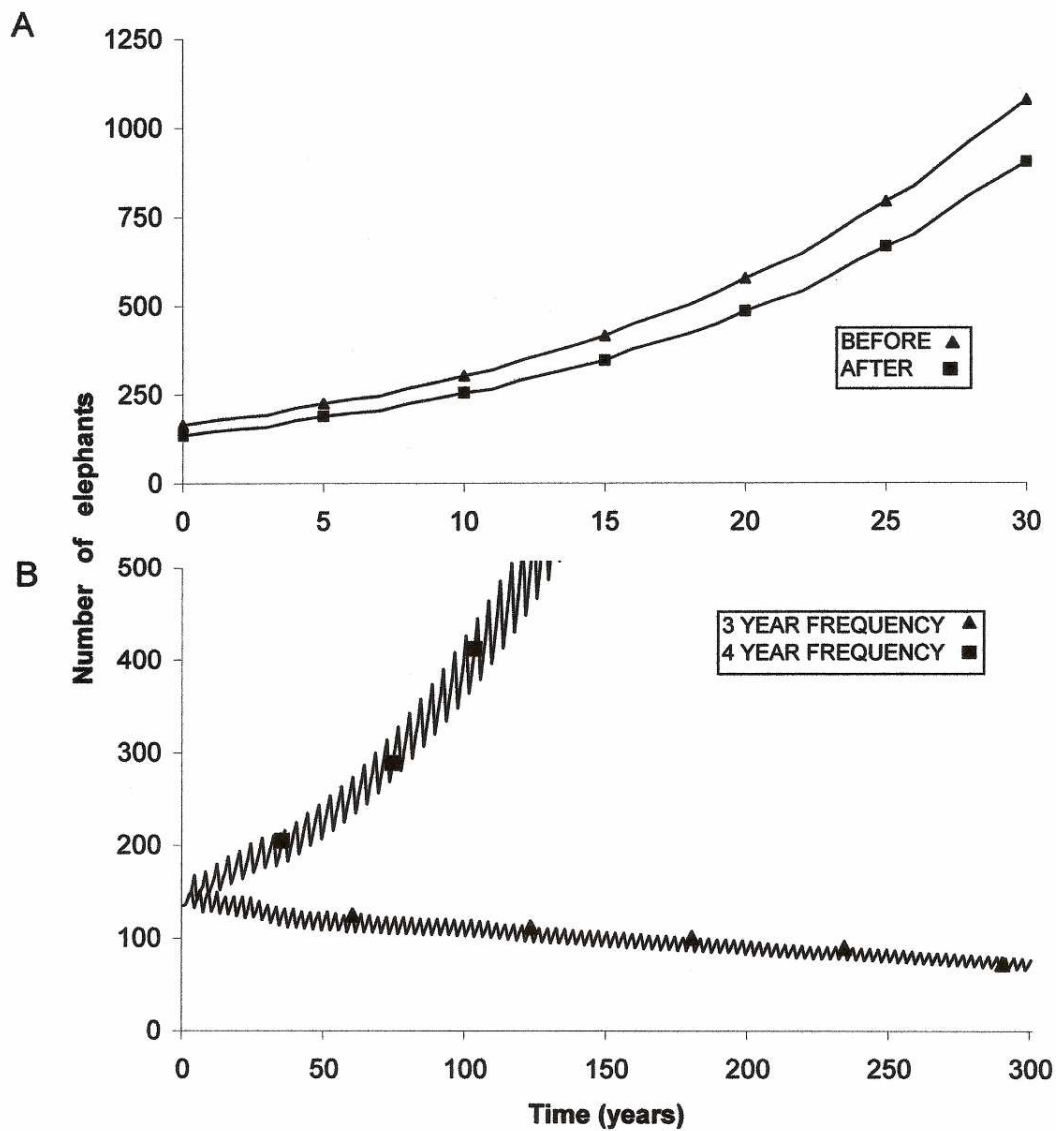


Figure 4. The effect of fire on the future Pilanesberg National Park elephant population: (A) comparative modelled projection over a 30 year period using population data before and then after the fire in September 2005; (B) effect of three year and four year fire frequency on population size over a 300 year period using population data before the fire, and the mortality parameters associated with this fire event.

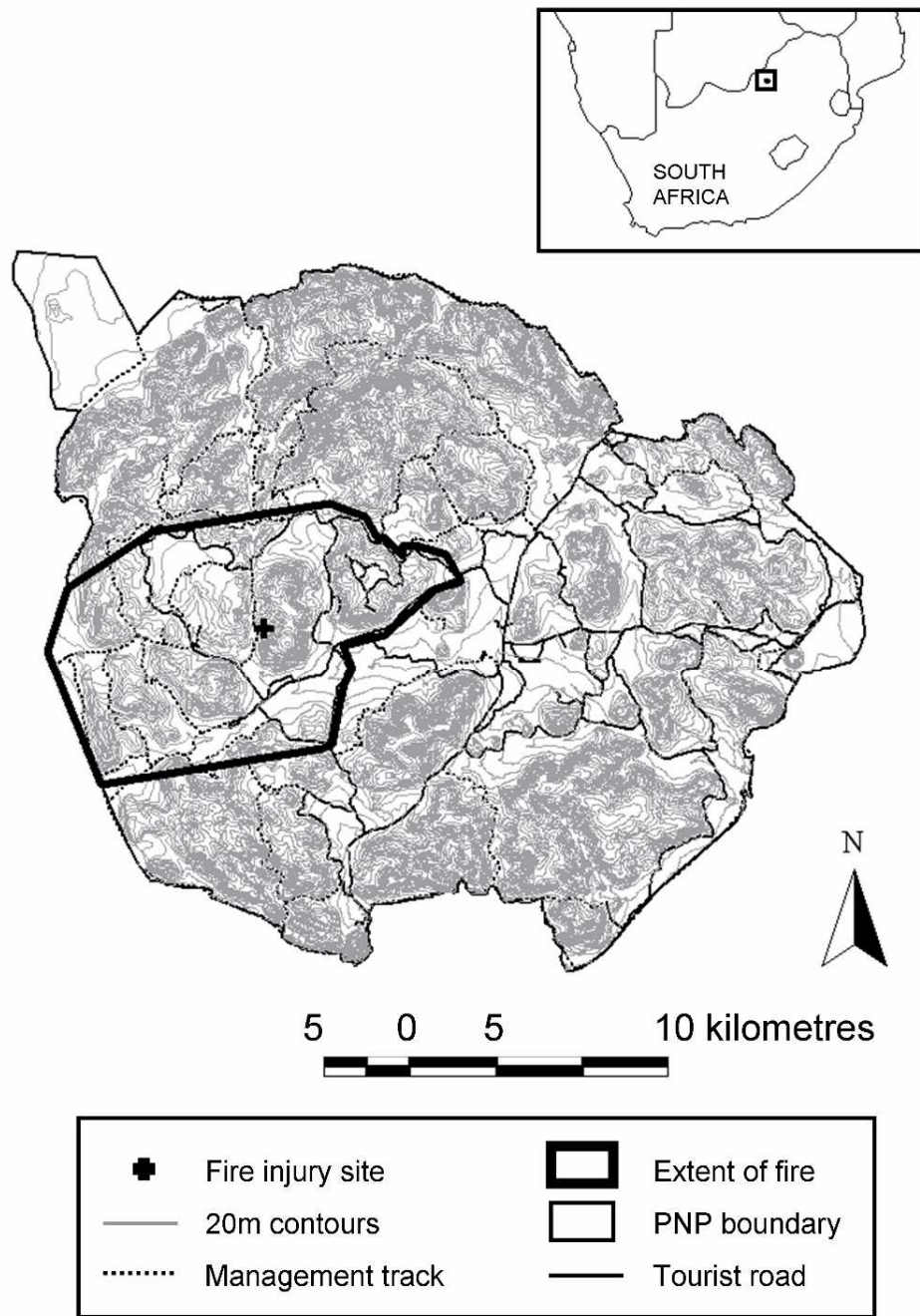


Figure 5. Map of Pilanesberg National Park incorporating 20m contours, tourist roads, management tracks, the site where elephants were injured in a fire on 21 September 2005 and the approximate extent of the fire.

Chapter 4

Intraspecific Strategic Responses of African Elephants to Temporal Variation in Forage Quality

Leigh-Ann Woolley^{1*}, Joshua J. Millsaugh², Rami J. Woods²,
Samantha Janse van Rensburg¹, Bruce Page¹, Rob Slotow¹

¹ *Amarula Elephant Research Programme, School of Biological and Conservation
Sciences, Westville Campus, University of KwaZulu-Natal, Private Bag X54001, Durban
4000, South Africa.*

² *Department of Fisheries and Wildlife Sciences, 302 Natural Resources Building,
University of Missouri, Columbia, Missouri 65211, USA.*

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ABSTRACT

Mammalian herbivores adopt foraging strategies to optimize nutritional trade-offs against restrictions imposed by body size, nutritional requirements, digestive anatomy, physiology, and the forage resource they exploit. Selective or generalist feeding strategies scale with body size across species. However, within-species where constraints should be most similar, responses to limitation have rarely been examined. We used African elephants (*Loxodonta africana*) to test for changes in seasonal diet quality of individuals of differing body size and sex through measurement of fecal nitrogen and phosphorus. We measured physiological stress response of these age and sex classes to seasonal change by fecal glucocorticoid metabolite levels (i.e. stress hormones). Large body size increased tolerance to lower quality forage. Adult males and females exhibited divergent trends; females had higher diet quality than males, irrespective of body size. When limited by forage availability or quality during the dry season, diet quality declined across all body sizes, but weaned calves ingested a higher quality diet than larger-bodied adults. On release from restriction during the wet season, weaned calf nitrogen concentrations were consistently high and stress hormone levels decreased, whereas adult female phosphorus levels were highest and less variable and stress hormone levels were unchanged. The ability to adjust forage quality is an important strategy used to ensure adequate nutritional intake according to body size limitations. Although body size is a key determining factor of dietary differences between adult elephants, foraging strategies are also driven by specific nutritional requirements, which may override the body size effects driving foraging decisions in some cases. The diversity of intraspecific response highlights ecologically segregated entities within a species and should be a concern for population management planning, particularly for threatened species. Fecal diet quality and stress hormone analysis could provide an early and sensitive indicator for monitoring age and sex class responses to resource restriction in high-density elephant populations.

KEY WORDS Allometry, dimorphism, foraging strategy, limitation, *Loxodonta africana*, nutrition, seasonal restriction, South Africa.

INTRODUCTION

Mammalian herbivores use various strategies to cope with changes in forage quality and quantity available at any one time. The ability of an herbivore to respond strategically to resource limitation can be critical to its fitness or survival (McNaughton and Georgiadis 1986). Body size and digestive strategy affect costs and benefits incurred by herbivore decisions to select higher quality forage (Clauss et al. 2003). Selective (i.e., active selection for high quality forage) or generalist (i.e., acceptance of lower quality forage in accordance with availability) feeding strategies scale with body size across species (Bodmer 1990, Gordon and Illius 1994, Robbins et al. 1995). In general, small herbivores are selective feeders, with their small size constraining digestive capacity (van Soest 1996, Clauss et al. 2003). Larger herbivores have the advantage of increased digestive capacity (mean retention) and therefore can use large quantities of lower quality forage (van Soest 1996, Clauss et al. 2003). Large herbivores with hindgut fermentation (e.g. African elephant [*Loxodonta africana*]) can utilize lower quality forage by maximising throughput rate. In contrast ruminants use more efficient foregut fermentation so large ruminants (e.g. giraffe [*Giraffa camelopardalis*]) can meet their nutritional requirements using a more selective foraging strategy (Clauss et al. 2007). Therefore, species-specific characteristics can constrain all individuals to follow a particular strategy regardless of body size. However, there may be a need to overcome the species-specific constraint due to the variable requirements of growth and reproduction. The same responses to being selective or generalist may thus apply to individuals of different body size within the same species, particularly in dimorphic species where body size can vary more within-species than among-species. Nutritional requirements vary not only according to body size but also the life-history stage of the animal, as predicted by high juvenile growth rates and adult reproductive demands (Meissner 1982). Therefore smaller-bodied, younger herbivores may adopt a different feeding strategy to larger-bodied, older herbivores in different stages of reproductive output. The influence of body size and nutritional requirement applies to both among-species differences, as well as to intraspecific differences among juveniles, adults, and different sexes within the same species.

To evaluate whether seasonal variation in forage availability results in an adjustment in forage quality selection strategy within a species, we used the African elephant as a test subject due to the large difference in body size between calves (200 – 800 kg), adult females (1,500 – 2,500 kg), and adult males (3,000 – 5,000 kg; Laws et al. 1975). The African elephant is also a generalist, mixed feeder with the ability to adjust the quality of forage ingested by varying the type of forage (browse–grass) ingested (Cerling et al. 2006), as well as plant part (even to the point of uprooting woody species to access roots; Stokke and du Toit 2000, Shannon et al. 2006a), to maximize nutritional intake. The higher tolerance of large-bodied herbivores to lower quality diets has been used to explain differences between species of different body size (e.g. Demment and van Soest 1985, du Toit and Owen-Smith 1989, Clauss and Lechner-Doll 2001), as well as sexual dimorphism in ungulates and the African elephant, where it was shown that smaller-bodied adult females selected a diet of higher quality than large-bodied adult males (e.g. Beier 1987, du Toit 1995; Stokke and du Toit 2000). Divergent growth patterns are exhibited for male and female elephants after adulthood is reached, whereupon males grow more quickly and continue to grow into old age, whereas female growth slows dramatically and stops at around 30 years (Lee and Moss 1995, Morrison et al. 2005, Shrader et al. 2006). Therefore older females may be similar in body size to younger adult males. Increased nutritional demands imposed on adult females by pregnancy or lactation means that adult male and female elephants of similar body size are likely to have differing nutritional requirements (van Soest 1996). Furthermore, few studies have investigated intraspecific differences in feeding ecology dictated by body size disparities between juveniles and mature individuals of the same species (e.g. Hooper and Welch 1983, Munn et al. 2006). Due to lack of gastrointestinal development and small body size, juveniles may be unable to cope with adult diets or diets of low quality (e.g. Munn and Dawson 2006). The stress response of herbivores to nutritional restriction may help forewarn of critical levels of diet quality changes and offers a unique view of the consequences of the foraging choices being made. Fecal glucocorticoid metabolite levels have been used to investigate African elephant stress levels during stressful events such as transportation and culling (e.g. Millspaugh et al. 2007, Burke et al. 2008) and have been linked to seasonal nutritional stress (Foley et al. 2001, Viljoen et al. 2008).

Therefore, our main aim was to assess whether elephants adjust the quality of their seasonal diet to cope with nutritional requirements dictated by body size and life-history stage and whether there is a corresponding change in stress hormone levels, which we evaluated through: 1) diet quality differences between adult males, adult females, and weaned calves measured using fecal nutrient analysis and 2) the resultant effect of such dietary differences on stress using fecal hormone analysis. We predicted: 1) diet quality would scale with body size (i.e. ad M would ingest the lowest quality diet and weaned calves the highest quality diet); 2) variability in nutritional requirements would differentiate diet quality in adult elephants of similar body size but different sex, and these relationships would be more pronounced in the dry season; and 3) seasonal nutritional stress would cause increased stress levels in the dry season.

STUDY AREA

Pilanesberg National Park (PNP, 25°24'S, 27°08'E, 570km²) was located in the North West Province of South Africa, in the transition zone between the dry Kalahari Thornveld to the west and the wetter Bushveld region to the east (Acocks 1988), providing unique overlaps in fauna and flora specific to each of these vegetation types. Pilanesberg National Park was a geologically important area, formed by volcanic activity 1,200 million years ago to produce an alkaline ring complex and resultant rugged landscape after weathering (Boonzaaier and Collinson 2000).

Rainfall averaged 630 mm annually, with approximately 90% falling during summer between November and April. There was one major river system in PNP and many ephemeral tributaries and streams, with several dams making water supply plentiful throughout the Park, especially in the wet season. The combination of rainfall, geology, and landscape gave rise to diverse habitat types ranging from broadleaf thickets to open grasslands, with rocky hillsides mainly consisting of broad-leaf species e.g. Red bushwillow *Combretum apiculatum*, Live-long *Lannea discolor*, Transvaal beech *Faurea saligna*, Lavender fever-berry *Croton gratissimus*, Small-leaved bride's bush *Pavetta zeyheri* and the bottomlands mainly accommodating fine-leafed species e.g. Umbrella

thorn *Acacia tortilis*, Sweet thorn *A. karroo*, Black thorn *A. mellifera*, whereas the herbaceous layer was dominated by tufted perennial grasses (Brockett 1993).

Between 1981 and 1998, elephants were reintroduced to PNP (Slotow and van Dyk 2004) and at the beginning of the study in September 2003, the population totaled approximately 150 individually identified elephants, of which 35 were independent adult males and 115 formed part of 18 stable matriarchal family groups. However, mortality due to a fire in September 2005 (Woolley et al. 2008) reduced the population from 165 to 136 elephants.

METHODS

We collected fecal samples opportunistically during the wet season (late Nov – early Apr) and dry season (late Jun – early Nov) from September 2003 to February 2006, with concentration of efforts during the late dry season from September to first spring rains (early Nov) and during the wet summer months from approximately 2 weeks after first spring rains (i.e. post green flush approx. late Nov) to February.

We measured the mean diameter of an intact bolus of fresh dung (< 6 hr since deposition) according to Morrison et al. (2005) to give an indication of body size (and approx. age) of the donor elephant. Mean dung bolus diameter is strongly correlated with African elephant body size (Morrison et al. 2005). A seasonal change in the fiber content of the diet causes the bolus produced by an individual to vary in fiber content (bulk density), but size of the bolus remains consistent in diameter and is thus depends on anal size (Wimberger 2001).

We collected samples of fecal matter from the inner core of a bolus, placed them in a cooler immediately, and stored them frozen within a few hours of collection. Some samples came from known individuals (diet quality samples $n = 67$, stress hormone samples $n = 82$), whereas others came from unknown donors (diet quality samples $n = 161$, stress hormone samples $n = 179$). In the case of unknown donors, we classified mean dung bolus diameters (MDBD) of 8 – 11 cm as belonging to weaned calves.

Weaning generally occurs at birth of the next sibling and with a mean calving interval of 3 years in the PNP population, the MDBD corresponding with age at first weaning of 3 years according to Morrison et al. (2005) was 7.5 – 8 cm (Lee and Moss 1986, Mackey et al. 2006). We calculated mean female age at sexual maturity of the PNP population at approximately 10 years, which corresponds with MDBD of approximately 11 cm (Morrison et al. 2005, Mackey et al. 2006). Therefore we classified samples >11 cm in diameter as those excreted by adult elephants. Adult elephants are sexually dimorphic and changes in MDBD follow the typical growth pattern observed in African elephants (Morrison et al. 2005). To distinguish between differences in adult sex classes, we evaluated the sex of anonymous adult donors according to the presence of single (indicative of independent ad M) or multiple (breeding herd) tracks, as well as size of the dung bolus. We ignored unknown samples with MDBD of 11 – 15 cm collected from breeding herd sites if we found young males associating with the source herd, to ensure that we used only female donors. We considered MDBD >16 cm to belong to an adult male, as all but one adult female in the PNP population were <30 years of age at the time of sampling (corresponding to a MDBD of approx. 14 – 15 cm). We classified adult males with MDBD 11 – 16 cm as smaller-bodied and MDBD >16 cm as large-bodied.

We used fecal nitrogen (N_f) and phosphorus (P_f) concentrations as indices of diet quality. Under conditions of consistent study site and herbivore population, and across broad seasonal trends, measurement of N_f has been a useful index of dietary nitrogen for both temperate (e.g. Mubanga et al. 1985, Leslie and Starkey 1987, Howery and Pfister 1990, Kamler and Homolka 2005) as well as southern African ungulates (e.g. Grant et al. 1995, Wrench et al. 1996, Wrench et al. 1997, van der Waal et al. 2003, Mbatha and Ward 2006). Fecal phosphorus concentrations are strongly correlated with dietary phosphorus concentrations and a further indication of dietary quality but are consistent across all feeding types (i.e. browser, grazers and mixed feeders; Belonje 1980, Howery and Pfister 1990, Grant et al. 1995, Wrench et al. 1996, Grant et al. 2000).

We dried fecal samples at 90° C for 36 hours and ground them through a 1-mm mesh in a Retsch Mill (Retsch Inc., Haan, Germany). We determined N_f in duplicate by the Dumas

Combustion method in a Leco FP-2000 Nitrogen Analyzer (Leco, St. Joseph, MO) by AOAC Official Method 990.03 (AOAC International 2002). From fecal material derived from the same dung samples used in N_f analyses (total $n = 228$), we determined P_f in duplicate using a Technicon Autoanalyser II (SEAL Analytical Limited, West Sussex, England) by AOAC Official Method 965.17 (AOAC International 2002), after initial digestion in sulphuric acid, hydrogen peroxide and a selenium catalyst using a block digester at 360° C. We present N_f and P_f results on a dry matter (DM) basis.

We measured levels of glucocorticoid metabolites from fecal samples using a modification of Schwartzenberger et al. (1991) described by Wasser et al. (2000), involving the use of a corticosterone I^{125} radioimmunoassay kit (MP Biomedicals, Solon, OH), which has been validated for elephants (Wasser et al. 2000, Millspaugh et al. 2007). Where possible we used fecal material derived from the same raw dung samples we used in diet quality analyses and we also included additional samples (total $n = 264$). However, unlike samples used in the diet quality analyses, we prepared stress hormone analysis samples differently. For glucocorticoid metabolite assessment, samples remained frozen until we freeze-dried them for 24 hours and sieved the feces to remove woody material prior to hormone extraction. Adult female stress hormone levels increased significantly after a catastrophic fire in September 2005, whereas adult male and weaned calf stress hormone levels did not change significantly (Woolley et al. 2008). Therefore we did not include postfire adult female samples in stress hormone samples, but we did include weaned calf and adult male samples to maximize power for statistical analyses. All work on live animals was approved by the Animal Ethics Committee of the University of KwaZulu-Natal (010/08/Animal).

We compared N_f , P_f , and stress hormone concentrations between the wet and dry season and among elephant classes (i.e. weaned calf, ad F, large-bodied ad M, small-bodied ad M) using 2-way analyses of variance (ANOVA). It was highly improbable that dung samples collected during the wet season came from identical individuals during the dry season and we considered these time periods independent; thus we did not use repeated-measures ANOVA. We validated assumptions using the Kolmogorov-Smirnov test for

normality and Levene's test for homogeneity of variances. We investigated significant differences detected by ANOVA further with post-hoc tests (Tukey). We could not perform post-hoc tests for season because there were <3 groups. Consequently, we could not perform post-hoc tests for class \times season interactions, but we tested the significance of these relationships further using independent-samples *t*-tests. We assessed variability in seasonal N_f , P_f , and stress hormone concentrations using the coefficient of variation. We assessed the magnitude of the effects of N_f and P_f on stress hormone concentrations using multiple linear regression and we used Pearson Correlation to test the significance and strength of relationship between N_f and P_f . We used SPSS 15.0 (SPSS Inc., Chicago, IL) for all statistical analyses with $\alpha = 0.05$ unless otherwise stated. We applied 1-tailed tests in circumstances where there was a clear uni-directional hypothesis and we were concerned with lack of statistical power (Sokal and Rohlf 1995).

RESULTS

We considered differences statistically significant at $\alpha = 0.05$. Comparison of data between years showed no difference ($P > 0.05$), therefore we pooled data from each season of each year over the study period.

Season and elephant class affected N_f whereas the interaction between class and season was not significant (Table 1). In general, large (>16 cm MDBD) and small (11 – 16 cm MDBD) adult males had 25% lower overall N_f than adult females and weaned calves (Table 1). Adult female N_f did not differ from those of weaned calves, nor did N_f of large adult males differ from small adult males (Table 1).

When analyzed on a seasonal basis, dry season N_f for all elephant states were 20% lower than wet season concentrations (Table 1). Weaned calf N_f was higher than other age and sex classes during both the dry (7% higher than ad F, 20% higher than ad M) and wet season (7% higher than ad F, 30% higher than ad M; Table 1, Fig. 1). Adult female dry and wet season N_f was 25% higher than that of small adult males and large adult males (Table 1, Fig. 1). However, N_f of large and small males did not differ in neither the dry nor wet season (Table 1, Fig. 1).

Season and elephant class affected P_f , but the interaction between class and season was not significant (Table 1). Adult males (large and small) had 30% lower overall P_f than adult females and weaned calves, whereas adult females and weaned calves, as well as large adult males and small adult males, were similar (Table 1).

Dry season P_f for all elephant states were 30% lower than wet season concentrations. Weaned calf P_f were highest during the dry season (Table 1, Fig. 1). During the wet season adult female P_f were highest, but not different from that of weaned calves (Table 1, Fig. 1). Weaned calf P_f increased by 25% from dry to wet season, whereas adult female P_f increased by 50%. Although wet season weaned calf P_f was 35% higher than that of large adult males, it was not different from that of small adult males (Table 1, Fig. 1). Adult female P_f was 30% higher than that of adult males (large and small) in the dry season (Table 1, Fig. 1). Large and small male P_f were not different from one another in the dry season or wet season (Table 1, Fig. 1). During the wet season, weaned calves consistently had higher N_f (lower CV in wet season), whereas adult female P_f were more consistently (i.e. lower CV) higher in the wet season (Table 1, Fig. 1).

Elephant class affected glucocorticoid metabolite (stress hormone) level, but season did not, and there was no interaction between class and season (Table 1). Both large and small adult males had 30% higher stress hormone levels than adult females and weaned calves (Fig. 1) but were not different from each other (Table 1, Fig. 1). Adult female stress hormone levels were 15% higher than those of weaned calves (Table 1, Fig. 1).

Overall dry season stress hormone levels were not different from wet season levels (Table 1). However, there was an 8% decline in weaned calf stress hormone level from dry to wet season (Table 1, Fig. 1). Stress hormone levels were affected by N_f but not P_f (Table 1). Factoring out N_f and P_f , class and season also had an effect on overall population stress hormone levels (Table 1).

There was a significant increase in N_f with increasing P_f across all samples, as well as within both the dry season and wet season (Table 1). There was a general trend of decline in N_f and P_f (diet quality) with increasing body size (Fig. 2). Weaned calves had a similar diet quality independent of sex, but divergence occurred approximately at adult body size (11 cm MDBD), whereupon adult males had a lower diet quality than adult females (Fig. 2).

DISCUSSION

Elephant diet quality fluctuated with seasonal variation in resources. We found a general scaling of elephant diet quality with body size, and clear sexual dimorphism. Within body size classes, sex of the elephant and therefore the reproductive state of the individual affected quality of diet ingested, as male and female diet quality differed between individuals of similar body size. A mean calving interval of 3 years in PNP suggests that nutritional demands are maximized by almost continuous pregnancy or lactation during a female's adult life (Mackey et al. 2006). Peak lactation can increase female elephant energy demands by 30% (Meissner 1982, Meissner et al. 1990). Due to these reproductive demands, adult females exploited a higher quality diet than similar-sized males. Pregnant and lactating goats (*Capra hircus*) in the Chihuahuan desert, Mexico, responded to increased nutritional requirements by adjusting their diet selection according to their metabolic needs (Mellado et al. 2005). Lactating grazers have been shown to increase intake rate through an increase in grazing time (Clutton-Brock et al. 1982, Pulido et al. 2001). The inclusion of smaller, slower calves within the elephant breeding herd dictates the rate of movement of the herd, which limits the adult females' ability to cover enough ground to increase ingestion of a sufficient quantity of forage to meet nutritional requirements. With this limitation on the quantity of forage ingested, compensation in forage quality is a reasonable strategic response.

One of the primary strategic responses exhibited by adult females and calves (breeding herds) to allometric influences on nutritional requirements is to increase forage quality ingested (Stokke 1999; Stokke and du Toit 2000; Shannon et al. 2006a, b). Foraging strategies influence ranging behaviour, with breeding herds moving quickly through an

area, selecting for higher quality forage and moving on, whereas adult males increase intake of lower quality forage, spending more time on one foraging bout, and can be more destructive in their foraging behaviour (e.g. uprooting large woody species; Stokke 1999; Stokke and du Toit 2000; Shannon et al. 2006a, b). Adult males therefore have a heterogeneous impact on the landscape, as some areas can be severely impacted and others are not, whereas breeding herds spend less time in one area and their need to cover more ground to increase forage quality intake means that vegetation impact is spread more evenly over the landscape (Slotow and van Dyk 2004; Shannon et al. 2006a, b).

During the wet season, African elephants predominantly feed on grass, which is generally higher in digestibility and dietary quality than browse at this time of year (van Soest 1996, Cerling et al. 2006), but switch to browse during the dry season when grass becomes fibrous and less nutritious (Cerling et al. 2006). Wet season diet is therefore expected to be of higher quality than dry season diet, as supported by our data. Elephant N_f from the southern Kruger National Park also showed a dramatic increase from dry to wet season (Codron et al. 2006). Seasonal trends in forage quality (N_f and P_f) were found on East African grasslands (Boutton et al. 1988) as well as in semi-arid savannas of South Africa for zebra (*Equus burchelli*), wildebeest (*Connochaetes taurinus*), impala (*Aepyceros melampus*), kudu (*Tragelaphus strepciseros*), and buffalo (*Syncerus caffer*; Bodenstein et al. 1999, Grant et al. 2000, van der Waal et al. 2003).

Overall, N_f and P_f values we found for elephants were lower than concentrations recorded for other large herbivores (e.g. Wrench et al. 1997, Bodenstein et al. 1999, Grant et al. 2000, van der Waal et al. 2003). A minimum level of 12 – 14 g/kg N_f has been associated with a deficiency in dietary nitrogen in zebra, buffalo, impala, kudu and cattle (*Bos indicus*; Wrench et al. 1997, Grant et al. 2000, van der Waal et al. 2003), whereas long-term $P_f < 2.0$ g/kg may be associated with deficiencies severe enough to cause a drop in body condition and low reproductive rates in wildebeest, zebra, impala and cattle (Moir 1966, Wrench et al. 1997, Dörgeleh et al. 1998, Grant et al. 2000). With N_f and P_f well below these thresholds, elephants of PNP showed a slight drop in body condition during the dry season, but excellent body condition in the wet season, normal juvenile growth

patterns, and no calf mortality from starvation (Woolley, University of KwaZulu-Natal, personal observation). Therefore, the thresholds discussed above should allow for the influence of body size on forage quality tolerance and nutritional requirements for large-bodied herbivores. Diet supplementation policies should extend thresholds of concern for larger, free-ranging herbivore species.

With an increase in nutrient availability during the wet season, adoption of a more selective foraging strategy to suit nutritional requirements becomes an option for smaller-bodied individuals who can invest time in the active search for higher quality forage. During the wet season, weaned calves consistently had higher N_f , whereas adult females consistently had higher P_f . Phosphorus requirements during pregnancy and lactation could be driving adult female elephants' foraging decisions, whereas N requirements for growth may be driving weaned calf foraging decisions. Phosphorus is a limiting mineral in PNP (Moolman 2007), therefore pregnant or lactating females may need to target sources of phosphorus to ensure requirements are met when availability is high, as it is possible that phosphorus stored during times of excess may be remobilized (Scholes and Walker 1993). Migration of wildebeest in East African savannas has been linked to phosphorus requirements during lactation (Voeten 1999), whereas greater densities of grazing ungulates occurred in a region of the Serengeti where greater nitrogen ingestion was possible (Seagle and McNaughton 1992). Elephant feeding preferences in the miombo woodlands of Kasungu National Park, Malawi, were positively correlated with leaf sodium, magnesium, crude protein, and sugar concentration (Jachmann and Bell 1985) but negatively associated with lignin and high levels of total phenols (Jachmann 1989). Elephant damage to trees in western Zimbabwe was found to correlate positively with leaf calcium, magnesium, potassium, and protein, but not sodium, phosphorus, or fiber (Holdo 2003). These studies did not differentiate intraspecific elephant impact, which may vary in accordance with nutritional requirements dictated by life-history stage. Nutrient limitation is clearly a broad driver in the ecosystem (McNaughton 1992, Scholes and Walker 1993, Singer and Schoenecker 2003), but our results indicate that within the overall nutrient landscape, individuals can select forage to increase intake of limiting nutrients (e.g. Augustine et al. 2003, Seagle 2003).

Elephant breeding herd fecal stress hormone levels were higher in the dry than wet season in the southern Kruger National Park (Viljoen et al. 2008). There is seasonality in forage quality and availability in PNP, but water is not restricted dramatically in the dry season, as it is in Kruger. Seasonal stress indicated in Kruger, but not PNP, suggests the importance of water as a vitally restrictive resource for elephant populations. The manipulation of active waterholes has been advocated as a method of elephant management in closed, fenced systems (Owen-Smith et al. 2006) and dry season waterhole activity has been linked to density-dependent elephant population limitation in open systems (Chamaille-Jammes et al. 2008).

Change in season had a greater impact on weaned calf than adult stress hormone levels, implying that nutritional stress is an important factor influencing weaned calf well-being. In general, adult female stress hormone levels were higher than that of weaned calves. With greater social responsibility, this higher stress level is expected for adult females, as an animal's reaction to stressors is influenced by its position in the social group and social status can influence glucocorticoid concentrations (Moss and Poole 1983, Goymann and Wingfield 2004, Wittemyer et al. 2005). Adult males engage in scramble competition for mates and establish a dominance hierarchy using aggression, where the oldest, largest males enter into a state of musth and search out receptive females (Poole 1989). We speculate that these social pressures are amongst some of the many possible explanations for the higher stress hormone levels evident in adult males than in females or calves. Population stress hormone levels varied with N_f in the diet. Therefore, although nutritional stress strongly affected the stress hormone levels of weaned calves, there are many other factors, such as sociality, that compound these effects and cause an adjustment in stress levels. Fecal stress hormone level measures may provide a useful indication of diet quality deficiency in the smallest-bodied individuals most sensitive to nutritional stress.

Based on our results, severe forage restriction (e.g. during drought) is more likely to affect younger elephants. Although adult females may cease lactation or abort a fetus in

times of severe nutritional stress (Lee and Moss 1986, Moss 2001), calves cannot reduce nutritional requirements. It is therefore unsurprising that juvenile elephant mortality is high during prolonged drought periods, whereas adult mortality remains low (Dudley et al. 2001, Moss 2001, Foley et al. 2008). One of the mechanisms involved in juvenile mortality patterns seen in predator-free, large herbivore population dynamics may therefore be the strong allometric relationships between requirements and responses driving patterns of forage quality ingestion (Gaillard et al. 1998, 2000).

MANAGEMENT IMPLICATIONS

Individual use of the environment can vary depending on body size, age, and sex (life-history stage), as well as the resultant nutrient and energy requirements driving foraging decisions. These effects need to be considered in population management planning, particularly for threatened species, where appreciation of the intricacies of intraspecific variation can improve decision-making if assumptions are made at the cohort level rather than a broad species level.

Diet quality and stress hormone assessment through fecal analysis provides a non-invasive management tool that could be very useful in the evaluation of the nutritional condition of elephant populations in resource-limited systems, such as in high density areas. Density-dependent feedbacks are the result of resource limitation due to competition and manifest in elephant populations as effects on vital rates (e.g. increased female age at first breeding, lengthened inter-calving intervals) and increased juvenile mortality (Laws et al. 1975). However, the exact stage at which these effects become evident in elephant populations living in different climates and habitats remains poorly understood. Further, there will be a lag in density-dependent effects manifesting in population vital rates, particularly in species with long gestation times such as elephants. Monitoring of diet quality and stress hormone levels can assist in the evaluation of the potential limit at which elephant populations become restricted, by providing an early, and sensitive, indicator for managers.

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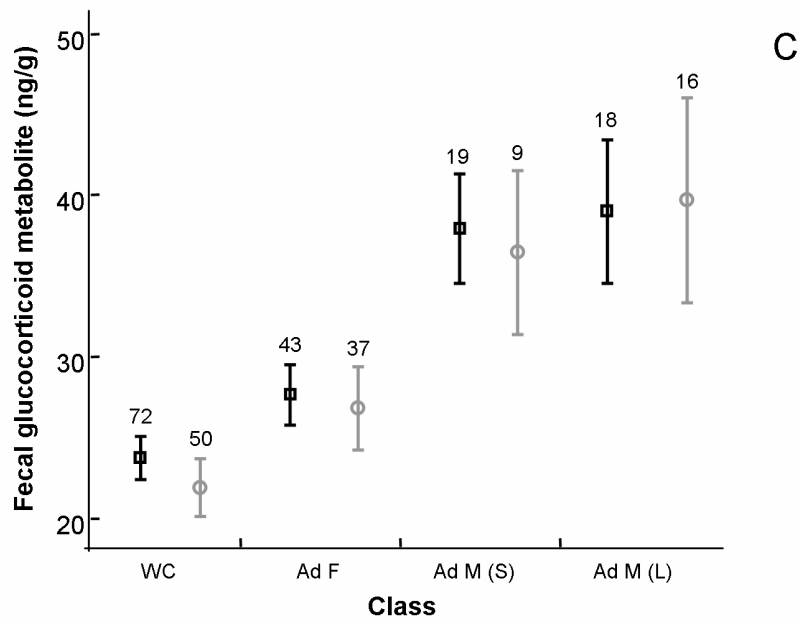
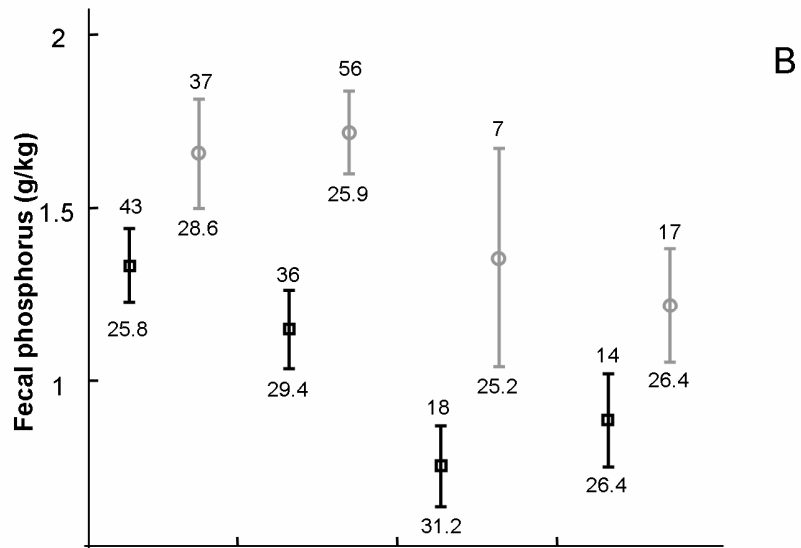
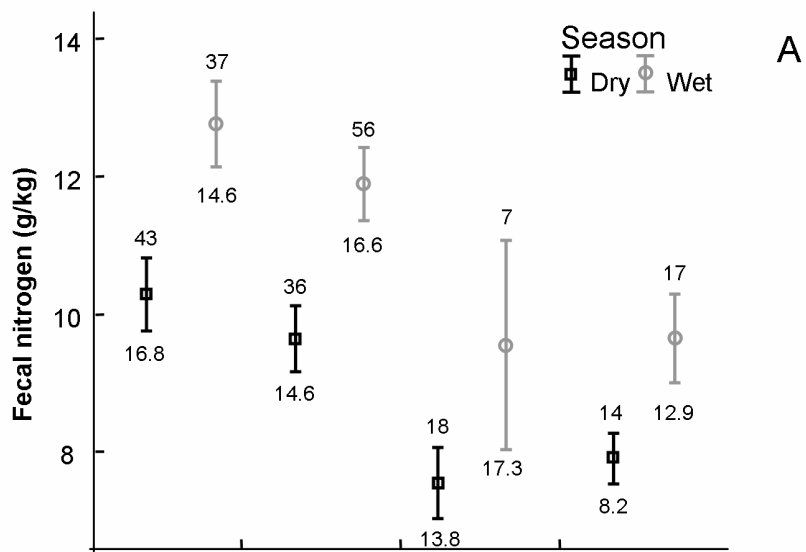
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Table 1. Statistical values for analyses of variance (ANOVA), post-hoc tests and t-tests on fecal nitrogen (N_f), fecal phosphorus (P_f) and fecal glucocorticoid metabolite concentrations (stress) from African elephant weaned calves (WC), adult females (Ad F), small adult males (Ad M S), and large adult males (Ad M L) in Pilanesberg National Park from Sep 2003 – Mar 2006. Statistical values for interaction relationships given for regression of N_f , P_f on stress and correlation of N_f and P_f .

	Fecal nitrogen (N_f)		Fecal phosphorus (P_f)		Glucocorticoid metabolites (stress)	
ANOVA						
Season	$F_{1,220} = 61.972$	$P < 0.001^*$	$F_{1,220} = 54.018$	$P < 0.001^*$	$F_{1,253} = 0.593$	$P = 0.442$
Class	$F_{3,220} = 31.462$	$P < 0.001^*$	$F_{3,220} = 15.394$	$P < 0.001^*$	$F_{3,253} = 63.547$	$P < 0.001^*$
Season \times class	$F_{3,220} = 0.382$	$P = 0.766$	$F_{3,220} = 1.978$	$P = 0.118$	$F_{3,253} = 0.264$	$P = 0.851$
Post-hoc						
Class (Tukey)						
WC – Ad F	$P = 0.349$		$P = 0.997$		$P < 0.001^*$	
WC – Ad M S	$P < 0.001^*$		$P < 0.001^*$		$P < 0.001^*$	
WC – Ad M L	$P < 0.001^*$		$P < 0.001^*$		$P < 0.001^*$	
Ad F – Ad M S	$P < 0.001^*$		$P < 0.001^*$		$P < 0.001^*$	
Ad F – Ad M L	$P < 0.001^*$		$P < 0.001^*$		$P < 0.001^*$	
Ad M S – Ad M L	$P = 0.319$		$P = 0.486$		$P = 0.730$	
Season						
Population	$F_{1,220} = 61.972$	$P < 0.001^*$	$F_{1,220} = 54.018$	$P < 0.001^*$	$F_{1,253} = 0.593$	$P = 0.442$
WC (dry vs wet)					$t_{(1),117} = 1.709$	$P = 0.045^*$
Dry						
WC – Ad F	$t_{(1),77} = 1.781$	$P = 0.040^*$	$t_{(2),77} = 2.402$	$P = 0.019^*$		
WC – Ad M S	$t_{(2),59} = 6.288$	$P < 0.001^*$	$t_{(2),59} = 6.536$	$P < 0.001^*$		
WC – Ad M L	$t_{(2),55} = 5.042$	$P < 0.001^*$	$t_{(2),55} = 4.532$	$P < 0.001^*$		
Ad F – Ad M S	$t_{(2),52} = 5.610$	$P < 0.001^*$	$t_{(2),52} = 4.455$	$P < 0.001^*$		
Ad F – Ad M L	$t_{(2),48} = 4.427$	$P < 0.001^*$	$t_{(2),48} = 2.672$	$P = 0.010^*$		
Ad M S – Ad M L	$t_{(2),30} = -1.138$	$P = 0.264$	$t_{(2),30} = -1.589$	$P = 0.123$		
Wet						
WC – Ad F	$t_{(2),91} = 2.122$	$P = 0.037^*$	$t_{(2),91} = -0.641$	$P = 0.523$		
WC – Ad M S	$t_{(2),42} = 4.247$	$P < 0.001^*$	$t_{(2),42} = 1.592$	$P = 0.119$		
WC – Ad M L	$t_{(2),52} = 6.238$	$P < 0.001^*$	$t_{(2),52} = 3.459$	$P = 0.001^*$		
Ad F – Ad M S	$t_{(2),61} = 3.001$	$P = 0.004^*$	$t_{(2),61} = 2.065$	$P = 0.043^*$		
Ad F – Ad M L	$t_{(2),71} = 4.393$	$P < 0.001^*$	$t_{(2),71} = 4.286$	$P < 0.001^*$		
Ad M S – Ad M L	$t_{(2),22} = -0.173$	$P = 0.864$	$t_{(2),22} = 0.941$	$P = 0.357$		
Regression						
$N_f - P_f - \text{stress}$	$r^2_{(2),157} = 0.240$		$F_{2,157} = 24.762$	$P < 0.001^*$		
$N_f - \text{stress}$	$\beta = -0.375$		$t_{160} = -4.058$	$P < 0.001^*$		
$P_f - \text{stress}$	$\beta = -0.154$		$t_{160} = -1.668$	$P = 0.097$		
Class – stress	$F_{2,154} = 10.180$	$P < 0.001^*$				
Season – stress	$F_{1,154} = 6.368$	$P = 0.013^*$				
Pearson Correlation (N_f against P_f)						
All samples	$r_{(2),228} = 0.669$	$P < 0.001^*$				
Dry	$r_{(2),111} = 0.626$	$P < 0.001^*$				
Wet	$r_{(2),117} = 0.497$	$P < 0.001^*$				

* Denotes significant difference at $\alpha = 0.05$

Figure 1. Effect of African elephant class (body size, age, sex) and season on fecal (A) nitrogen (N_f), (B) phosphorus (P_f) and (C) glucocorticoid (stress hormone) levels ($\bar{x} \pm 95\% \text{ CL}$) collected in Pilanesberg National Park from Sep 2003 – Mar 2006. WC = weaned calf, Ad F = adult female, Ad M (S) = adult male (small), Ad M (L) = adult male (large). Sample size is indicated above the error bars, with the same samples used for N_f and P_f analysis, but extra samples added to stress hormone analysis. Coefficients of variation (%) are given below nitrogen and phosphorus error bars indicating the extent of variability in the N_f and P_f data for dry and wet seasons.



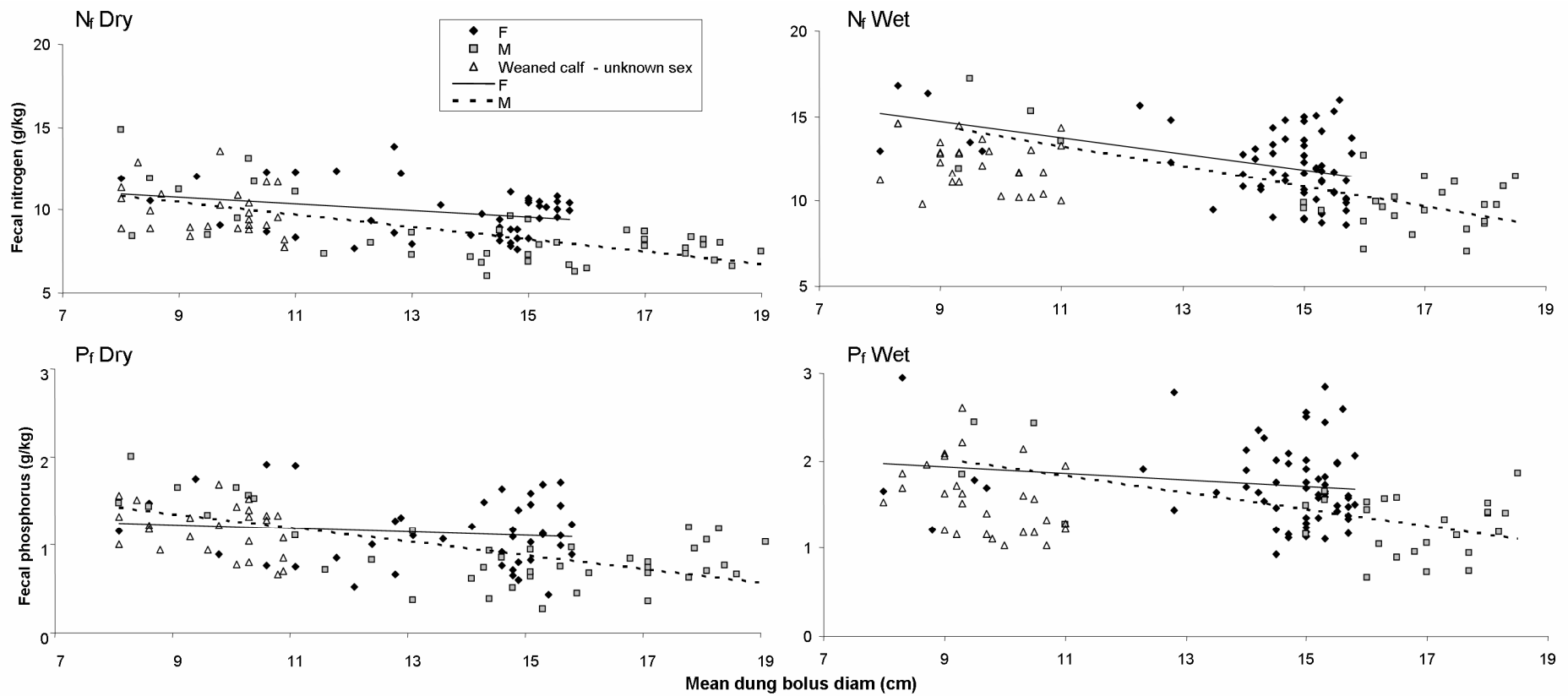


Figure 2. Effect of African elephant body size (indicated by mean dung bolus diam) and sex on diet quality as measured by fecal nitrogen (N_f) and fecal phosphorus (P_f) concentrations sampled during dry and wet seasons in Pilanesberg National Park from Sep 2003 – Mar 2006. We categorized samples according to sex for all adult body sizes (> 11 cm mean dung bolus diam) and where possible for weaned calf body sizes (8 – 11 cm mean dung bolus diam). A trendline shows the general relationship between body size and diet quality for males and females (weaned calves of known sex included).

Chapter 5

Foraging strategy within African elephant family units: why body size
matters

Leigh-Ann Woolley^{*}, Bruce Page & Rob Slotow

*Amarula Elephant Research Programme, School of Biological and Conservation
Sciences, Westville Campus, University of KwaZulu-Natal, Private Bag X54001, Durban
4000, South Africa.*

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ABSTRACT

Differences in intraspecific foraging strategies have been documented between the sexes of strongly dimorphic large herbivore species. However, body size implications on diet quality requirements can be extended to within-species age-specific comparisons. Here we investigated the hierarchical separation of foraging behaviour at the scale of plant type, plant species, plant part and vertically through the canopy, of African elephant adult females (lower quality diet required) and weaned calves (higher quality diet) within the elephant family unit, which is socially constrained to traverse the landscape together. Grass and browse were used with similar seasonal frequency by females and calves. Both females and calves tracked the phenology of woody species, including these species in the diet when new growth was available. Forage selection differed at the plant part level, with calves selecting for less fibrous and more nutritious plant parts (e.g. stripped leaves), while adult females selected branches, bark and roots with greater frequency. Adult females foraged at higher levels in the canopy when feeding < 3 m away from weaned calves. Elephant family unit foraging strategies are driven by body size, age-specific nutritional requirements and complex social interactions. This has broader application to other large herbivore species with great variance in intraspecific body size. Management and conservation of these species must replace traditional broad species-level assessments with intraspecific assessments of ecologically segregated classes to incorporate differential ecosystem utilization.

Key words: allometry, competitive displacement, ecological segregation, intraspecific, plant part, *Loxodonta africana*, South Africa.

INTRODUCTION

In order to maximise nutritional intake, mammalian herbivores have evolved foraging strategies to exploit the resources available to them, according to the versatility and diversity of their morphophysiology and body size (van Soest 1996; Clauss and others 2003). Selective or generalist foraging strategies scale broadly with body size across species (Bodmer 1990; Gordon and Illius 1994; Robbins and others 1995). Large herbivores have lower energy requirements per unit body mass, but increased gut capacity for ingesta retention, facilitating a higher tolerance for lower quality (high fibre content) forage (Parra 1978; Demment and van Soest 1985; Illius and Gordon 1991). Therefore, large herbivores tend to ingest a diet lower in quality than smaller herbivores, trading-off quality against quantity, as the benefits of ingesting abundant forage resources outweigh the costs of searching for forage of higher nutritional return which are usually rare in the environment (Demment and van Soest 1985; Owen-Smith 1988). Small herbivores are generally more selective feeders, maximising quality in response to digestive capacity constraints brought about by small body size and higher relative energy demands (Demment and van Soest 1985). However, absolute energy requirements increase with increasing body mass and consequently large herbivores must employ a strategy to increase time spent foraging, increase the efficiency of nutrient extraction or consume more nutrients per unit foraging time than smaller herbivores (Owen-Smith 1988).

Nutritional requirements vary not only according to body size but also the life-history stage of the animal, as predicted by high juvenile growth rates and adult reproductive

demands (Meissner 1982). Therefore smaller-bodied, younger herbivores may adopt a different feeding strategy to larger-bodied, older herbivores in different stages of reproductive output (Clauss and others 2003). The influence of body size and nutritional requirement could apply to both between species differences (Gordon and Illius 1994; Robbins and others 1995), as well as to intraspecific differences between juveniles and adults (Munn and others 2006) and different sexes of mature individuals within the same species (Shannon and others 2006a).

African elephants (*Loxodonta africana*) are considered “ecosystem engineers”, due to their extreme ability to physically alter the environment in which they live on a large scale (Jones and others 1994). Their removal or significant increase in a system may have consequences for other components (Mills and others 1993). However, intraspecific differences in behaviour arise due to social (e.g. Stokke and du Toit 2002; Shannon and others 2006a,b) and physiological reasons (e.g. Stokke 1999; Stokke and du Toit 2000) and therefore can influence the impact of different age-sex classes on the system. The elephant is strongly sexually dimorphic (Poole 1994; Lee and Moss 1995; Shannon and others 2006b) and the scaling of elephant diet quality holds true for extremes in body size, but intermediate-sized adult females consistently ingest a higher quality diet than males of similar body size due to increased nutritional demand (Woolley and others, unpublished manuscript). This intraspecific variation in diet quality implies an age-specific difference in foraging strategy, with the possibility of a more selective approach by smaller-bodied elephants. Being a large, generalist, mixed feeder, elephants have the ability to adjust the quality of forage ingested by varying the plant type (browse or grass)

ingested (Cerling and others 2006), as well as plant species or plant part (Owen-Smith 1988; Stokke and du Toit 2000; Shannon and others 2006a). Adult males consistently have a less diverse diet in terms of woody plant species than members of elephant family units, they consume more fibrous plant parts, plants with larger stem diameters and spend more time foraging on a single woody species (Stokke and du Toit 2000), consistent with a diet of lower quality. However, little attention has been given to investigation of dietary differences between the members of elephant family units, dictated by contrasting body sizes.

To evaluate the influence of body size on foraging strategy, we used the African elephant as a test subject and focussed on extending body size contrasts from adult sex classes to intraspecific differences within the elephant family unit. Intraspecific contrast controls for morphology other than body size. Because family units move and feed together, we control for the spatial and temporal separation of individuals at larger spatial scales. Therefore, we were able to directly compare the foraging strategy of the largest and smallest-bodied forage-dependent members of the family unit over a foraging hierarchy of plant type (grass vs. browse), plant species and plant part, as well as vertically through the canopy by comparing feeding heights. We quantified the differences in seasonal foraging through direct observation of the feeding bouts of individual adult females and weaned calves to: (1) compare differences in foraging strategies, (2) evaluate the scale at which differences occur, (3) compare the use of trees of different heights by individuals of different sizes.

METHODS

The study was conducted in Pilanesberg National Park (PNP, 25°24'S, 27°08'E, 570km²) in the North West Province of South Africa. PNP is located within the mouth of an extinct volcano and the resulting landscape is rugged (Boonzaaier and Collinson 2000). Together with the park's location within the transition zone of the dry Kalahari Thornveld and the wetter Bushveld regions (Acocks 1988), unusual habitats and combinations of fauna and flora result. Water is available throughout PNP from one major river system and many ephemeral tributaries and streams, as well as several dams. Rainfall averages 630 mm p.a. (~ 90% falls during the wet season November – April). Average rainfall in the 2003/4 and 2005/6 wet seasons were above average (824 mm and 654 mm respectively), while in 2004/5 it was below average (555 mm). There are many broad habitat types ranging from broadleaf thickets to open grasslands, with rocky hillsides mainly consisting of broad-leaf species e.g. *Combretum apiculatum*, *Croton gratissimus*, *Faurea saligna*, *Lannea discolour*, *Pavetta zeyheri* and the bottomlands mainly accommodating fine-leafed species e.g. *Acacia karroo*, *A. mellifera*, *A. tortillis*, *Dichrostachys cinerea*, with the herbaceous layer dominated by tufted perennial grasses (Brockett 1993).

Between 1981 and 1998, elephants were reintroduced to PNP during “Operation Genesis” where wildlife was returned to the area after cessation of commercial farming practices (Slotow and van Dyk 2004). Towards the end of 2003, the elephant population was estimated at 150 individually identified elephants (35 independent adult bulls and 115 members of 18 relatively stable matriarchal family units). However, after fire mortality

incurred in September 2005, the population was reduced from 165 to 136 elephants (Woolley and others 2008).

We located elephant family units opportunistically on a daily basis during the late dry and early wet season (August – March) from September 2003 to March 2006. All family units had been individually identified according to sex, approximate age, unique ear notches and tusk configuration prior to sampling. For the greatest body size contrasts, we used the adult females and just-weaned calves in a family unit as focal animals. Elephant calves are usually weaned after the birth of the next sibling (Lee and Moss 1986), thus we differentiated weaned from unweaned calves by making sure that the focal calf had a younger sibling and was not still suckling.

We recorded the time spent by each individual on a continuous feeding bout to the nearest second. The first trunk-load taken by an elephant initiated a woody species feeding bout until termination of the feeding bout with transfer to the next plant or the display of a different behaviour (e.g. interaction with herd members, movement away from forage plant). When feeding occurred on a woody species, we recorded the target species name, tree height, feeding height and plant part taken. Herbaceous layer feeding bouts were comprised of continuous time spent feeding on grasses, forbs or sedges. It was not possible to identify each herbaceous species fed upon; therefore a single feeding bout was terminated by transfer to a woody species or engagement in a different behaviour.

We evaluated seasonal and monthly use of plant type (herbaceous vs. woody) by adult females and weaned calves by comparison of the proportion of total feeding time spent on these plant types. We used a Kolmogorov-Smirnov 2-sample test to compare the differences in frequencies of use across elephant age class.

We compared the frequency of woody plant species use by adult females versus weaned calves on a seasonal basis using the percentage of total feeding time spent on the ten highest-use species. The wet season was defined as the period from late November to early April and the dry season from late June to early November when the first rains fell. We used a G-test to examine the frequency of use across elephant age classes. To examine whether the phenology of a woody species influenced its inclusion in the diet of elephant family units at different times of year, we linked monthly woody species use to the monthly phenology of the species by comparing the proportion of time spent on species with new growth (i.e. new leaves) or flowers, fruit and pods. We recorded the phenological state of the most common woody forage species in the sites most frequently used by elephant family units during a single month. On average, approximately ten sites were assessed each month and at least three trees of each species were measured. During these phenology assessments, we estimated the proportion of each tree that was comprised of woody (i.e. main stem, branches, twigs) versus non-woody (i.e. leaves, flowers, fruits) plant parts, and then estimated the proportion of the non-woody component made up by buds, young leaves, mature leaves, senescent leaves, flowers, fruit and pods.

We compared the proportion of adult female feeding time spent on different plant parts (pooled across all woody species) to that of weaned calves on a monthly basis. We tested the comparative monthly use of stripped leaves, the highest quality part, using a Mann-Whitney U-test. We compared the seasonal use of plant parts from the ten highest-use woody species across elephant age class.

We estimated the height of each tree fed upon and the feeding height used by the focal elephant. We compared the mean tree and feeding heights obtained for each high-use woody species utilized by adult females and weaned calves in each season. We investigated possible vertical displacement of adult females to higher foraging levels in the canopy by estimating the distance between a focal adult female and the closest calf, as well as the shoulder height of this calf. With a calving interval of approximately 3 years in the PNP population (Mackey and others 2006), weaning should occur at ~ 3 years of age after the birth of the next sibling (Lee and Moss 1986). Therefore weaned calves were estimated to have a shoulder height > 1.2m (Lee and Moss 1995; Schrader and others 2006). We assessed the effect of distance (under 3m) to weaned calves on adult female feeding height through linear regression analysis.

All statistical analyses were run using SPSS 15.0 software (SPSS Inc., Chicago, Illinois, USA) with $\alpha = 0.05$. This study was approved by the Animal Ethics Committee of the University of KwaZulu-Natal.

RESULTS

Adult females and weaned calves used herbaceous and woody plants with similar frequency during the dry and wet season ($Z_3 = 0.5$, $P = 0.964$), as well as in each month ($Z_{15} = 0.42$, $P = 0.674$) (Figure 1). However, the switch to include a greater proportion of herbaceous material in the diet at the onset of the wet season in November saw weaned calves spending more time on the herbaceous layer than adult females and maintaining a high frequency of use into the wet season (Figure 1).

Woody species were used at a similar frequency by adult females and weaned calves on a seasonal basis (Dry season: $G_9 = 8.029$, $P = 0.531$; Wet season: $G_9 = 3.417$, $P = 0.945$) (Figure 2). The monthly woody species use of both adult females and weaned calves tracked plant phenology, as species were included in the diet when new leaves or flowers, fruits and pods (FFP) first became available (Figure 3). In the late dry season, evergreen species such as *R. lancea* were included in greater proportions in the diet of both adult females and calves when availability of all else was low, even though no new leaves were available from these species (Figure 3). Species producing flowers during the late dry season featured with greater frequency in the diet of adult females and calves at this time (Figure 3). During the late dry season, weaned calves maximised their use of *A. karroo* in September, then increased their use of *A. caffra* in October (Figure 3). Adult females spent most of their time on *A. karroo* during the late dry season, but spent more time on *A. tortilis* during September than weaned calves did (Figure 3).

Adult females spent a greater proportion of their feeding time on cellulose-rich plant parts, such as branches and bark, than weaned calves did (Figure 1). Leaves and branches were taken together most frequently by adult females and weaned calves, however weaned calves took only leaves at a significantly greater frequency than adult females ($U_{17} = 11.5, P = 0.031$) (Figure 1).

In the late dry season (August – November), weaned calves incorporated bark and roots in their diet, with frequency of use decreasing towards the onset of the wet season (Figure 1). In the early wet season (November – March), roots and bark were not used by weaned calves, but bark featured in the diet again with progression of the wet season (Figure 1). Adult females incorporated bark into their diet throughout the late dry and early wet season, with peak usage in the late dry season (Figure 1). Roots were used less frequently by adult females after the first rains in November and usage dropped off from December to February and featured again in March (Figure 1). FFP were used, but with less frequency than other plant parts, during the late dry season by weaned calves and adult females (Figure 1).

From the ten highest-use woody species in the dry and wet season, weaned calves utilized these species differently to adult females by taking a greater proportion of higher quality plant parts (i.e. stripped leaves, FFP), while adult females included more fibrous plant parts in their diet from those species (i.e. branches, bark) (Figure 2).

A. karroo, *R. lancea*, *A. caffra*, *A. tortilis* and *D. cinerea* were the woody species used most frequently by adult females and weaned calves during both the dry and wet season (Figure 2). Although adult females and weaned calves utilized the same plant parts from these highest-use species in the dry season (with exception of inclusion of stripped leaves of *A. tortilis* and *D. cinerea* by weaned calves), the difference in their feeding strategies was evident in the proportion of time spent on these plant parts, with adult females spending more time on branches and weaned calves spending more time on stripped leaves (Figure 2). However, during the wet season adult female and weaned calf selection for plant parts was different. Weaned calves took fewer branches and selected for leaves when adult females did not, while adult females utilized bark and roots when calves did not, and also included more branches in their diet (Figure 2).

Most *A. caffra* and *A. karroo* used by adult females and weaned calves were small trees (< 2 m) (Figure 4). In the dry season, adult females spent 13 and 20 % (and weaned calves 16 and 30 %) of their feeding time selecting for coppice growth from *A. caffra* and *A. karroo* respectively at feeding heights < 1 m (Figure 4). Adult females generally fed higher in the canopy and selected taller trees than weaned calves did (dry season: mean (\pm SE) tree height of 2.2 ± 0.04 m, mean (\pm SE) feeding height of 1.2 ± 0.03 m, $n = 1207$; wet season: mean (\pm SE) tree height of 2.0 ± 0.07 m, mean (\pm SE) feeding height 1.0 ± 0.04 m, $n = 542$). Weaned calves selected trees of mean (\pm SE) height of 1.9 ± 0.05 m (dry, $n = 855$) and 1.5 ± 0.06 m (wet, $n = 397$), and fed at a mean (\pm SE) height of 0.8 ± 0.02 m (dry) and 0.5 ± 0.03 m (wet). There was significant regression relationship between distance to weaned calf and adult female feeding height ($F_{1, 57} = 20.9$, $P <$

0.001; $\beta = 0.637$, $t_{57} = 4.574$, $P < 0.001$). When adult females were < 3 m away from a calf, they tended to feed above the shoulder height of the calf (Figure 5). Adult females fed on smaller trees (< 2.5 m in height) when in close proximity (< 0.5 m) to unweaned calves or when further away (> 3 m) from weaned calves (Figure 5). Taller trees were selected when foraging less than 3 m away from weaned calves (Figure 5).

DISCUSSION

African elephants adjust their selection of plant types, species and plant parts with seasonal variation in forage quality and availability (Owen-Smith 1988; Cerling and others 2006; O'Connor and others 2007). With consistency in resource availability to the individuals within elephant family units, there should be many similarities in feeding choices, however the influences of body size on foraging strategies (Demment and van Soest 1985; Gordon and Illius 1994; van Soest 1996; Clauss and others 2003) predict intraspecific differences. Differences in the foraging strategies of adult females and weaned calves were not evident in their use of plant types or plant species. However, decision-making at the plant part level was different.

Much plant-available nitrogen is released in a “flush” of new growth at the beginning of the wet season (Scholes 2003). With easier access to a greater biomass intake from grass plants than browse due to herbage density, protein intake can be maximised at start of the rainy season through the ingestion of grass (Field 1971). Weaned calves included a higher proportion of herbaceous material into their diet than adult females did at the onset of the wet season. When unrestricted by availability in the wet season, weaned calves

selected more consistently for nitrogen, while adult females selected for phosphorus (Woolley and others, in press). Macrominerals such as phosphorus were available at higher concentrations in summer than winter within plant communities in Nylsvlei Nature Reserve, South Africa (Dorgeloh 1999). Although high levels of protein (nitrogen) are available from both grass and browse in the wet season, adult females included a greater proportion of browse in their diet (requiring greater harvesting effort) than that of weaned calves. This suggests that browse may have contained higher levels of phosphorus during the wet season than the herbaceous layer, thereby attracting greater utilization of browse by adult females than weaned calves during the wet season. Elephant impact in the Kalahari Sand woodlands of Zimbabwe was associated with leaf mineral and to a lesser extent crude protein concentrations (Holdo 2003). Nutrient hot-spots may therefore drive forage selection at both the broad landscape level (Grant and Scholes 2006) as well as the more specific level of the plant part selected for. Nutrient requirements at different life-stages (e.g. protein for growth, phosphorus for pregnancy/lactation) are therefore important influences on foraging decisions (Pond and others 1995; Dorgeloh 1999).

Although adult females and calves used the same woody plant species, they used these species differently. Adult females incorporated more fibrous plant parts into their diet, while weaned calves took more nutritious cell soluble plant parts. Body size influences on tolerance to a lower quality diet and the high absolute quantity of forage required by large-bodied individuals, determines the less selective foraging strategies employed by larger-bodied herbivores (Demment and van Soest 1985; Owen-Smith 1988; Illius and

Gordon 1991). Therefore, while smaller-bodied weaned calves can afford to invest more time and energy into selecting higher quality plant parts, adult females trade-off selectivity against the need to maximise the absolute quantity of forage ingested (O'Connor and others 2007). Nutritious plant parts (e.g. flowers, fruit) are less available, making the ingestion of vast quantities of these plant parts impossible for adequate adult nutrition. Elephant foraging pressure was not linked to plant species' shoot vigour in Chobe National Park, Botswana, but it was suggested that elephant respond rather to the combined quality of branches, bark and leaves when foraging (Makhabu and others 2006). However, this has greater application to adult rather than juvenile foraging decisions. In our study weaned calves utilized higher quality plant parts and exploited new growth at greater frequencies than adult females, suggesting that weaned calves can afford to make quality decisions on a finer plant part scale than larger-bodied adult females, where whole plant quality is likely to be more important.

In some cases fire damage or the pollarding of woody species can result in a tree coppicing i.e. new growth (i.e. leaves and stems) from the base. This was exploited by adult females and weaned calves, with foraging occurring at ground level at the base of the trees. Generally, adult females and weaned calves (but more so calves) foraged at low levels on smaller trees of the highest-use species such as the Acacias. It is possible that selective suppression of these species may be occurring in PNP as a result of the repeated targeting of small individuals, preventing recruitment into larger size classes and "escape" from elephant impact (Caughley 1976), as found elsewhere in Africa (e.g. Dublin and others 1990; Tchamba 1995; Campbell and others 1996; Holdo 2003). In

PNP, concern has been raised over the low density of tall trees and dominance of shrubby plants (Moolman 2007) and further investigation into impacts on larger size-class recruitment is required.

Adult female foraging strategy was additionally influenced by displacement to higher feeding levels in the canopy when in the close proximity to calves. Adult females have previously been found to forage at lower levels in the canopy when feeding alone than when feeding close to subadults and juveniles (Stokke and du Toit 2000). We speculate that this behaviour may be a direct result of intraspecific competition, or more likely an evolutionary response on the part of adult females to ensure calf survival. If calves take higher quality plant parts from lower levels in the canopy, it may be more profitable for adult females to feed on intact canopy at higher levels. Therefore calf presence could displace adult females and promote browsing stratification from below. This is the basic premise behind the competitive displacement of giraffe bulls which feed higher in the canopy than cows and their offspring (Woolnough and du Toit 2001) and is consistent with studies on grazing guilds, where selective grazing by smaller-bodied grazers causes the depletion of overall forage quality available to larger grazers (Murray and Illius 2000). Therefore, adults may derive a nutritional advantage from ensuring they feed above the reach of calves when feeding together, but this may also be an altruistic behaviour by adult females ensuring adequate calf nutrition. Further research is required to establish whether displacement of adult females may be a direct response to a reduction in forage quality at lower heights. Competitive displacement is unlikely to consistently influence all adult female foraging events, due to plant recovery post-

herbivory, but may be more influential when calves are feeding simultaneously in close proximity to a female.

Proximity to calves that were weaned caused greater displacement of adult females to elevated feeding heights and taller trees. Unweaned calves rely on milk to supplement the diet and increase diet quality, whereas weaned calves must exploit the available vegetation to a greater extent than unweaned calves in order to maximise diet quality. Weaned calves are therefore likely to be more selective than unweaned calves. This degree of selectivity could influence adult female decisions to feed more consistently above the height of weaned than unweaned calves. Weaned calves are consequently most susceptible to a decline in forage quality during times of nutritional stress (e.g. during drought). Juvenile mortality is a key factor in the population regulation of predator-free, large herbivore systems (Gaillard and others 1998, 2000) and the allometric and nutritional drivers of selectivity are therefore important mechanisms of elephant population limitation.

Intraspecific divergence in foraging strategy between the strongly dimorphic adult elephant sexes is sufficient to cause spatial segregation of the sexes (Stokke 1999; Stokke and du Toit 2000, 2002; Shannon and others 2006 a,b), but our study also proves a clear age-specific influence on foraging strategy. Although family units utilized the landscape on the broadest scales in a similar manner, differences arose on a reduced decision-making scale, with family unit foraging decisions separated at the plant part level, as well as vertically through the canopy. The foraging decision-making process is therefore

driven by age-specific nutritional requirements, body size and intraspecific competition. This type of intraspecific divergence in the behaviour may also apply to other large herbivore species where body size varies considerably from the largest adults to the smallest weaned individuals. Differences could therefore arise in the way species cohorts utilize and impact an ecosystem. Instead of a broad species-specific view, assessments must include an appreciation of the potential for intraspecific variation in responses and the possibility of ecologically separated classes within the same species which may have decidedly different impacts on the system. It is therefore vital that an understanding of intraspecific segregation is applied to the management and conservation of large herbivore species.

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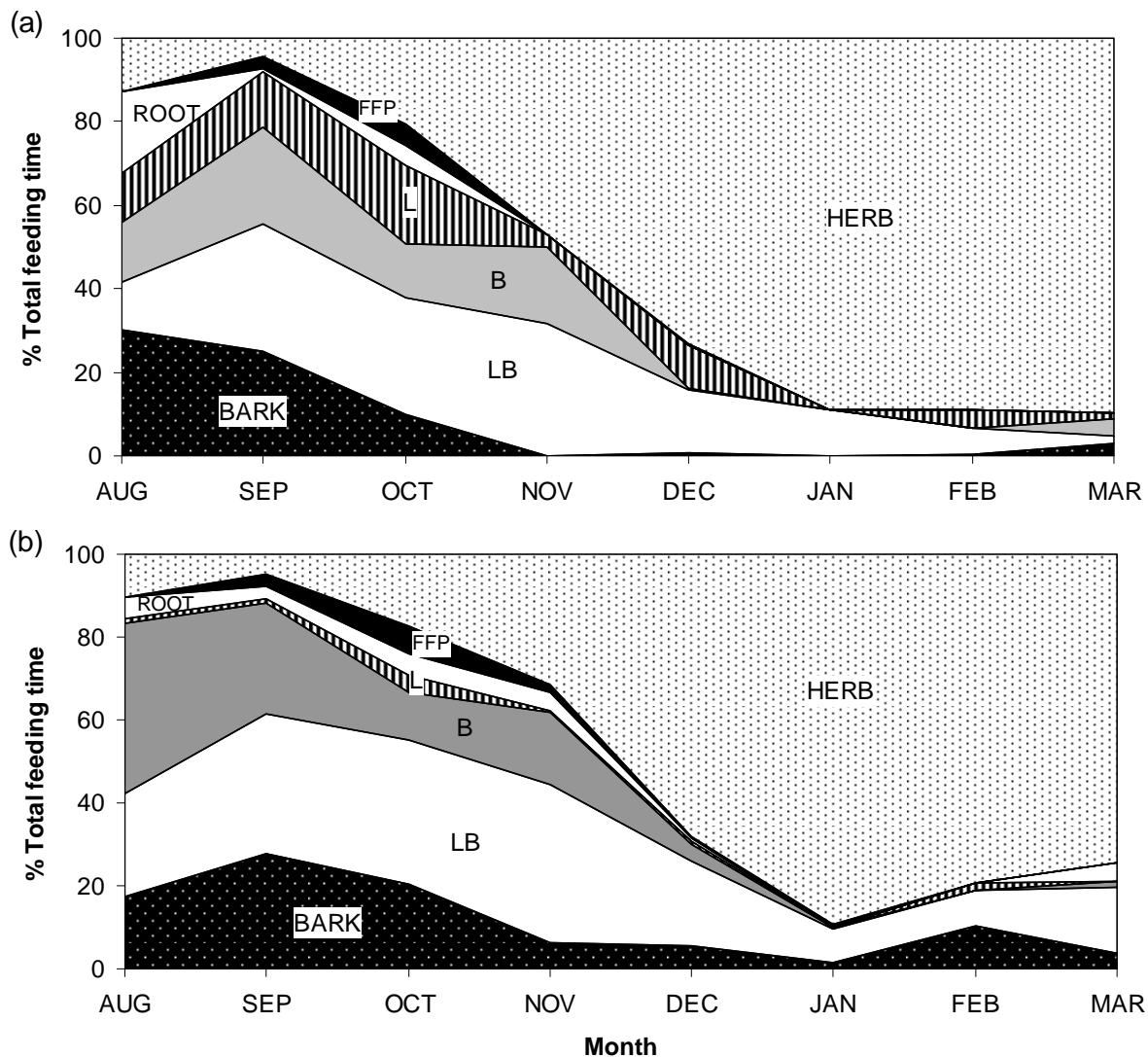
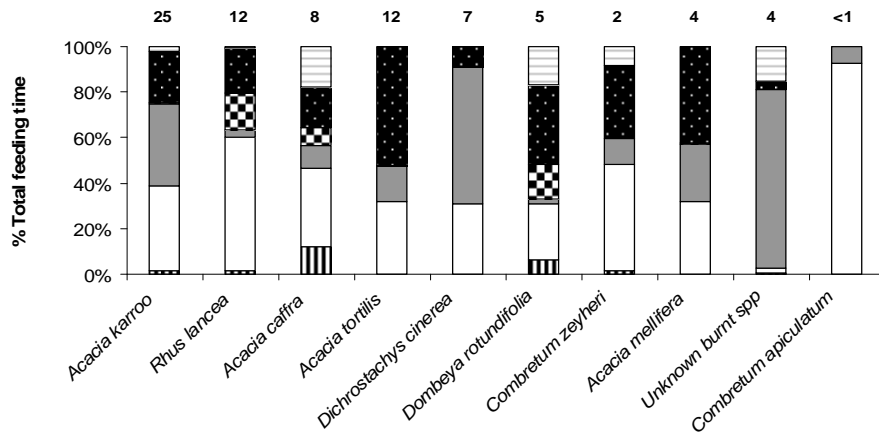
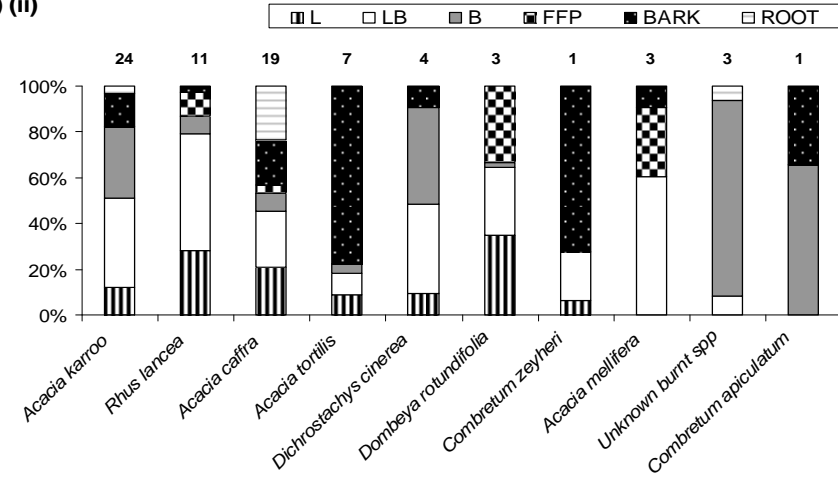


Figure 1 Plant type and woody plant part use. The percentage of total feeding time spent on the herbaceous layer and woody plant parts is given for: (a) weaned calves and (b) adult females. In sequence from top, HERB = herbaceous; FFP = flowers, fruit, pods; ROOT = roots; L = leaves only; B = branches only; LB = leaves and branches combined; BARK = bark.

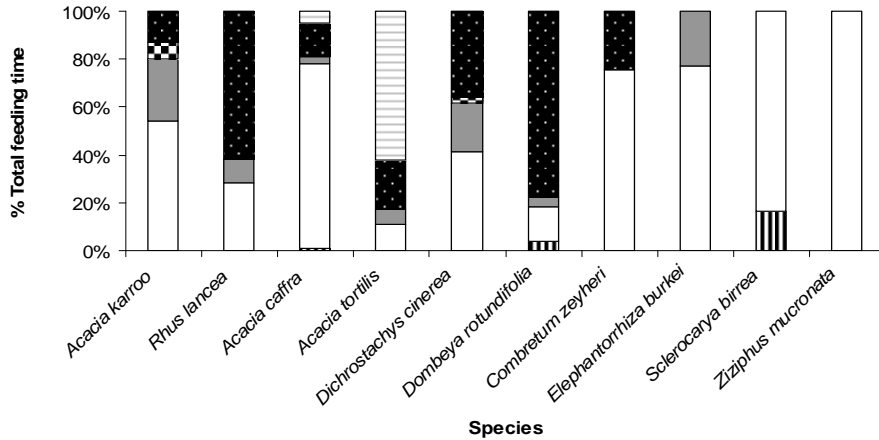
(a) (i)



(a) (ii)



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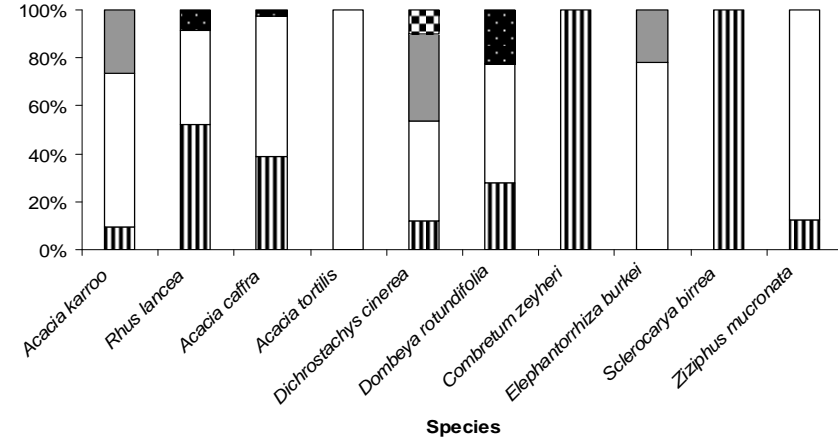


Figure 2 Seasonal woody species and plant part use. The percentage of total feeding time spent on woody plant parts for ten species is given for the: (a) dry and (b) wet season and for (i) adult females and (ii) weaned calves. L = leaves only; LB = leaves and branches combined; B = branches only; FFP = flowers, fruit, pods; BARK = bark; ROOT = roots. Feeding time spent on each species (% of all feeding observations including herbs) is given above each species bar.

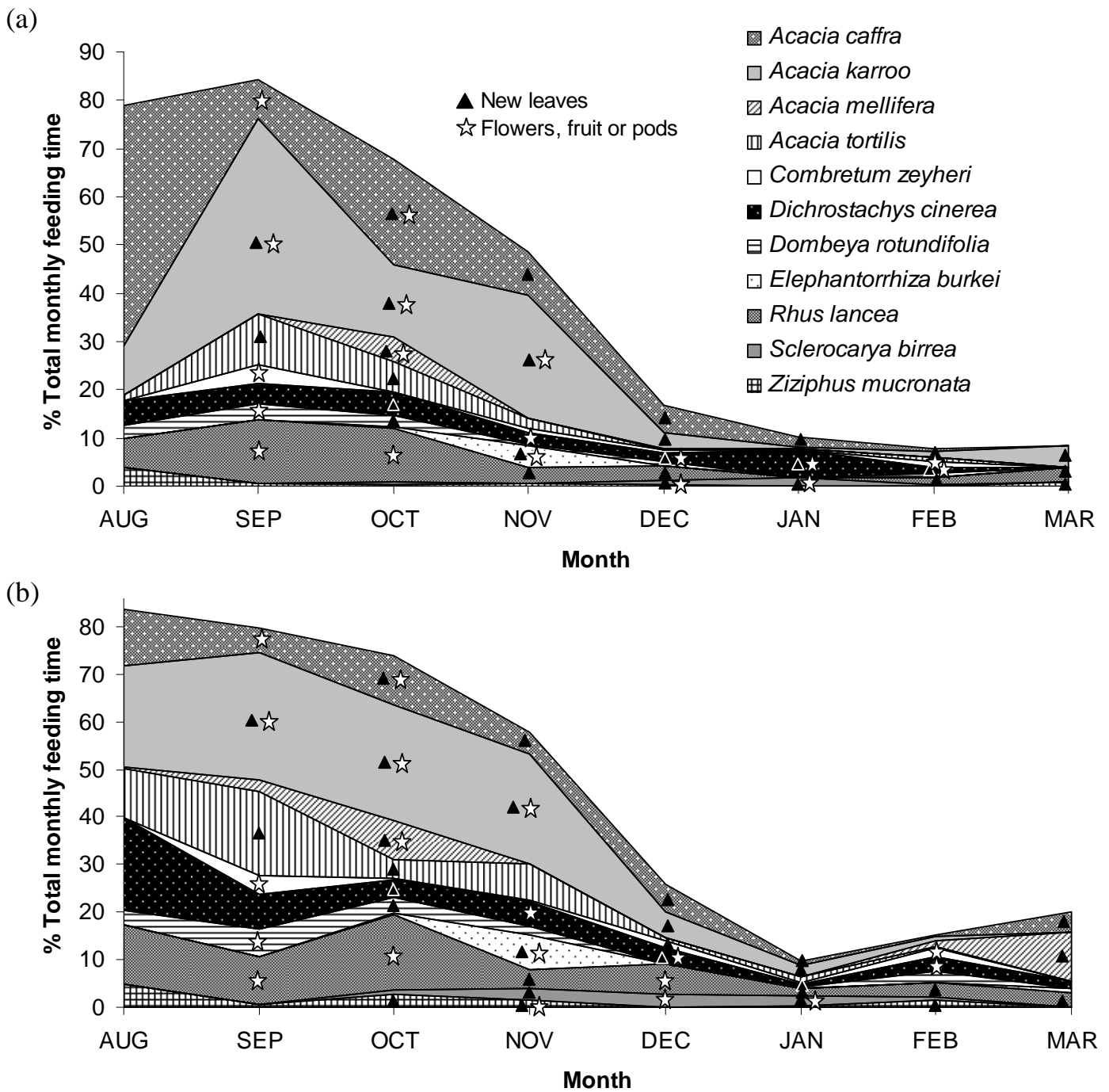


Figure 3 Monthly woody species use. The percentage of total feeding time spent on 10 high-use species is given for: (a) weaned calves and (b) adult females. The production of new leaves or flowers, fruit and pods by each species is indicated each month.

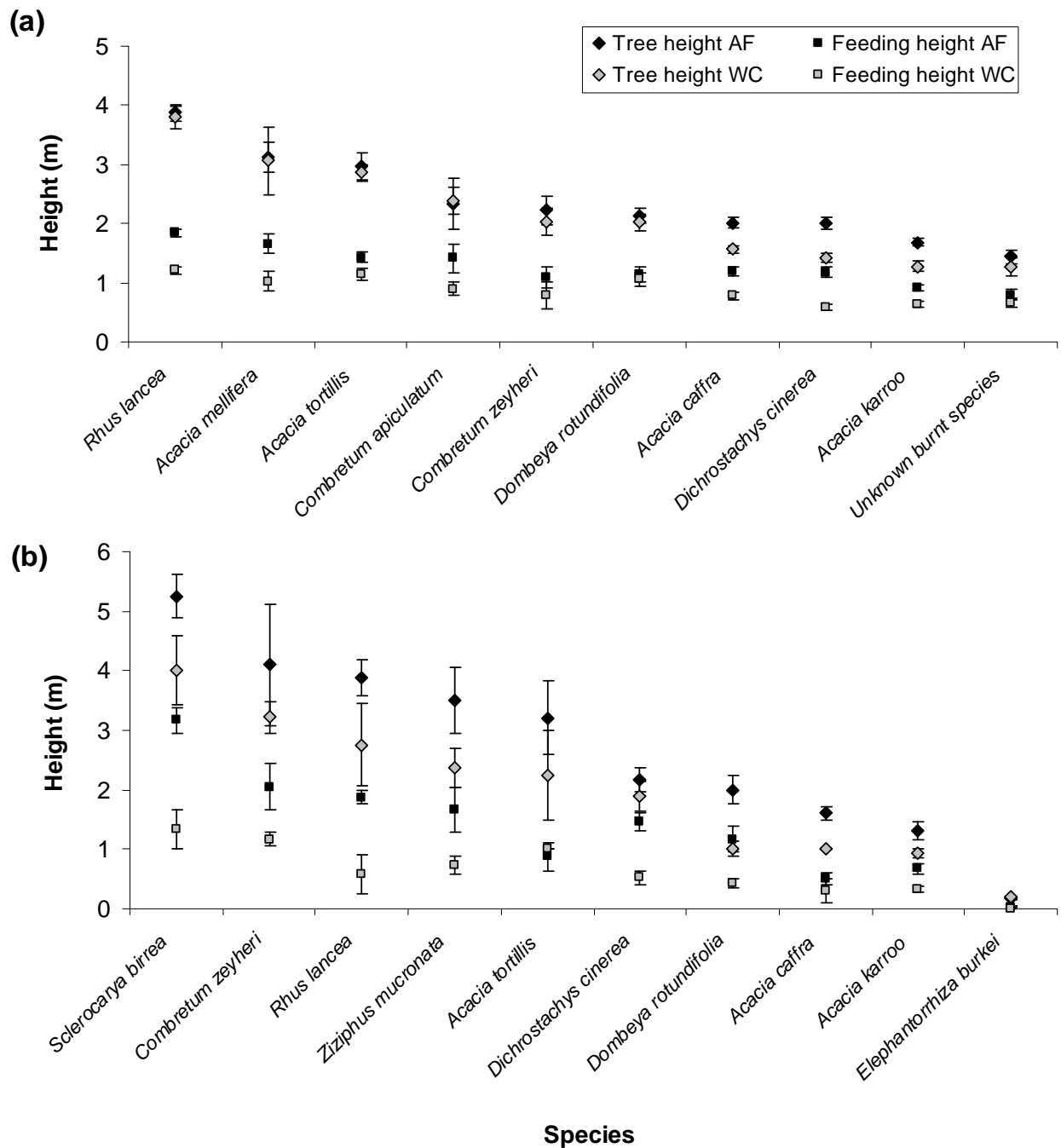


Figure 4 Mean (\pm SE) tree and feeding height for high-use species utilized by adult females and weaned calves in (a) dry and (b) wet seasons. AF = adult female, WC = weaned calf.

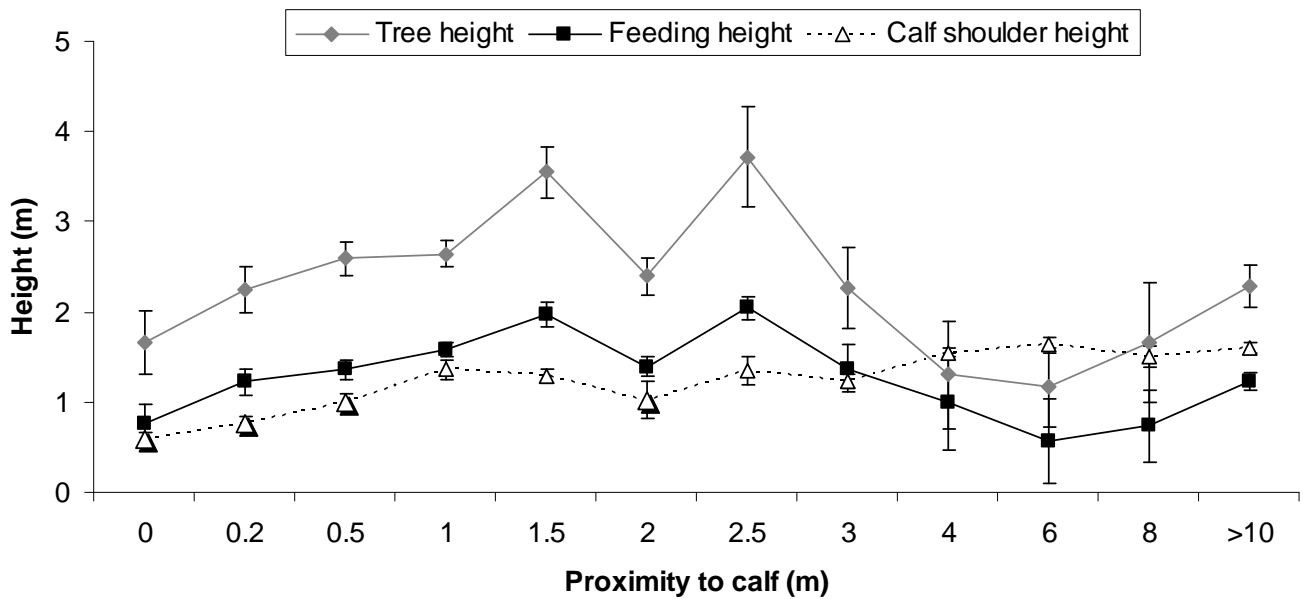


Figure 5 Effect of weaned calf presence on adult female feeding height. The mean (\pm SE) tree height and feeding height selected by adult female elephants when in proximity to a calf (mean (\pm SE) calf shoulder height given). Mean calf shoulder height is separated into that of unweaned (< 1.2 m, shadowed data points) and weaned calves (> 1.2 m, unshadowed data points).

Chapter 6

General Discussion and Conclusions

Ironically, both extinction and overpopulation are issues influencing the successful conservation management of the African elephant (*Loxodonta africana*) across the African continent (Carruthers *et al.*, 2008; Pimm, 2008). It is vital that we have a sound understanding of the causes and effects of population persistence, stability and variability if we are to effectively manage this species (Owen-Smith *et al.*, 2006; van Aarde *et al.*, 2006; Biggs *et al.*, 2008).

Because the elephant is a long-lived species (maximum age of approximately 60 – 65 years in the wild (Laws *et al.*, 1975), there are very few studies documenting elephant populations over long time periods (Whitehouse & Hall-Martin, 2000; Moss, 2001; Wittemyer, 2001). Therefore indirect or short-term studies become very valuable in the assessment of the processes involved in African elephant population dynamics. In general, we know that large-bodied, long-lived species possess a unique combination of life-history characteristics such as long generation times, low fecundity and high adult survival (Moss, 2001; Wittemyer *et al.*, 2007) which prolong demographic response to perturbation (Coulson *et al.*, 2004; Forsyth & Caley, 2006; Ratikainen *et al.*, 2008; Slotow *et al.*, 2008). Populations with slow turnover tend to exist close to the limit set by resources and competition and density dependence are greatest close to this limit (Fowler & Smith, 1973; Fowler, 1981; Sibley *et al.*, 2005).

When disturbed, population inertia and strong density-dependent responses ensure that long-lived populations return to equilibrium more quickly than short-lived species with fast turnovers, i.e. there is greater population stability in long-lived species (Saether *et al.*, 2002; Sibley *et al.*, 2005). The interactions between demography and environment determine the effects of stochastic environmental events and density dependence

(Coulson *et al.*, 2001). For example, sustained harvesting can introduce nonlinearity and fluctuations in abundance in natural populations (Anderson *et al.*, 2008) and overcompensatory responses to environmental stochasticity can drive fluctuations in population size (Bull & Bonsall, 2008).

The applicability of these processes to elephant population dynamics suggests that elephant populations live on a demographic “knife edge” (Pimm, 2008; van Aarde *et al.*, 2008), where comparatively small changes in parameters may have quite a large influence on population trends, potentially resulting in overpopulation or decline (Slotow *et al.*, 2005; Carruthers *et al.*, 2008). This is particularly pertinent in human-modified, small, fenced reserves where problems associated with overpopulation can become very acute, very quickly (Slotow *et al.*, 2005). But at the same time small, fragmented populations can be especially susceptible to environmental catastrophes (e.g. Coulson *et al.*, 2001). Chapter 3 (Woolley *et al.*, 2008b) illustrates this point in the response of the increasing elephant population of Pilanesberg National Park to a catastrophic fire, where a total population mortality of 18 % occurred in this single event. At the same time, Chapter 2 (Woolley *et al.*, 2008a) demonstrates that a severe event per generation or more frequent, less severe events (but still requiring the mortality of ~ 85 % of infants and weaned calves twice a generation) can regulate elephant populations.

Predation on elephants, e.g. by humans, has been proposed as a historical factor limiting elephant numbers (Kay, 2002; Surovell *et al.*, 2005; Cumming, 2007). Predation by lions is not extremely common in all elephant systems, but does occur in low magnitude in some areas and most commonly involves juvenile elephants (Ruggiero, 1991; Wittemyer *et al.*, 2005). For example, in the Samburu and Buffalo Springs National Reserves 23.8 % of calf mortalities recorded over 1998-2003 were attributed to lion and these mortalities accounted for only 4 % of total population mortality, with an average annual mortality of only 2.6 % p.a. (Wittemyer *et al.*, 2005). Lion predation on elephant calves is known to increase during drought periods and in Hwange National Park, Zimbabwe, lions target weaned calves in particular between the ages of about six and eight years, while hyaena have also developed strategies to take very young elephant calves during dry years

(Salnicki *et al.*, 2001; Loveridge *et al.*, 2006). Human predation and mortality due to injuries inflicted by humans mainly affects adults, with poaching for ivory having reduced numbers of large adult elephants in the 1970's and 1980's, especially in East Africa (Ottichillo *et al.*, 1987; Moss, 2001; Wittemyer *et al.*, 2005; Gobush *et al.*, 2008). However, most elephant populations today are fairly well-protected from poaching (Carruthers *et al.*, 2008).

A combination of different types of stochastic environmental events, such as drought and fire (possibly fairly severe and frequent) can play an important role in the population regulation of elephant populations. This may have particular applicability to the many small, closed systems in South Africa where eruptive population growth is exhibited (Mackey *et al.*, in press). These populations have not reached resource limitations and density dependent effects do not dominate population regulation as yet (e.g. van Jaarsveld *et al.*, 1999; Gough & Kerley, 2006). The management of these populations must balance the possibility of population crashes with the environmental consequences from a population undergoing exponential growth, for example the biodiversity impacts associated with increased elephant densities (Mills *et al.*, 1993; Guldemond & van Aarde, 2007; Kerley *et al.*, 2007; Landman *et al.*, 2008).

The scale at which elephant population regulation occurs remains unclear, but scale is no doubt an important factor to consider. Open systems with free-ranging elephant populations include dispersal as a factor in population response to changing environmental conditions (Chamaillé-Jammes *et al.*, 2008). Fences force the system into a state where emigration and immigration opportunities are removed (Slotow *et al.*, 2005; van Aarde *et al.*, 2006). This effectively decreases the temporal and spatial scale at which elephants can operate, by forcing them to revisit the same foraging patches more often, and changes the primary demographic and environmental processes regulating populations (Slotow *et al.*, 2005; Owen-Smith *et al.*, 2006; van Aarde *et al.*, 2006; Slotow *et al.*, 2008; van Aarde *et al.*, 2008; Mackey *et al.*, in press). When we restrict an elephant's range we increase the localised impacts of the elephant on the system (Skarpe *et al.*, 2004; van Aarde *et al.*, 2006; Guldemond & van Aarde, 2007; O'Connor *et al.*,

2007; Harris *et al.*, 2008). In large, open systems elephants can vary habitat use on a spatial and temporal basis, spreading impacts across the landscape (O'Connor *et al.*, 2007; Harris *et al.*, 2008; Valeix *et al.*, 2008). This is not to say that impacts are only evident in high-density situations. Even a single elephant can have visible impacts on an ecosystem, and landscape with and without elephants will differ (O'Connor *et al.*, 2007).

The management of elephant populations will therefore depend on the scale of the system, as well as site-specific local habitats, climate and human-mediated impact, i.e. fences, water supplementation (Owen-Smith *et al.*, 2006; Biggs *et al.*, 2008). Active adaptive management, where managers test and push the system to learn more and adapt management strategies accordingly, has been advocated for both small, closed and large, open systems with overabundant elephants (Owen-Smith *et al.*, 2006; Biggs *et al.*, 2008). Metapopulation management, where local movements and regional dispersal are facilitated by the linkage of conservation areas to allow movement, has particular application to large, open systems where elephant populations can be locally overabundant and increasing spatial dynamics can potentially stabilize numbers regionally while reducing local impacts (van Aarde & Jackson, 2007; Chamailié-Jammes *et al.*, 2008).

In both closed and open contexts, the regulation of elephant populations living in variable environments governed by climate-driven environmental stochasticity seems closely tied to resource availability (Fowler, 1981; Fritz *et al.*, 2002). Both mortality and fecundity effects are involved in limitation either as a direct result of an environmental disturbance or density dependence (Dudley *et al.*, 2001; Moss, 2001; Wittemyer *et al.*, 2007; Chamailié-Jammes *et al.*, 2008; Foley *et al.*, 2008; Junker *et al.*, 2008). Resource availability can drive both density-dependent feedbacks (e.g. Chamailié-Jammes *et al.*, 2008), and limitation during stochastic environmental events (e.g. Dudley *et al.*, 2001; Foley *et al.*, 2008), by affecting fecundity and mortality.

Fecundity is significantly influenced by female age at first calving and the interval between successive calves, which can substantially impact population growth rates (van

Aarde *et al.*, 1999; Mackey *et al.*, 2006; Woolley *et al.*, 2008a). Due to the effects of resource limitation at high densities these variables can increase, thereby decreasing fecundity (van Aarde *et al.*, 2008). Resource limitation during climatic events or in severe environments (e.g. Kalahari desert, Namibia) can also affect fecundity (e.g. Leggatt, 2003; Wittemyer *et al.*, 2007). In fact, Wittemyer *et al.* (2007) suggest that elephant population dynamics is driven by interactions between female fecundity and environmental variability, rather than fluctuations in mortality. The severe physiological impact of an environmental disturbance such as that caused by elephant injury and mortality in a fire (Woolley *et al.*, 2008c) also has the potential to affect female fecundity. For example, two adult female elephants that were pregnant with their first calf (assessed by enlarged mammary glands in the absence of a suckling calf) before the fire in Pilanesberg National Park in which they were injured (Woolley *et al.*, 2008b), were not seen with calves within 2 years (approximate gestation period of the elephant (Laws *et al.*, 1975; Lee & Moss, 1986)) post-fire and lactation had ceased within a few months of the fire (L. Woolley, pers. obs.). Significantly lower reproductive output was recorded in young adult females in Mikumi National Park, Tanzania, where high levels of poaching were experienced in the past (Gobush *et al.*, 2008). This low reproductive output was attributed to low average group relatedness, associated low bond strength, disrupted social structure and high physiological stress levels due to historical poaching impacts (Gobush *et al.*, 2008). Most of the fecund females in this population were over 30 years of age (Gobush *et al.*, 2008), which is much older than that seen in Addo Elephant National Park, South Africa, or Amboseli National Park, Kenya, where females in the 20 – 29 year old age class are the most fecund of the population (Whitehouse & Hall-Martin, 2000; Moss, 2001).

Mortality in elephant populations is age-dependent, and although population growth is most sensitive to adult mortality (especially young, fecund females (van Aarde *et al.*, 1999; Woolley *et al.*, 2008a)), high temporal variation in juvenile survival typically occurs (Moss, 2001; Dudley *et al.*, 2001; Wittemyer *et al.*, 2005; Foley *et al.*, 2008). Juvenile mortality is the primary result of both density dependence (Chamaillé-Jammes *et al.*, 2008) and stochastic environmental events such as drought (Dudley *et al.*, 2001;

Moss, 2001; Leggatt, 2003; Foley *et al.*, 2008) or fire (Woolley *et al.*, 2008b). The classic mortality pattern seen in large herbivore systems worldwide (especially temperate species) mainly involves juveniles, while adult survival is buffered and possibly canalized against such variation (Saether, 1997; Gaillard *et al.*, 1998, 2000; Gaillard & Yoccoz, 2003). Our findings seem contiguous with these generalizations, as fire functioned in a similar manner to other stochastic, environmental events (e.g. drought), with high juvenile and low adult mortality the result (Woolley *et al.*, 2008b). The youngest are typically the most susceptible to resource restriction, with high infant and weaned calf mortality common in these situations (Dudley *et al.*, 2001; Moss, 2001; Leggatt, 2003; Wittemyer *et al.*, 2005; Foley *et al.*, 2008; Woolley *et al.*, 2008b). Infants rely on milk as the basis of their diet (Lee & Moss, 1986), but just-weaned calves must utilize environmental resources to survive, and can thus be severely impacted by resource restriction e.g. high levels of weaned calf mortality due to dehydration occurred in the Kalahari Sands in Hwange National Park when their trunks could not reach the water in dry river bed craters dug by the adult elephants (Conybeare & Haynes, 1984).

Water is a critical resource for elephants, and surface water is one of the primary drivers of elephant spatial use (Redfern *et al.*, 2005; Chamaillé-Jammes *et al.*, 2007). Climatic variability affects surface water availability which determines seasonal use of the environment by elephants (Redfern *et al.*, 2005; Chamaillé-Jammes *et al.*, 2007; Smit *et al.*, 2007). The foraging range determined by water availability caused localised population aggregation, ultimately influencing the strength of density dependence and the local regulation of elephants in Hwange National Park (Chamaillé-Jammes *et al.*, 2008). Surface water manipulation has powerful potential in elephant management (Owen-Smith *et al.*, 2006; Chamaillé-Jammes *et al.*, 2007; Smit *et al.*, 2007).

Nutritional restriction also plays a critical role in both density-dependent and independent elephant population regulation (Whitehouse & Hall-Martin, 2000; Dudley *et al.*, 2001; Moss, 2001; Wittemyer *et al.*, 2005; Chamaillé-Jammes *et al.*, 2008; Foley *et al.*, 2008). Forage limitation is likely to take a longer time to be physiologically damaging to a large herbivore than water limitation would, because fat reserves can be mobilised to meet

shortfalls in energy requirements, whereas severe dehydration may act more speedily to result in death (Willmer *et al.*, 2000). Further investigation into the primary physiological functioning involved in the energy and hydration requirements of elephants is required. There may be a critical level where food or water use (scaled according to body size) could result in mortality. Small body size will intensify the effects of dehydration and starvation, as larger animals may have larger fat reserves (e.g. Shrader *et al.*, 2006a) and be less susceptible to water loss and heat dissipation due to smaller body surface area to volume ratios (Williams, 1990; Phillips & Heath, 2001).

Similarly, susceptibility to nutritional restriction is age-dependent, as Chapter 4 (Woolley *et al.*, 2008c) and Chapter 5 (Woolley *et al.*, 2008d) indicate. In general, larger-bodied herbivores can tolerate a lower quality diet, mainly due to larger gut capacity and the resultant increased forage retention and greater digestive efficiency (Demment & van Soest, 1985). Seasonal environmental stochasticity results in a dry season drop in forage quality and quantity in African savannas (Scholes, 2003). Large-bodied herbivores cope by ingesting a lower quality diet, thus being constrained by quantity rather than quality (Owen-Smith & Novellie, 1982).

Large adult male elephants focus on increased throughput of vast amounts of forage ingested in proportion with environmental availability (Stokke & du Toit, 2000), thereby ingesting a lower quality diet than smaller-bodied adult females or juveniles (Stokke & du Toit, 2000; Woolley *et al.*, 2008c). African elephants are strongly sexually dimorphic, with divergence in male and female growth patterns occurring at adulthood when male growth accelerates resulting in ultimately greater male body sizes (Lee & Moss, 1995; Morrison *et al.*, 2005, Shrader *et al.*, 2006b). Younger males similar in body size to adult females also ingest a lower quality diet than the females in both wet and dry seasons (Woolley *et al.*, 2008c). The sex of the elephant, and thus the reproductive state, affects the quality of diet ingested (Stokke & du Toit, 2000; Woolley *et al.*, 2008c). Although smaller adult males would have higher metabolic requirements (per unit body mass) than large adult males, they ingest a similar quality diet (Woolley *et al.*, 2008c). Young males

thus must increase the relative (but not absolute) forage quantity ingested, rather than adjusting the quality of forage ingested to increase energy intake (Woolley *et al.*, 2008c).

In contrast, adult females employ a foraging strategy to increase diet quality (Woolley *et al.*, 2008c,d). These females are socially constrained to move across the landscape with their calves and thus are restricted to move at the rate the smallest calves in the herd are capable of (Moss & Poole, 1983). This limits the distance a female can cover to ingest adequate quantities of forage, therefore forage quality is increased to obtain adequate nutrition (Woolley *et al.*, 2008c,d). Weaned calves ingested a higher quality diet than the larger-bodied elephants within the population (Woolley *et al.*, 2008c). This was achieved by selecting higher quality plant parts which contain more cell soluble components and less fibre (Woolley *et al.*, 2008d).

The gastrocentric model (Barboza and Bowyer 2000, 2001) explains sexual segregation in ruminants on the basis of allometry, minimal forage quality, digestive retention and differing reproductive requirements of the sexes. This model suggests that smaller-bodied females are better adapted to increased intake of higher quality forage to meet energy and protein requirements for reproduction, while the digestive morphology and physiology of males is better suited to consumption of abundant, low quality forage because gut capacity promotes digestion and is poorly equipped to handle forage of too high a quality (Barboza and Bowyer 2000). In support of this theory, I found a general scaling of elephant diet quality with body size, as well as the clear sexual dimorphism exhibited by the higher quality diet of adult females (Woolley *et al.*, 2008c). Within body size classes, the sex of the elephant and therefore the reproductive state of the individual affected the quality of diet ingested, as male and female diet quality differed significantly between individuals of similar body size (Woolley *et al.*, 2008c). However, we require further investigation of alternative mechanisms of age and sexual segregation e.g. social constraints, reproductive strategy (Perez-Barberia & Gordon, 1999).

Individual strategic response to environmental stochasticity therefore varies according to body size and life-history stage, which determines nutritional requirements (in terms of

nutrients and energy) driving foraging selection strategies (Woolley *et al.*, 2008c,d). Intraspecific (and possibly interspecific) interactions may affect foraging decisions, with the displacement of adult females to higher levels in the canopy when feeding close to calves (Stokke & du Toit, 2000; Woolley *et al.*, 2008d). Relationships between these social foragers must not be underestimated and further investigation of the possibility that feeding height selection is influenced by sociality is required, together with the influence of intra- and interspecific competition on elephant foraging strategy. This may have particular impact on calves in high-density situations when competition for forage at lower heights in the canopy would be most intense.

During severe, prolonged periods of nutritional restriction due to a reduction in the availability of forage quantity and quality (e.g. during drought) weaned calves are likely to be severely compromised, due to their more selective foraging strategy (Woolley *et al.*, 2008c,d). Their requirements for a higher quality diet and frequent hydration, suggests that resource restriction would have the greatest impact on this elephant cohort (Woolley *et al.*, 2008c,d). These physiological requirements could explain the increased susceptibility of this age class to stochastic environmental variability and the resultant highest incidence of mortality in the juvenile age class during drought periods. Our studies (Woolley *et al.*, 2008c,d) provide the first mechanistic explanations linking the physiological constraints faced by juvenile elephants with stochastic environmental resource restriction and ultimately the factors affecting recruitment and influencing elephant population dynamics.

In isolation, juvenile mortality would be required at high levels (e.g. 17.1 % p.a., Woolley *et al.*, 2008a) and frequencies (e.g. 84 % every eight years (Woolley *et al.*, 2008a) to regulate African elephant populations. Such incidence of juvenile mortality does not currently occur naturally (Dudley *et al.*, 2001; Moss, 2001; Whyte, 2001; Leggatt, 2003; Slotow *et al.*, 2005; Wittemyer *et al.*, 2005; Gough & Kerley, 2006; Mackey *et al.*, 2006; Foley *et al.*, 2008; Woolley *et al.* 2008a). The artificial increase of juvenile mortality through culling (i.e. human predation) could produce the required mortality scenario, but this practice would be highly controversial due to, amongst other

things, the social impacts on elephant populations (Slotow *et al.*, 2008). However, juvenile mortality alone does not act in isolation to drive elephant population regulation, for reproductive delays which reduce female fecundity also play a significant role (Leggatt, 2003; Wittemyer *et al.*, 2007; Chamaillé-Jammes *et al.*, 2008).

In combination, juvenile mortality and female fecundity are the basic processes functioning during both stochastic environmental events and in situations where the strength of density dependent impacts is maximized (Dudley *et al.*, 2001; Moss, 2001; Leggatt, 2003; Wittemyer *et al.*, 2007; Chamaillé-Jammes *et al.*, 2008; Junker *et al.*, 2008; van Aarde *et al.*, 2008). These processes are initiated in different ways in open versus closed systems (van Aarde *et al.*, 2008). With dispersal options removed in closed systems, elephant populations can increase in size until density-dependent feedbacks may result in a decrease in population growth rates (Fowler & Smith, 1973; Owen-Smith *et al.*, 2006; Biggs *et al.*, 2008; van Aarde *et al.*, 2008; Mackey *et al.*, in press). But this is likely to occur at the very limit of resource capacity and the associated concentration of elephant impacts may be detrimental to the biodiversity of the system (e.g. Gough & Kerley, 2006). The absence of natural density-dependent feedbacks at moderate population densities, i.e. lower than the limits resulting in habitat transformation and elephant mortality due to resource limitation, may necessitate the initiation of management interventions to prevent such impacts on the biodiversity or landscape structure of the system (Owen-Smith *et al.*, 2006; Biggs *et al.*, 2008; Slotow *et al.*, 2008).

In closed systems, juvenile mortality resulting from stochastic environmental events may be the primary natural process functioning to reduce population size. However, population recovery from this type of mortality event is fairly fast (in the context of the long generation time of elephants) e.g. four years for recovery to pre-fire population level after fire mortality in Pilanesberg National Park (Woolley *et al.*, 2008b). Stochastic events such as drought and fire occur too rarely and cause too low a level of mortality to result in the prevention of population growth in these systems (Dudley *et al.*, 2001; Moss, 2001; Wittemyer *et al.*, 2005; Woolley *et al.*, 2008b). When they are severe, they are “large, infrequent disturbances” (Gillson, 2006) and by definition rare in occurrence. The

impact of these events on longer-term female fecundity requires further investigation. If reproductive delays occur in a substantial proportion of fecund females in the population, the frequency rather than the magnitude of mortality during these events would drive population dynamics, if the resultant combined effect on population growth rate is substantial enough. However, with climate change, droughts are expected to become more frequent in most arid and semi-arid ecosystems (Easterling *et al.*, 2000). If drought frequency and/or severity increases, this may play a vital role in the natural population regulation of large herbivores. Global climate change could therefore have a significant impact on ecosystems across the African continent, with increasingly severe, frequent droughts contributing to a new dimension of challenges facing large herbivore management.

In small, closed systems, the introduction of reproductive delays through female contraception may be a valuable (and reversible) option available in the management of elephant populations if the rate of population increase is of concern (Delsink *et al.*, 2006; Owen-Smith *et al.*, 2006; Mackey *et al.*, in press). In open systems, density dependence may play a significant role in elephant population regulation (e.g. Junker *et al.*, 2008; Chamaillé-Jammes *et al.*, 2008). The local abundance of elephant populations dictated by seasonal conditions can cause the mortality of juveniles and incur female reproductive delays (Chamaillé-Jammes *et al.*, 2008). With female fecundity closely linked to vegetative productivity, high density situations would result in female reproductive delays due to intraspecific competition for resources (Wittemyer *et al.*, 2007). Although low levels of juvenile mortality also occur in high-density populations, impacts on female fecundity may be of greater significance to population regulation than first thought (Chamaillé-Jammes *et al.*, 2008). Reproductive delays function over a longer timescale than the immediate effects of a single mortality event (Leggatt, 2003; Mackey *et al.*, 2006; Woolley *et al.*, 2008a), although drought mortalities can occur over a few consecutive years depending on conditions (Dudley *et al.*, 2001; Moss, 2001). Therefore, reduction in female fecundity can have a longer-term influence on population dynamics, extending limiting effects over at least one calving interval.

The typical juvenile-mortality-driven pattern of population regulation in large ungulate systems is therefore not truly representative of the processes driving African elephant population dynamics. The combination of juvenile mortality and female fecundity, rather than one or the other in isolation, functions to regulate African elephant populations naturally, together with dispersal in open systems. There is much uncertainty surrounding the exact stage at which these processes function in different elephant systems (Owen-Smith *et al.*, 2006; Kerley *et al.*, 2008; Slotow *et al.*, 2008; van Aarde *et al.*, 2008). Further investigation will provide insight into the mechanisms driving these processes, to allow sound scientific support of elephant management decisions to be made throughout Africa.

With similar demographic drivers in operation in all long-lived, megaherbivore species (Owen-Smith, 1988), it is critical that the role of juvenile mortality and female fecundity is well understood. Whether locally overabundant (e.g. elephant (Blanc *et al.*, 2008), giraffe (Fennessy & Brown, 2008)), vulnerable (e.g. white rhino (Hoffmann & Stuart, 2008a), hippopotamus (Lewison & Oliver, 2008)) or critically endangered (e.g. black rhino (Hoffmann & Stuart, 2008b)), the functioning of these population processes will determine regulation, and consequently the long-term survival of these species. The manipulation of female fecundity through management intervention may assist in the regulation of overabundant species, for example through direct contraception of females (Grobler *et al.*, 2008) or by increasing density-dependent effects, e.g. water point manipulation (Owen-Smith *et al.*, 2006; Chamaillé-Jammes *et al.*, 2007). Management of mortality impacts can also function as a valuable tool in population regulation (Slotow *et al.*, 2008). However, predation on adult cohorts has the potential to cause major shifts in demographics (Owen-Smith *et al.*, 2005), with the result that poaching is a considerable threat to megaherbivore populations (Hoffman & Stuart, 2008a,b). The demographic disruption can be long-lasting due to the long generation times of these species, and social influences can be significant and persist over many generations (e.g. Gobush *et al.*, 2008). An increase in these types of mortality events has the potential to shift a population from overabundance to decline within a relatively short timeframe (Owen-Smith, 1988; Owen-Smith *et al.*, 2005; Gobush *et al.*, 2008; van Aarde *et al.*, 2008),

which can have far-reaching consequences for systems where these megaherbivores function as keystone species (Kerley *et al.*, 2008). Therefore, it must be appreciated that the demographic processes driving megaherbivore population regulation are complex and sensitive. Successful conservation management will require careful consideration of the interactions between environmental stochasticity and active manipulation and the resultant effects on population persistence.

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