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Culling and the dynamics of the Kruger National Park African elephant population

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Abstract

South Africa's National Parks Board has opted to control African elephants (*Loxodonta africana*) through culling in the Kruger National Park (KNP). Killing elephants is highly controversial. The Board must balance this controversy against the probable destruction of vegetation and the consequent depletion of biological diversity that high elephant densities cause. Annual aerial counts provided the population estimates on which the culling quotas were based. For management purposes, the elephant population of the Park is divided into four sub-populations. From 1984 to 1994, the annual quota was usually taken from only one of these sub-populations during a given year. This resulted in 3 to 5 years elapsing between culls in each sub-population. We investigated the year-to-year changes in densities after culling. These changes were density dependent. Density dependence implies that immediate culls following estimated high densities may be premature. If left alone, the densities would decline naturally. Indeed, culling becomes self-reinforcing as it moves population densities towards the level where reproduction is greatest. Data confirm this intuition: at densities greater than 0.37 elephants/km^2 elephant numbers generally declined without culling. Many culls were unnecessary. Culling, as implemented in the past, may have had consequences for elephants and their habitat that were different to those expected from a mere reduction in their numbers. Densities in the year immediately after a cull tended to decline – not increase as would be expected from density dependence alone. Undoubtedly, this unexpected decline was the consequence of disturbance and subsequent emigration. In following years, the densities rose as animals moved back into the sub-population. A management programme where culling will be instituted only when densities exceed 0.37 elephants/km^2 in selected regions in the park for at least 1 year, may be more acceptable than the programme used up to 1995. However, we do not know if the vegetation of KNP can withstand the resulting episodic high densities. With densities presently exceeding the cut-off values calculated for both the south and the northern management regions vegetation changes there need to be monitored.

INTRODUCTION

For 30 years, managers have promoted culling as a management tool for African elephant populations confined to areas set aside for conservation (e.g. Buechner *et al*., 1963; Glover, 1963). Based on the findings of Van Wyk & Fairall (1969), the South African National Parks Board initiated a programme of elephant culling as a means of curtailing the anticipated destruction of the vegetation in the Kruger National Park (KNP). In 1967, they had already decided to maintain the KNP population at about 7000 individuals (0.32 elephants/km^2) based on studies on plant–elephant interactions conducted elsewhere in Africa. A new master plan for the management of the KNP came into effect during 1986. It confirmed the decision to continue to keep the population at 7000, but accepted fluctuations ranging from 6000 to 8500 individuals (Joubert, 1986). That decision resulted in 17 219 elephants being culled or removed from the KNP between 1967 and 1996. Increasing public pressure and the lack of proof of the damaging effects of high elephant densities resulted in the culling being temporarily discontinued in 1995. Since then, however, Cumming *et al*. (1997 and references therein) have demonstrated how high densities dramatically reduce biological diversity. The 'elephants *versus* biodiversity' debate remains controversial.

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Annual aerial surveys provided the culling quotas needed to maintain elephant densities within the suggested range. From 1967 to 1984 elephants were culled from areas throughout the KNP, however, from 1985 to 1994, KNP staff identified four management regions separated by rivers and covering the park's entire area (Fig. 1). The total quota for a given year was taken from just one of these regions and meant removal of between 6 to 32% of the local population.

We examined the response of elephants to culling by determining how post-culling densities affected population growth rate. Our analyses suggest an alternative management strategy for the elephants in the KNP. Left alone, high densities of elephants will usually decline. There will often, but perhaps not always, be no need for human intervention.

MATERIALS AND METHODS

Censuses

We base our analyses on information collected as part of the conservation management operations of the KNP. Aerial surveys conducted over a period of 1 month dur-

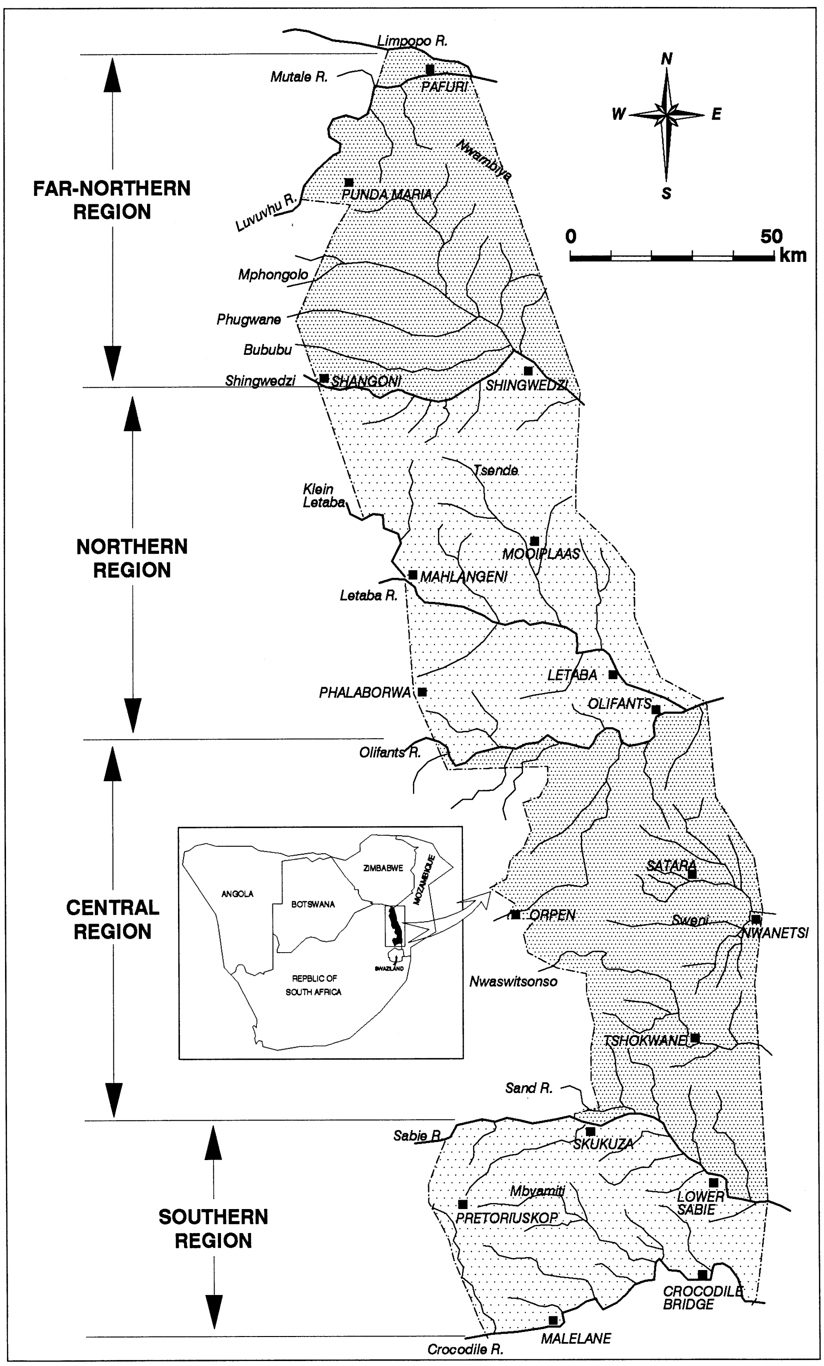

Fig. 1. The four elephant culling regions of the Kruger National Park.

ing August and September, when elephants concentrate along the watercourses of the park, yielded annual population estimates for the period from 1967 to 1998. Visibility is also at its best at the end of the austral winter when most deciduous trees have shed their leaves.

A four-seater Bell 206 Jet Ranger helicopter flown at an altitude of between 200 and 300 m, depending on the terrain and visibility permitted visual coverage of about 1 km on each side of the aircraft. Flight paths followed the drainage courses throughout the park. With flight lines less than 2 km apart, the entire park was covered during each census. The hovering ability of the helicopter allowed for counting of each group encountered, with the final number obtained through consensus amongst three observers. These yearly counts lasted 18 days, with an area of approximately 1100 km^2 being covered each day at a search rate of 2.6 km^2/min. I. Whyte (pers. obs.) has reported the precision and accuracy of these counts. Differences between recorded and expected population sizes over a period of 15 years only twice exceeded 6% (mean (± SE) = 1.67 (± 1.13)%).

Culling

Annual culling quotas ranged from 16 to 1846 individuals. Between 1967 and 1984, culls took place throughout the park. From 1984 to 1994, the total quota each year rotated around the four management regions in the KNP (Fig. 1). In practice, this resulted in 3–5 years elapsing between culls of a population in a given region. As a result of this, and of the discontinuation of the culling programme since 1995, a specific region experienced from 1–7 years of no disruption by culling after a specific cull. We refer to each of these regions as a sub-population.

Data analyses

Density dependent mortality suggests that there is a population density, K, below which densities X_t in year t, tend to increase to the following year (t+1) and above which they tend to decrease, i.e.: when $X_t < K$, $X_{t+1} - X_t > 0$ and when $X_t > K$, $X_{t+1} - X_t < 0$.

The year-to-year change in population density, $X_{t+1} - X_t$ we call D. The null hypothesis of no density dependence suggests a population model:

$$X_{t+1} = X_t + \sigma$$

where σ is random variation. Under the null hypothesis $D = \sigma$, a population follows a one-dimensional Brownian walk over time and the variance of population size constantly increases.

Naively, one would expect that linear regression of D against initial density X_t should not reject the null hypothesis if this model obtains. Were D to decline significantly as X_t increases, we would reject the null hypothesis, accept density dependence and use the value of X_t where $D = 0$, as an estimate of K. The method is intuitively reasonable, but statistically flawed. The method uses $X_{t+1} - X_t$ (= D) as the dependent variable and X_t as the independent variable. Put this way, they are obviously dependent on each other. This is old ground in population ecology and we tread it again only because we take a different route across the difficult terrain.

The flaw is that population densities are measured with error. So, for instance, a serious accidental underestimate of the true density in one year will lead *simultaneously* to a low value of X_t and corresponding high value of D. Consequently, regressions of population change (D) against initial population density X_t show strong, spuriously significant negative correlations by chance alone when sampling error is large relative to the actual population changes.

We know that for elephants the sampling error is small (< 5%), while the numbers fluctuate by many hundred animals from one year to the next in a population of roughly 7000. We have simulated this scenario using population sizes, fluctuations and sampling errors broadly similar to those that are observed. These simulations still show the spurious negative correlation of population change against initial population size. The spurious effect is small, however. (The percentage of variance explained by regressions of D *versus* X_t is never more than 5% and usually much less.) In the actual data, when a low density is followed by a population increase, then both the low density and the subsequent increase are real.

The flaw arising from the dependence on estimates of consecutive population densities is further weakened because in 1 out of 4 years, the initial population estimate is that after the cull and not the previous year's value. Culls act as experimental interventions, answering the question: by how much does a population increase afterwards when we reduce the population density to some prescribed low level? Simply, the low post-cull densities are known to be real ones – and not sampling artefacts.

Taken together, we believe we can analyse these data in the way outlined above. We use linear regression analyses of D against post-culling densities. Our method has small flaws but, we contend, these will not obscure the general results, and it has the advantage of being simple and intuitive.

RESULTS

Population growth

Culling did not halt population growth for elephants in the KNP, which fluctuated between 6586 and 8821 animals. Successive years of decrease in numbers were followed by successive years of increase in numbers (Fig. 2). The fraction of the total population removed through culling during a given year ranged from 0.2% to 20.9%. Expressed as a fraction of the sub-population affected by a given cull, the values ranged from 5.9 to 31.6%.

Table 1 presents the annual population density before

Table 1. Annual population density, culling density and change in population density expressed as the difference between post-cull density and the density after a cull for the four management districts of the KNP

Management district (area)	Year (t)	Density (elephants/km^{-2})				Change in density, D
		Year t (before the cull)	Culled C_t	Year t (post-cull)	Year t + 1 (after the cull)	
Far North (4190 km^2)	1984	0.522	0.165	0.357	0.227	–0.130
	1985	0.227	0.000	0.227	0.268	0.041
	1986	0.268	0.000	0.268	0.237	–0.031
	1987	0.237	0.000	0.237	0.264	0.026
	1988	0.264	0.000	0.264	0.372	0.108
	1989	0.372	0.074	0.298	0.232	–0.066
	1990	0.232	0.000	0.232	0.346	0.114
	1991	0.346	0.000	0.346	0.363	0.018
	1992	0.363	0.000	0.363	0.351	–0.012
	1993	0.351	0.062	0.289	0.298	0.009
	1994	0.298	0.010	0.289	0.275	–0.014
	1995	0.275	0.000	0.275	0.284	0.009
	1996	0.284	0.000	0.284	0.267	–0.016
	1997	0.267	0.000	0.267	0.308	0.041
	1998	0.308	0.000	0.308	–	
North (5980 km^2)	1984	0.324	0.035	0.289	0.335	0.047
	1985	0.335	0.020	0.316	0.308	–0.008
	1986	0.308	0.000	0.308	0.359	0.051
	1987	0.359	0.000	0.359	0.362	0.003
	1988	0.362	0.046	0.316	0.257	–0.059
	1989	0.257	0.000	0.257	0.358	0.101
	1990	0.358	0.000	0.358	0.312	–0.045
	1991	0.312	0.000	0.312	0.330	0.017
	1992	0.330	0.051	0.279	0.281	0.002
	1993	0.281	0.000	0.281	0.317	0.036
	1994	0.317	0.000	0.317	0.369	0.053
	1995	0.369	0.000	0.369	0.392	0.022
	1996	0.392	0.000	0.392	0.401	0.009
	1997	0.401	0.000	0.401	0.458	0.057
	1998	0.458	0.000	0.458	–	
Central (5475 km^2)	1984	0.342	0.022	0.320	0.354	0.034
	1985	0.354	0.000	0.354	0.389	0.035
	1986	0.389	0.070	0.319	0.245	–0.075
	1987	0.245	0.000	0.245	0.303	0.058
	1988	0.303	0.000	0.303	0.322	0.019
	1989	0.322	0.000	0.322	0.266	–0.056
	1990	0.266	0.000	0.266	0.256	–0.011
	1991	0.256	0.057	0.198	0.304	0.105
	1992	0.304	0.000	0.304	0.365	0.061
	1993	0.365	0.000	0.365	0.352	–0.013
	1994	0.352	0.000	0.352	0.333	–0.019
	1995	0.333	0.000	0.333	0.341	0.009
	1996	0.341	0.000	0.341	0.315	–0.027
	1997	0.315	0.000	0.315	0.322	0.007
	1998	0.322	0.000	0.322		
South (3840 km^2)	1984	0.326	0.0490	0.277	0.221	–0.056
	1985	0.221	0.000	0.221	0.379	0.158
	1986	0.379	0.000	0.379	0.326	–0.053
	1987	0.326	0.066	0.260	0.330	0.071
	1988	0.330	0.009	0.322	0.366	0.045
	1989	0.366	0.000	0.366	0.393	0.027
	1990	0.393	0.081	0.312	0.400	0.088
	1991	0.400	0.000	0.400	0.360	–0.041
	1992	0.360	0.000	0.360	0.370	0.011
	1993	0.370	0.060	0.311	0.393	0.082
	1994	0.393	0.033	0.360	0.449	0.090
	1995	0.449	0.000	0.449	0.477	0.027
	1996	0.477	0.000	0.477	0.514	0.037
	1997	0.514	0.000	0.514	0.485	–0.029
	1998	0.485	0.000	0.485		

Annual counts were conducted during August/September of year t while culling took place during April/May of year t+1. Entry of these values in the same row facilitated further calculations.

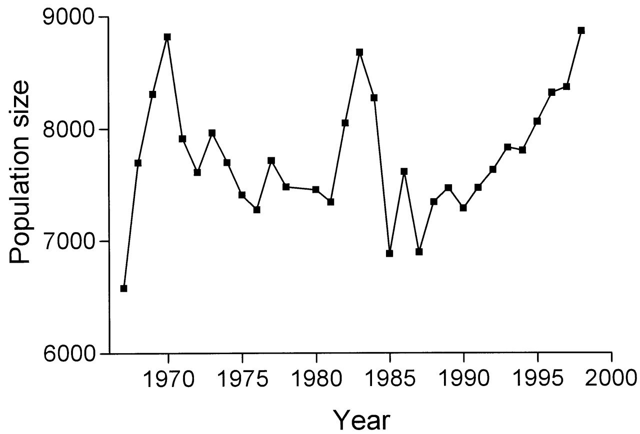

Fig. 2. Trend in the total population size for African elephants in the KNP based on aerial surveys conducted annually between 1967 and 1998. The population was exposed to culling as a management option from 1967 to 1994.

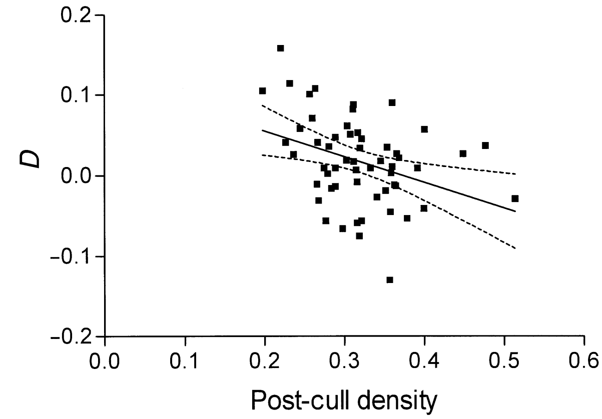

Fig. 3. The relationship between change in population density (D) and post-cull density for all sub-populations of African elephants in the KNP.

the cull, the density of elephants culled, C, and, from their difference, the population density after the cull. It also shows the pre-cull density for the following year and finally the change in population density. Annual counts were in August/September of year t while culling took place between April and June of year $t+1$. Entry of these values in the same row facilitates further calculations. Pre-cull densities ranged from 0.221–0.552 elephants/km^2, with a mean value of 0.339 (± 0.009) elephants/km^2. Post-cull densities during the period of culling ranged from 0.198–0.400 elephants/km^2, with a mean value of 0.307 (± 0.007). Annual growth rates expressed as yearly differences in post-cull densities in year t and pre-cull densities in year $t+1$ ranged from –0.13 to +0.158 (see Table 1).

Density dependence

Population growth rate, D, decreased significantly with an increase in post-cull density (Fig. 3; Table 2). Population densities above 0.37 elephants/km^2 usually declined during the next year when not culled. However, there were exceptions. The North sub-population increased from a density of 0.37 in 1995 to 0.39 (1996), 0.40 (1997) and 0.48 (1998). The South sub-population's density increased from 0.36 in 1994 to 0.45 (1995), 0.48 (1996) and 0.51 (1997) before declining again. There is evidence for density dependence, but it is a far from perfect regulator for those who must consider the long-term consequences to the park's vegetation of these transient high densities.

The simple regression technique readily allows further statistical exploration. First, we ask: do the four regions differ in their degree of density dependence? The slopes of the lines describing the above relationship for each of the management areas did not differ significantly from each other (F = 1.029; d.f. = 3 and 48; P = 0.388). This analysis of covariance shows that the four regions were homogenous and the density intercept for all districts combined suggests inhibition of growth at a density of 0.374 elephants/km^2 (Table 2).

Statistically, we should not read anything more into the regional slopes and intercepts. However, managers might see the differences between them supporting independent observations. Table 2 shows the regional results for this purpose. Only the regressions for the Far North and Central regions differed significantly from zero (see Table 2), tentatively suggesting that density dependence may be more powerful here. The density-intercepts for the four regions ranged from 0.293 to 0.445, suggesting that there might be regional differences in the density at which growth may be inhibited (Table 2).

Second, what is the impact of the cull itself? The residuals about the D *versus* post-cull density plot can themselves be plotted against culling density. The residuals decrease as culling intensity increases (Fig. 4), suggesting that culling intensity does affect population changes. An analysis of the influence of culling on

Table 2. Linear regression variables for the relationship between change in population density and post-cull density for elephant sub-populations in the KNP as presented in Table 1

District	Slope	y-intercept	x-intercept	r^2	F-value for deviation of slope from zero
Far North	–0.900 ± 0.324	0.264 ± 0.093	0.293	0.392	7.728*
North	–0.267 ± 0.265	0.107 ± 0.087	0.402	0.078	1.016
Central	–0.625 ± 0.242	0.206 ± 0.076	0.324	0.356	6.644*
South	–0.374 ± 0.189	0.119 ± 0.037	0.445	0.246	3.909
All districts	–0.317 ± 0.113	0.167 ± 0.069	0.374	0.128	7.940*

*P < 0.01.

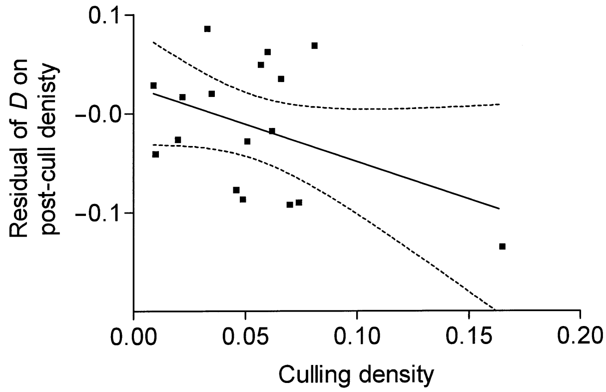

Fig. 4. The relationship between the residuals of *D* on post-cull density and culling density described by a linear regression line with the equation $y = 0.0357 - 0.759x$ ($r^2 = 0.173$).

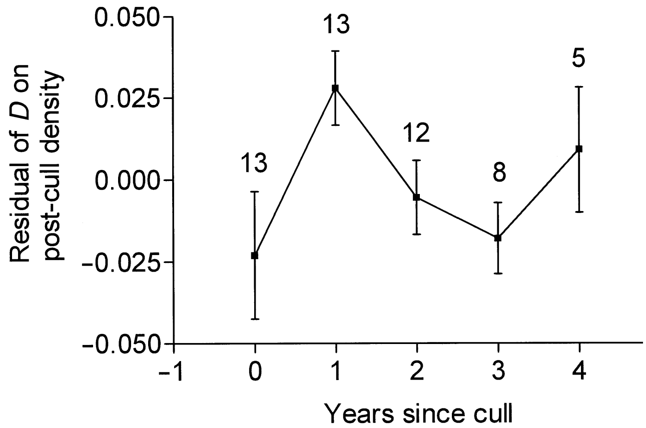

Fig. 5. The influence of culling on population change expressed as the mean values of *D* on post-cull density against the number of years that have elapsed since culling. The values above the standard error bars denote sample size.

population change showed that population change was affected by the time that had elapsed since the cull. Figure 5 plots the residuals of population change *versus* post-cull density, against the number of years that have elapsed since culling. Culling was followed by a sharp relative decrease in the rate of change in the year following a cull (Fig. 5). Mean values 2 and 3 years after the cull were higher.

The simplest interpretation of Fig. 5 is that relative to the expected density change, populations tend to be smaller than expected in the year immediately after the cull and to recover the following year. It seems likely that elephants initially move *out* of regions where other elephants have been killed – and not *in* to those regions, as would be expected if they responded solely to the increased availability of resources. This behavioural effect makes culling seem more effective than it is.

DISCUSSION

Culling raises ethical, social, and economic problems (see Cumming *et al.*, 1997; Butler, 1998; Whyte, van Aarde & Pimm, 1998) well beyond the scope of this paper. But so, too, does the loss of biodiversity. The South African National Parks aims to maintain biodiversity by preventing habitat destruction. The culling of elephants from 1967 to 1994 kept the population at between 7000 and 8500 individuals (see Fig. 2) and thus within the apparent limits of accepted influence on their environment in the KNP.

The obvious questions are was this the right range of population densities and was the management plan the best way to achieve that range?

Is the right range of densities correct?

The practice of limiting culling to a given area, followed by a number of years of no culling in that area, provided us with the opportunity for assessing the response of sub-populations to culling. From our analyses it is apparent that numerical changes in elephant sub-populations in the KNP are density dependent. At densities >0.374 elephants/km^2 (Fig. 3) the population tended to decrease. This value might differ for the different management regions of the KNP (see Table 2). This density is equivalent to an elephant population of very nearly 8000 for the KNP, and thus within the limits set for the population by park managers (see Smuts, 1975; Joubert, 1986).

Density induced regulation of reproductive output through changes in age at sexual maturity, pregnancy rates and inter-calving interval have been recorded for elephants elsewhere in Africa (see Laws, 1969; Dunham, 1988; Dobson, 1993, and references therein). Such density dependence may be important in population regulation (Hanks & McIntosh, 1973). Our analysis implies that in the KNP density dependence of population growth rate only begins to operate at densities greater than 0.37 elephants/km^2. In terms of the total park it is of interest to note that such a density was only achieved in 1968. Since then densities have been maintained at values ranging from 0.31 to 0.40 elephants/km^2.

Van Jaarsveld, Nicholls & Knight (1999) found no evidence for density dependent effects in South African elephant populations, with a mean density of 0.33 elephants/km^2 (Hall-Martin, 1992). Such a conclusion matches ours. The suggestion by Smuts (1975) that a density of 0.4 elephants/km^2 still had no regulatory effect on reproduction does not agree with the results of our analyses, since the inhibition in population change conceivably results from differences between birth and death rates. However, our analyses were conducted on the sub-population level and changes in population size for a given region may have resulted from intra-population movements rather than changes in demographic variables.

Our value of 0.37 elephants/km^2 as the density at which population growth rate is depressed is very much lower than the value of 0.57 proposed by Fowler & Smith (1973) as an 'equilibrium' density for the African elephant. It also differs considerably from the value of

1.19/km^2 suggested by Armbruster & Lande (1993) as an equilibrium value for elephants in semi-arid regions.

These higher values however are very similar to the equilibrium density estimated by Laws (1969) for Tsavo in East Africa. The discrepancy between our value and those mentioned above may be due to differences in habitat quality or due to the effect of long term management (culling) of numbers on our analysis.

In summary, comparisons of studies elsewhere do not sensibly inform management within the KNP. There may be differences of opinion about what is a reasonable density, but it seems more likely that there are real, underlying differences in ecology. What this study shows is that densities in the KNP will tend to be regulated at around 0.37/km^2.

What does this value mean? Habitat deterioration associated with densities slightly higher than the value of 0.37/km^2 in the KNP is of concern and implies that the present conservation paradigm (maintenance of biological diversity) requires some management action when elephant densities exceed the value of 0.37. Indeed, efforts to maintain the population substantially below this level – at 7000 to 7500 individuals – were based on Van Wyk & Fairall's (1969) suggestion that densities of elephant >0.29 individuals/km^2 may result in the destruction of vegetation.

Surveys have illustrated that widespread scarring of trees in the park by elephants only commenced during 1973 (Coetzee *et al.*, 1979) when densities were at the level of expected density dependent feedback. Densities above 0.37 have occurred since 1995 in two sub-populations and habitat damage has been continuing ever since (pers. obs.). Thus, maintaining the population at a level where density dependent effects are apparent may cause habitat destruction.

Are culls necessary?

When densities exceed 0.37 they typically decline the following year when not culled. Thus, the strategy of culling immediately after high densities is premature. Wait a year and the populations will often decline without such controversial intervention.

Moreover, the effectiveness of culls is often spurious. The immediate response of sub-populations of elephants to the cull was that of a local *decrease* in numbers, followed by a dramatic increase in population growth rate. The rates of increase recorded in response to culling (Table 1) often exceeded the maximum rate of increase of 7% estimated by Calef (1988) for the species. This implies that the calculated response of sub-populations to culling results not from an immediate increase in birth rate or a decrease in calving intervals, but rather from inter sub-population immigration, either by 'vacancies' created through the culling of sub-populations being occupied by members of neighbouring sub-populations, or by culling pressures inducing movements across sub-population boundaries. Thus, culling of a given sub-population may reduce environmental pressures exerted on neighbouring areas, while increasing that on the areas occupied by the culled sub-population. This idea requires further investigation, especially in terms of the consequences such fluctuations in the disturbances brought about by elephant may have for local diversity.

Can culls be eliminated entirely? Even though our analyses show that at densities >0.37 elephants/km^2 the killing of elephants may often be unnecessary, high densities have persisted for several years on occasion. We do not know if the vegetation of the KNP can withstand such high densities. With densities presently exceeding the cut-off values calculated for both the south and the northern management regions (see Table 2), vegetation changes there need to be monitored.

In summary, our management recommendations are simple. Culls should be considered only if a high elephant density persists for two consecutive years. They should not be an immediate response to high densities because typically such densities decline without intervention. The effects of persistent high densities on vegetation must be measured.

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