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Demography and population dynamics in the elephants *Loxodonta africana* of Addo Elephant National Park, South Africa: is there evidence of density dependent regulation?

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Abstract Density dependence of the Addo Elephant National Park (South Africa) elephants *Loxodonta africana* was assessed using a long-term data set. Estimated carrying capacity is 0.1–0.5 elephants km^{-2} but stocking rates have been up to 4 elephants km^{-2}. Population growth rate was found to be positively correlated with increasing density. There was no relationship between birth rate, the age of first calving or calf sex ratio and elephant density but there was a positive relationship between birth rate and rainfall during conception year. Mortality rates, particularly for juveniles, were low, and mean inter-calf interval was 3.3 years. There is no evidence of density dependent regulation in this population, despite the population being consistently above the estimated sustainable carrying capacity and a loss of phytomass and biodiversity. This is interpreted in light of the characteristics of the aseasonal habitat, succulent thicket vegetation and the ability of elephants to utilize accumulated vegetation biomass. These findings indicate that density dependence should not be considered as an option in the control of elephant numbers in this Park, or where elephant resources are not seasonally limited.

Keywords Addo Elephant National Park, density dependence, elephant, *Loxodonta africana*, population regulation, South Africa.

Introduction

Elephant *Loxodonta africana* population regulation is increasingly becoming an issue in many conservation areas throughout Africa. Given their large body size elephants have the ability to transform habitats, particularly when at high densities. Successful management leads to large elephant populations within confined areas, which may lead to a loss of biodiversity (Van Wyk & Fairall, 1969; Laws, 1970; Barnes, 1983; Western & Gichohi, 1989; Lewis, 1991; Ben-Shahar, 1993; Moolman & Cowling, 1994; Cumming *et al.*, 1997). The challenge to conservation managers is to limit elephant population size without resorting to culling. One management approach may be to rely on the regulation of population size through density dependent effects (Laws, 1970; Hanks & McIntosh, 1973; van Aarde *et al.*, 1999). Consequently, understanding how density dependence influences elephant population dynamics is critical to the future management of elephants. Here we assess the evidence for density dependent effects in a small, closed population of elephants in South Africa.

Fowler (1987) reviewed the evidence for density dependence in large mammals and concluded that the vital rates (fecundity and mortality) may change as a result of changes in food resources. Gaillard *et al.* (1998, 2000) determined that, although adult survival rate has a greater effect on population growth rate than juvenile survival rate, it had higher elasticity and appeared to be buffered against temporal variation. They concluded that juvenile survival was more sensitive to density dependence. There is a sequence of changes in vital rates as population density increases towards maximal levels: increase in juvenile mortality rate, increase in age of first reproduction, decrease in adult female reproductive rate, and increase in adult mortality rate (Gaillard *et al.*, 2000; Eberhardt, 2002). These changes have been reported in a number of species (e.g. red deer *Cervus elephus*, Clutton-Brock *et al.*, 1987; Soay sheep *Ovis aries*, Clutton-Brock *et al.*, 1996).

The nutritional status of females may influence the sex of offspring (Trivers & Willard, 1973); hence, populations operating under density limited resource availability may show skewed sex ratios. Changes in the birth sex ratio have been attributed to density dependence (Kruuk *et al.*, 1999; Mysterud *et al.*, 2000). Males are more expensive than female offspring in terms of parental investment and future breeding opportunities for a number of species, including elephant (Clutton-Brock *et al.*, 1981; Lee & Moss, 1986; Wolff, 1988; Clark *et al.*, 1990). We therefore hypothesize that a population

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operating under density limited resource availability may show a higher proportion of females at birth.

Density induced population regulation has been noted in a number of elephant populations (Buss & Savidge, 1966; Laws, 1969; Hanks & McIntosh, 1973; Dunham, 1988; van Aarde *et al.*, 1999). The density at which these effects operate varies with the population and habitat type. Van Jaarsfeld *et al.* (1999) found no evidence of density dependent effects in South African elephant populations with a mean density of 0.33 elephants km^{-2}. However, van Aarde *et al.* (1999) found evidence to suggest density dependence at the sub-population level in the Kruger National Park at a density of 0.37 elephants km^{-2}. The elephants of Addo Elephant National Park, the population reported on here, have been stocked at much higher levels, up to 4.0 elephants km^{-2}, during the Park's 73-year history.

The Park's elephant density has been consistently higher than any estimated carrying capacities (*sensu* Zacharias, 2004) recommended to maintain the vegetation (e.g. 0.4 elephants km^{-2}, Penzhorn *et al.*, 1974; 0.25–0.54 elephants km^{-2}, Boshoff *et al.*, 2002). Since 1976 the population has been the subject of a number of intensive demographic studies (Hall-Martin, 1980; Whitehouse, 2001; K.F. Gough, unpub. data). This well studied population, occurring at high densities and faced with declining resources (Penzhorn *et al.*, 1974), presents an ideal opportunity to investigate density dependent influences. This paper presents the findings of such an analysis.

Methods

Population history

The Addo Elephant National Park is *c*. 60 km north of Port Elizabeth in the Eastern Cape Province, South Africa. The Park was proclaimed in 1931 to protect the remaining 11 elephants in the region (Hoffman, 1993). It was fenced in 1954, restricting the then population of 22 elephants to 22.7 km^2 (Hall-Martin, 1980) and preventing any natural emigration or immigration. The elephants of the Park were intensively studied from 1976 to 1979 (Hall-Martin, 1980) and from 1996 to the present (Whitehouse, 2001). The history of the population was reconstructed (Whitehouse, 2001), allowing detailed examination of long-term demography. Since the Park was fenced it has undergone five expansions, starting in 1977 (Lombard *et al.*, 2001). The elephant population numbered 381 in December 2002, confined to a fenced area of 103 km^2.

Analysis

Demographic analysis for the period 1976–2002 is presented here. Although the history of the population has been reconstructed, data prior to 1976 is not used as it is less reliable (Whitehouse & Hall-Martin, 2000). The observed annual exponential rate of increase (r) and the percentage population growth were calculated (Caughley & Sinclair, 1994) as $r = \log_e(N_{t+1}/N_t)$, where N = population size and t = time, and % population growth = $(e^r - 1)100$, respectively. The relationship between annual percentage population growth and density was investigated using linear regression. The influence of a delay in density dependent regulatory effects on population growth was assessed by lagging density data during calculations by 1, 2 and 3 years.

Female fecundity, as age of first calving, inter-calf interval, and birth rate were examined. The age of first calving and the inter-calf interval are maximum estimates as cows may have given birth to additional calves between recorded offspring or prior to their first recorded offspring (Whitehouse & Hall-Martin, 2000). The calf sex ratio was expressed as a proportion (males/(males + females)) where 0.5 reflects an equal sex ratio, higher values are male biased, and lower values are female biased (Wilson & Hardy, 2002). The birth rate was derived following Moss (2001), adjusted to remove females unavailable for conception due to pregnancy. Thus, birth rate was calculated as (cows that gave birth in year x)/(cows available to give birth in year x), where available is defined as all cows of breeding age minus cows that had given birth in the previous 22 months (gestation length). Breeding age was 9–55 years, the youngest and oldest ages of calving, respectively, recorded in the Park (1976–2003). Multiple linear regressions were used to compare the birth rate with density (elephants km^{-2}) and rainfall (data from South African Weather Service) in the conception year as elephant conception rate can be influenced by rainfall (Moss, 2001). Rain occurs throughout the year in the Park with an annual mean of 392 ± SD 111 mm (calculated for 1959–2003). There is no permanent natural surface water and water is provided by bore-holes that feed 11 artificial water points.

The total number of elephants entering each of 17 age classes (year 0, 1, 2, 3, 4 and thereafter in 5 year categories, 5–9, 10–14,…, 60–64) between 1976 and 2002 was summed and the total number of deaths in each age class used to calculate age-specific and sex-specific mortality.

Results

Elephant density fluctuated widely between 1976 and 2002 (Fig. 1) as the population grew and the area available increased through Park expansions. Mean density for the period 1976–2002 was 2.4 ± SD 0.48 elephants km^{-2} (range 1.8–4). Annual population

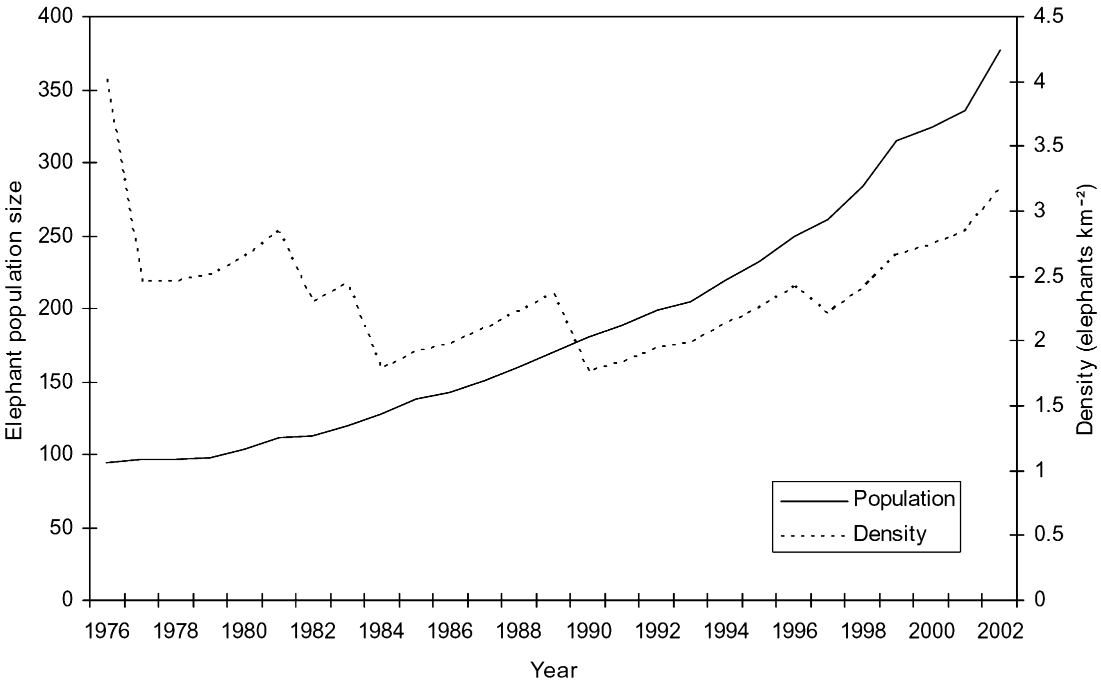

Fig. 1 Addo Elephant National Park elephant population size and density during 1976–2002. The park was enlarged in 1977, 1982, 1984, 1990 and 1997 (Lombard *et al.*, 2001).

growth rate for the same period was 5.8 ± SD 3.14% (range 0–13.3; Table 1). The population grew exponentially (exponential $R^2 = 0.99$, Fig. 2) and r ranged from 0.0 to 0.12 (Table 1). A 3-year running mean produced a range of r of 0.01–0.08 (Fig. 3).

Density and annual percentage population growth had a positive relationship ($R^2 = 0.17$; df = 27; P = 0.03). There was no significant relationship between population growth rate and density when this was lagged by 1 ($R^2 = 0.01$; P = 0.93), 2 ($R^2 = 0.02$; P = 0.5) or 3 years ($R^2 = 0.04$; P = 0.3). The number of years since each expansion was not a significant predictor of percentage population growth (Pearson product-moment correlation = −0.32; n = 23; P = 0.13).

Population density and r had a positive relationship ($R^2 = 0.20$; df = 27; P = 0.02), where the mean r for the 1976–2002 period was 0.05 ± SD 0.03 (range 0–0.12; Table 1). No significant relationships were found when the density data was adjusted for time lags of 1 ($R^2 = 0.01$; P = 0.78), 2 ($R^2 = 0.02$; P = 0.54) or 3 years ($R^2 = 0.05$; P = 0.28).

The proportion of breeding females was calculated to determine if an increase in the proportion of breeding females over time could explain the significant relationship with population growth. The percentage of breeding females was 25.0 – 34.5% (mean 30.9%) and there was no relationship with population growth rate (Spearman's rank correlation = − 0.074; P = 0.71; n = 28).

Mean calf sex ratio for 1976–2003 was 0.54 ± SD 0.188 (range 0.25 – 1.0; 200 male calves; 176 female calves). The higher number of male calves born did not differ significantly from parity ($\chi^2 = 1.4$; df = 1; P > 0.05). The sex ratio fluctuated annually (Table 1) but this was not related to density or rainfall. There was no relationship between the sex ratio of calves and density in conception year (Pearson product-moment correlation = 0.021; P = 0.28), density in birth year (Pearson product-moment correlation = −0.088; P = 0.66), rain in conception year (Pearson product-moment correlation = −0.016; P = 0.94) or rain in the year prior to conception (Pearson product-moment correlation = 0.155; P = 0.56).

Mean age of first calving was 12.3 ± SD 1.73 years (n = 62). A birth rate for an age of first calving of 9 years was calculated but as only 0.89% of cows reproduced at this age birth rates for 10 and 11 years were also calculated (23.21% of cows had had their first calf by 11 years, 50.89% by 12 years, and 91.07% by 15 years). The mean inter-calf interval for the period 1976–2003 was 3.3 ± SD 0.77 years.

Elephants had a higher birth rate in wet years at all three ages of maturation (9 years $R^2 = 0.26$, $\beta = 0.61$, P = 0.01; 10 years $R^2 = 0.24$, $\beta = 0.59$, P = 0.01; 11 years $R^2 = 0.25$, $\beta = 0.59$, P = 0.01). However, the age of a cow at the birth of her first known calf was not correlated with rain in conception year (Spearman's rank correlation = −0.005; P = 0.97; n = 86; 1976–2003). There was no correlation between birth rate and population density in

Table 1 End of year population sizes, annual births, deaths, calf sex ratio (> 0.5 male biased; < 0.5 female biased), and growth and mortality rates for the Addo Elephant National Park elephant population, 1976–2003.

Year	Population size at end of year	Births	Deaths	Sex ratio (M/(M+F))	Exponential rate of increase (*r*)	Population growth (%)	Mortality (%)
1976	94	11	0	0.45	0.12	13.3	0.0
1977	96	4	2	0.50	0.02	2.1	2.1
1978	96	2	2	1.00	0.00	0.0	2.1
1979	98	9	7	0.38	0.02	2.1	3.1
1980	103	5	0	0.40	0.05	5.1	0.0
1981	111	12	4	0.25	0.07	7.8	3.6
1982	113	4	2	0.75	0.02	1.8	1.8
1983	120	8	1	0.75	0.06	6.2	0.8
1984	128	9	1	0.67	0.06	6.7	0.8
1985	138	10	0	0.30	0.08	7.8	0.0
1986	142	11	7	0.50	0.03	2.9	4.9
1987	151	10	1	0.50	0.06	6.3	0.7
1988	160	11	2	0.36	0.06	6.0	1.3
1989	170	10	0	0.40	0.06	6.3	0.0
1990	181	11	0	0.36	0.06	6.5	0.0
1991	189	8	0	0.50	0.04	4.4	0.0
1992	199	12	2	0.83	0.05	5.3	1.0
1993	205	13	7	0.69	0.03	3.0	3.4
1994	220	15	0	0.67	0.07	7.3	0.0
1995	232	18	6	0.69	0.05	5.5	2.6
1996	249	19	2	0.32	0.07	7.3	0.8
1997	261	17	5	0.56	0.05	4.8	1.9
1998	284	29	6	0.36	0.08	8.8	2.1
1999	315	32	1	0.66	0.10	10.9	0.3
2000	324	15	6	0.40	0.03	2.9	1.9
2001	336	16	4	0.81	0.04	3.7	1.2
2002	377	42	1	0.62	0.12	12.2	0.3
2003	388	18	7	0.42	0.03	2.9	1.8

conception year (9 years $R^2 = 0.26$, $\beta = -0.31$, $P = 0.15$; 10 years $R^2 = 0.24$, $\beta = -0.24$, $P = 0.26$; 11 years $R^2 = 0.25$, $\beta = -0.23$, $P = 0.29$). No significant relationship was found between the age of a cow at the birth of her first known calf and density in the year of conception (Spearman's rank correlation = −0.136; P = 0.21; n = 86, 1976–2003).

Mean annual mortality rate for 1976–2003 was 1.43 ± SD 1.49% (Table 1). Annual percentage mortality rate was not dependent on density ($R^2 = 0.01$; df = 26; P = 0.84). Male and female mortality rates differed at each age class (Table 2) with males tending to have higher rates (Mann-Whitney U test $T = 246.0$; n = 14; P = 0.051). The juvenile mortality rate (0–9 years) was 1.02 ± SD 1.94% with no statistical difference between male and female rates ($z = 0.52$; P = 0.61). The adult (⩾10 years) mortality rate was 1.6% ± SD 1.68 and the male rate (2.81%) was significantly higher ($z = 3.93$; $P < 0.001$) than the female rate (0.80%).

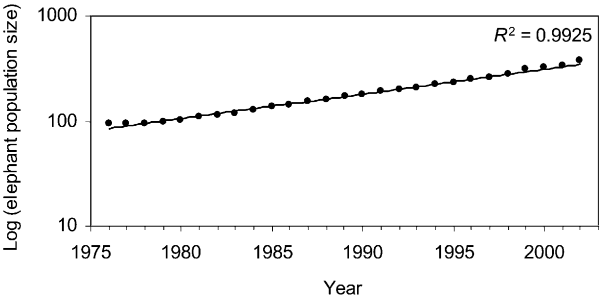

Fig. 2 Logged growth curve of the elephant population of Addo Elephant National Park for 1976–2002.

Discussion

The elephant mean population growth of 5.8% per annum in Addo Elephant National Park approaches the estimated maximum rate of increase of stable age elephant populations (7%; Calef, 1988). Furthermore, density did not affect the growth rate or any of the other demographic rates examined. The mean age of first calving was younger (12.5 vs 13.7 years) and the mean inter-calf interval (3.3 vs 3.5–4.5 years) was slightly shorter in the Park compared to other populations (Hanks, 1972; Moss, 2001).

The elephant birth rate in the Park correlated positively with rainfall in the year of conception, as found in Amboseli (Moss, 2001). High rainfall may

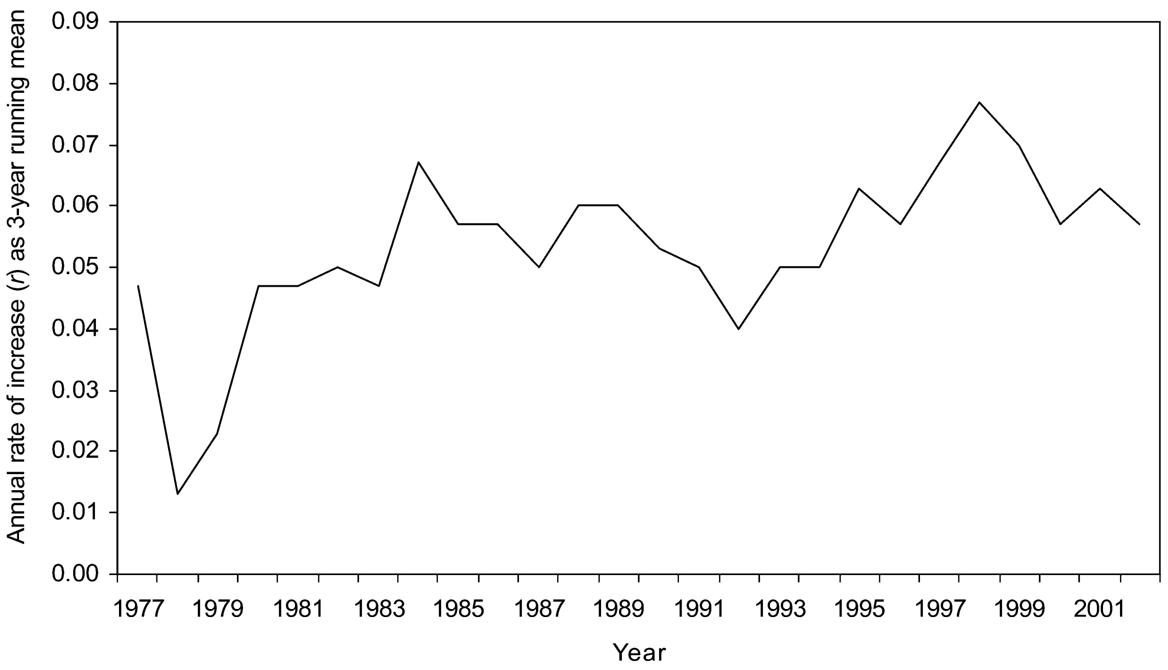

Fig. 3 Exponential rate of increase, *r*, using a 3-year running mean, for the Addo Elephant National Park elephant population during 1976–2002. The park was enlarged in 1977, 1982, 1984, 1990 and 1997 (Lombard *et al.*, 2001).

Table 2 Age and sex specific mortality rates for the Addo Elephant National Park elephant population for 1976–2003. *Z*-tests were used to determine if there were significant differences between male and female rates.

	Mortality rate (%)				
Age class	Male	Female	Total	*z*	P
0	3.5	4.6	4.0	0.23	0.82
1	0.0	0.6	0.3	0.05	0.96
2	1.8	0.0	1.0	1.05	0.29
3	2.0	0.4	1.7	4.98	0.001*
4	0.7	0.0	0.4	2.89	0.004*
5–9	0.4	0.2	0.3	0.04	0.97
10–14	0.8	0.0	0.4	6.05	0.001*
15–19	1.9	0.6	1.1	1.11	0.27
20–24	3.4	0.0	1.4	2.51	0.01*
25–29	4.7	0.5	2.1	2.18	0.03*
30–34	5.4	0.0	1.9	1.64	0.03*
35–39	10.6	2.3	5.3	1.65	0.10
40–44	7.7	2.4	4.3	0.04	0.67
45–49	0.0	3.2	2.6		
50–54	n/a	0.0	0.0		
55–59	n/a	0.0	0.0		
60–64	n/a	41.7	41.7		

*Male mortality rates significantly higher than those of females.
n/a, not available; i.e. no animals in the population have reached this age class or have died.

increase plant nutrient levels, thereby positively influencing birth rates, as shown for a number of rodent species (Reichman & Van De Graff, 1975; Taylor & Green, 1976). McCullagh (1969) observed a period of growth and higher cellular metabolism during the wet season in elephants of Murchison Falls National Park, Uganda, which he linked to the availability of new, nutritious vegetation.

The sex ratio of calves did not deviate from parity and no relationship between the sex ratio and density or rainfall was found. Lee & Moss (1986) found that during dry years male calves had elevated mortality levels in the first year of life, possibly because mothers could not provide enough milk. Unlike the Amboseli population the elephants of Addo Elephant National Park have year round access to drinking water and drought resistant vegetation (Stuart-Hill & Aucamp, 1993) in an environment that receives year-round rainfall. This probably explains the extremely low calf and juvenile mortality rates found in the Park compared to other populations, e.g. 4% for 0–1 years compared to 10% (Moss, 2001) and 1.0% for 0–9 years compared to 10% (Laws & Parker, 1968; Douglas-Hamilton, 1972). The male mortality rate tended to be significantly higher than that of females, which supports findings by Moss (2001), although adult mortality rates in the Park are also lower than those described elsewhere (1.6% compared to 3–5%, Laws & Parker, 1968; Douglas-Hamilton, 1972).

The findings indicate that the vital rates of the elephants of the Park are not following the expected sequence (Gaillard *et al.*, 2000; Eberhardt, 2002) of a population operating under density dependent mechanisms: the juvenile mortality rate is low, the age of first breeding is young, birth rate is high and not influenced by density, and adult female mortality rate is low. Furthermore, all these parameters are independent of density.

The demographic data indicates that the elephant population of Addo Elephant National Park is healthy and will continue to increase exponentially. This suggests two things: either that the population has not reached a sustainable carrying capacity, assuming that regulatory mechanisms will be evident once it does, or that elephants will not respond to density dependent processes until the ecosystem is highly altered and damaged. Given that elephant density within the Park is much higher (2.4 elephant km^{-2}) than recommended to maintain the vegetation (Penzhorn *et al.*, 1974; Boshoff *et al.*, 2002) and that the population is still growing rapidly, we conclude that resource requirements are currently being met. It is also apparent that the demographic data do not provide any insights into the appropriate densities for these landscapes.

Addo Elephant National Park is situated in a succulent thicket vegetation type (Hall-Martin, 1980, 1992; Cowling, 1984) that is evergreen and nutritious (Koen *et al.*, 1988; Seydack & Bigalke, 1992; Stuart-Hill & Aucamp, 1993). It has a high standing biomass (mean wet plant biomass of 18 kg m^{-2}, Penzhorn *et al.*, 1974) that accumulates over a number of years, despite a relatively low productivity (Stuart-Hill & Aucamp, 1993; Henley, 2001). The high nutritional value of thicket can influence herbivore life history; Seydack & Bigalke (1992) found that bush pig *Potamochoerus porcus* living in the succulent thicket of the Eastern Cape had higher reproductive rates than those living in the Southern Cape forest. Undisturbed thicket maintains its forage production in drought and has a relatively consistent forage flow between seasons. However, once it has become overgrazed it loses secondary productivity (Stuart-Hill & Aucamp, 1993), an apparently irreversible, positive feedback process that once initiated, continues (Lechmere-Oertel *et al.*, 2005). Numerous studies within Addo Elephant National Park describe a loss of plant biodiversity (with up to 70 plant species at risk) and biomass, and attribute this to high elephant density (Penzhorn *et al.*, 1974; Midgley & Joubert, 1991; Lombard *et al.*, 2001; Kerley & Landman, 2006; M. Landman, unpub. data). The amount of forage available has been substantially reduced yet the elephant population of the Park continues to increase. Because of their large body size, hind-gut digestion, and rapid throughput, elephants are able to utilize a wide range of forage quality (Owen-Smith, 1988). The ability of elephants to utilize a diverse range of plants in the diet (146 species in Addo Elephant National Park, M. Landman, unpub. data) further enhances their ability to extract nutrients from resources with declining availability and variation in quality.

The observed decline in plant biomass and the lack of response in elephant demography allows us to predict that at some point elephants will severely deplete the accumulated forage resources (the basis for further productivity). Until the resource base in the Park is irreversibly damaged, the elephant population will probably continue to reproduce and grow at a high rate, at the expense of biodiversity. A key finding of this study is that elephant demographic data cannot be used to predict when this resource base will collapse; other elements of biodiversity are already providing warnings that densities in the Park are too high. Although there was evidence for density dependence in Kruger National Park (van Aarde *et al.*, 1999), Whyte *et al.* (2003) surmised that it may be too late for some plant and animal species by the time the elephant population stabilizes. This will be the case in the Addo Elephant National Park and management strategies here or in other aseasonal environments should not therefore rely on the elephant population stabilizing through density dependence before serious damage to the habitat has occurred.

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