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Managing the elephants of Kruger National Park

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Abstract

The elephant population in Kruger National Park, Republic of South Africa, is growing rapidly. To prevent damage to the Park's ecosystems, the management has culled about 7% of the population annually. Such culls are very controversial. At first glance, contraceptives seem an attractive alternative means of control. We examine contraception as a management option, review the relevant aspects of elephant reproduction, physiology and demography and conclude that this optimism is probably misplaced. First, contraceptives have a wide range of physiological and behavioural side-effects that may prove to be damaging to the individual female and those around her. Second, the elephants in the Park have near-maximal growth rates with inter-calving intervals of less than four years. To achieve zero population growth, about three-quarters of the adult female elephants would need to be on contraceptives. There are no simple alternatives. The smallest numerical target for controlling population numbers is to kill or sterilize females about to become pregnant for the first time. Such a solution is unlikely to appease those who consider killing elephants to be unethical. It may, however, be the one closest to the natural patterns of elephant mortality.

INTRODUCTION

The problem of managing the elephant population in Kruger National Park (KNP), South Africa has unusual dimensions. On the continental scale, elephants are losing the competition for space with Africa's burgeoning human population (Parker & Graham, 1989). Yet within KNP, over the last three decades, culls removed an average of 7% of the population per year (from hundreds to ~1800 animals). The elephant population still increased. Without such intervention, the numbers might have doubled in as little as ten years.

Experiences in a variety of relatively dry landscapes show that high numbers of elephants can change species-rich woodlands to species-poorer grasslands (see Cumming *et al.*, 1997). Park management chooses to prevent these changes (Joubert, 1986) and so controls elephant numbers. Management interventions that prevent nature from taking its course will always be controversial among ecologists. Moreover, elephant culls raise social and economic issues that transcend the KNP's boundaries, further constraining the management's options, and leading to yet more controversy.

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The use of elephant products and hunting income might benefit the peoples next to the park, some of whom make only a subsistence living. Such income might engender a view of the elephant as a resource, rather than a competitor. Yet local actions have unintended global consequences. Across most of Africa, elephants are in a rapid decline, usually attributed to poaching and the illegal ivory trade (Lewis, 1984; Douglas-Hamilton, 1987; Barnes & Kapela, 1991; Caughley, Dublin & Parker, 1991). Selling ivory where elephants are protected and increasing creates an unregulated market that will probably lead to poaching and subsequent extinction elsewhere.

There are ethical issues, too. Many people, including those who might never visit the park, strenuously object to killing any large mammals. Ethics and economics may also interact. The tourists who do visit may feel offended that the animals they have travelled so far to see are locally deemed pests and so shot. KNP may not be the untouched wilderness of these tourists' imaginations and their not visiting it as a consequence might lead to a loss of revenue. Finding common ground between those for whom hunting is a passion and for those who passionately oppose it may be impossible. This issue extends well beyond elephants, of course.

Here, we will ask two sets of more limited questions. The more difficult is why should we control elephants in the first place? The second is how do we go about doing it?

'Playing God' is the frequent criticism – including by an anonymous reviewer of this paper – of those wildlife managers who would intervene in the natural course of things. The elephant problem in KNP is self-imposed: the decision to control elephants is based on speculation about what would happen if the elephants were to increase. Yet such speculation may be unavoidable. The obvious experiment of letting the elephants increase could have unfortunate consequences to the ecosystem and the species that depend on it that persist for decades or longer.

These consequences raise more questions. Did elephants effect such ecosystem changes in the past? Even if they did, should they do it now? What were the natural processes that regulated elephant numbers in the past? And what is 'natural' today in an Africa with a large and rapidly growing human population and few well-protected parks?

Given the choice of controlling elephant numbers, does KNP's management have alternatives to killing elephants that will still keep their numbers low? The use of contraceptives has been touted as a promising solution (Short, 1992; The Economist, 1996). Consequently, much effort has been spent to investigate the endocrinology of elephants and to evaluate the potential use of substances such as RU3486 that may block implantation (Greyling, van Aarde & Potgieter, 1997; Greyling, Ford *et al.*, in press). Other methods based on either immuno-contraception or slow-releasing estrogen implants are presently under trial in KNP.

We outline the serious and unpredictable consequences to the individuals of these methods. These include changes in behaviour, social status within the breeding herd, and in the steroidogenic activities of the ovary and uterus. Females treated with estrogen implants may remain in permanent estrus. We cannot predict either their behaviour or the consequences that this may have for the park's male elephants. Moreover, contraception is impractical. We will present models of elephant demographics to show that perhaps 75% of female elephants would need to be treated. Even at this level, the number to be treated would grow for well over a decade before we would achieve zero population growth.

Finally, we ask what is the smallest number of animals one should kill or sterilize if the goal is to control the population. In this answer is more than just a practical solution to controlling the population. For it identifies the weak link in the chain of life-history – the age and sex group where natural processes would make the largest difference to whether the elephant population increased or decreased.

WHY CONTROL ELEPHANT NUMBERS?

In at least some dry forests, increasing numbers of elephants progressively destroy the forest and convert it into more open habitats (Laws, 1970; Barnes, 1980, 1983; Douglas-Hamilton, 1987; Dublin, Sinclair & McClade, 1990; Jachman & Croes, 1991; Dublin, 1994; Leuthold, 1996; see Lawton & Gough (1970), Guy (1982) and Ben-Shahar (1996) for alternative explanations). In KNP, elephants also suppress the rejuvenation of selected woodland trees (Viljoen, 1988; Trollope *et al.*, in press). By comparing ecosystems on either side of an elephant fence, Cumming *et al.* (1997) demonstrated significant reductions in the species richness of birds, ants and other taxa, where elephants have removed the tree canopy.

There are several reasons why we may wish to prevent these changes. We might justify the low elephant numbers from assessments of biodiversity. Naturally high elephant numbers may have made woodlands and their inhabitants scarce or local. On a continent where so little protected habitat remains, there may be the need to conserve a set of species more localized and so more vulnerable to extinction than elephants (Hoeft & Hoeft, 1995). This justification explicitly recognizes that restoring nature to its original state on its original scale may now be impossible.

Alternatively, the target size that the population must not exceed may be historically justified. Phrased another way, conditions may be different now and we need to restore them to their former, natural state. We are reasonably sure that elephant densities are now different from the *recent* past. Evidence suggests that KNP held only low numbers of elephants at the turn of the century (Vaughn Kirby, 1896; Whyte, in prep.). Pienaar, van Wyk & Fairall (1966) estimated the 1947 population to be 560 elephants. During the 1960 (first) aerial survey the population comprised 1186 individuals (Pienaar *et al.*, 1966). Whether these were natural low numbers or, as Spinage (1973) has argued, the consequences of the ivory trade is still debatable.

If the latter explanation holds, then elephants would naturally have been abundant. So why were there originally any areas with extensive woodlands? Elephants might increase over century long time scales, destroying the woodlands in the process, and thus causing their own decline (Caughley, 1976). Elephants and forests might co-exist only over very large spatial scales that permit large mosaics of soon-to-be-destroyed woodland, about-to-recover near-treeless ecosystems and everything in between. Finely resolved palynological data might elucidate such changes, but we are not aware of such studies over sufficiently large areas.

In any case, even parks as large as KNP's 20 000 km^2 may be too small to allow such cycles to operate. The idea of trans-frontier conservation areas ('peace parks') – huge protected areas that stretch across international barriers – may take care of some of these problems of geographic scale. The realization of such parks is still in the future.

If the explanation that elephants were always at low numbers is correct, then what were the reasons why elephants remained scarce and what has changed? To answer these questions we need to consider elephant demography.

ELEPHANT DEMOGRAPHY

One does not need a detailed demographic model to expect that elephants, like humans, can increase rapidly in numbers. The parameters are broadly similar. Laws & Parker (1968), Laws, Parker & Johnstone (1975), Hachman (1980), Dunham (1988) and references therein summarize them. Like humans, female elephants have a life span of ~60 years, with between 2·5 and 5% of the population dying each year. They have a mean age of first calving from 11 to 20 years old. Gestation is 22 months, and the inter-calving interval can be as short as three years or as infrequent as nine years. Unlike humans, they remain fertile until into their late fifties.

In KNP, some females have given birth in their 12th year and most have given birth by the time they are 13 years old (Smuts, 1975). A culled sample of 966 adult cows shows an almost exact equality in the numbers of those pregnant (484) and non-pregnant (482). This means that, on average, a cow is pregnant for half of her adult life. Thus the calving interval will be twice the gestation time of 22 months, i.e. 44 months or 3·67 years (Whyte, in prep.)

There is no long-term, cohort-based study of survivorship. One way to estimate the annual mortality is from the size of the cull itself and how fast the numbers grow despite it. Two factors increase the population: births and immigration from areas outside the park. Immigration from Mozambique was a probable cause of the increase of ~6600 in 1967 to 8800 in 1970. It is less likely to explain the changes in the last two decades (Walker *et al.*, 1987). There are few elephants in the conservation and agricultural areas to the west of the KNP. KNP fenced the long eastern and shorter northern and southern boundaries in 1970. We suggest that immigration made, at best, only a small contribution to the population's growth rate after 1972. Whatever the contribution of immigration, practically, we must include it in our calculations as if it were a birth rate, for there is no way we can exclude more animals.

From 1973 to 1994 inclusive, the cull averaged 6·7% of KNP's elephants. The population ended this period at much the same size (7800) as it started (7600) and fluctuated between a low of 6900 and a high of 8700 animals. From year to year, the population always increased when the cull was less than 5%. It increased one year to the following year in nine different years when the cull was 0, 4, 4, 4, 4, 5, 5, 5 and 6% of the animals, respectively. Given the inevitable uncertainties in counting animals, increases may reflect under-counting in one year followed by over-counting in the following year. We discount the single high value of 6% because of this possibility. The consistent increases in population when between 4 and 5% of the animals are killed makes 5% a reasonable estimate of the population's growth rate. A population growing at 5% annually, all females calving first in their 12th year and at 3·67 years thereafter, allows a back calculation of annual mortality of 1·5%.

If these rapidly growing elephant populations are not typical of KNP's original state, then what has changed? For this question a simple demographic model provides interesting answers. The model assumes constant survivorship up to 60 years (and no survivors beyond that age), and specifies the age of first calving and calving interval. In nature, these parameters are not independent: poor food conditions and high elephant densities will probably affect all three. In particular, Dobson (1993) summarizes data showing how the age at first calving declines with increasing elephant densities. The effect of density on inter-birth interval is less obvious. We assume no marked changes in numbers – for that is the management objective – and so, for simplicity, we fix each parameter at a given value.

The fetal sex ratio for elephants in KNP is 1:1 (Smuts, 1975; Whyte, in prep.). This ratio persists until 14 years old, when the young males leave the breeding herds and join bachelor groups. The mortality of bulls in bachelor groups is unknown. It is likely to be slightly higher than in adult cows, but still low, as KNP has recorded few natural deaths of adult bulls. In our model, we need assume only that there are sufficient males in the population to permit the females to produce young whenever they are able to do so.

We explored the growth rates under the combinations of maximum and minimum values of the three reproductive parameters we have discussed so far. Our objective was to find the parameter changes which were most likely to effect changes in KNP's elephant numbers.

With our model, elephants can increase when mortality is as high as 5% per year and when the age at first calving is as late as 20 years. In contrast, when the inter-calving interval is as long as nine years, the population can only grow slowly under the best circumstances of low mortality and young age of first breeding. Given the natural range of parameters, the inter-calving interval should play the major role in driving the population changes – a conclusion of Dobson (1993) and Hanks & McIntosh (1973).

If KNP is now different for elephants than in the past, then changes in calving interval are the prime suspect. Notice, first, that long calving intervals are demographically equivalent to short calving intervals combined with high pre-breeding mortality. The interval between a female producing a youngster of breeding age is long in both circumstances. Juvenile (i.e. pre-breeding) mortality might have been consistently higher in the past.

Hunting by Stone- or Iron-age cultures might have elevated juvenile mortality. So, too, might the long distances between water sources – for young elephants are prone to die during droughts (Dunham, 1988). KNP's extensive network of engineered water holes may have tweaked the parameter – pre-breeding mortality – that can effect the greatest change in the growth rate of a population. The drought in the early 1980s had little effect on the growth rate of KNP's elephants, though, interestingly, they did unusual amounts of damage to trees in that period (Walker *et al.*, 1987).

The demographic model suggests that juvenile mortality caused by droughts could be episodic and still slow growth rates to near zero. One episode in every 11 years would be enough to severely impact all the pre-breeding age classes.

The parameters for KNP's elephants of age at first calving, inter-calving interval, and annual survival are close to or exceed the maximum observed elsewhere. Calef (1988) suggests 8% as the theoretical maximum growth rate for elephants. We agree with Dobson (pers. comm.) that this seems to be far too high. We employ age-structured models similar to those of Dobson (1993). The models suggest that KNP's particular problem is to regulate elephants at a density at which resource limitation is minimal. The management problem is thus maximally difficult. Do contraceptives provide a practical solution?

CONSEQUENCES OF CONTRACEPTION FOR THE INDIVIDUAL

Contraceptive use aims to control the elephant population without the killing of animals that so many find objectionable. It also holds the promise of being reversible. Were some natural event to greatly reduce the population, the contraceptive programme could be stopped and the population could recover quickly. In spite of limited information, we may predict some of the physiological and behavioural consequences of the substances presently on trial as contraceptives. These consequences will probably thwart the promise of contraception as both humane and reversible.

Studies on endocrine correlates of elephant reproduction show that blood levels of both estrogens and progestins are extremely low in the African elephant (Plotka *et al.*, 1975; De Villiers, Skinner & Hall-Martin, 1989). In contrast to most other mammals, relatively high concentrations of the 5-reduced metabolites of progesterone rather than progesterone appear to maintain pregnancy in the elephant (Hodges, van Aarde *et al.*, 1994; Hodges, Heistermann *et al.*, 1997; Greyling, van Aarde *et al.*, 1997). As yet, we cannot discount the role of progesterone in the maintenance of pregnancy. Elephants may be extremely sensitive to this steroid, resulting in extremely low concentrations being sufficient to support pregnancy. This may also be true for the interactions between estrogens and ovarian function. Such a possibility requires further investigation, preferably on captive animals.

Circulating concentrations of oestradiol-17 are extremely low (Plotka *et al.*, 1975; McNeilly *et al.*, 1983) and endometrial receptor affinity is highly specific (Greyling, van Aarde *et al.*, 1997; Greyling, Ford *et al.*, in press). Estrogens in the elephant, as in other mammals, probably originate from developing ovarian follicles. Ovulation and incidences of estrus may be associated with a surge in their plasma concentrations but circulating levels are extremely low (see Hess, Schmidt & Schmidt, 1983).

The slow-releasing capsules recently implanted in ten lactating elephants in KNP resulted in continued high concentrations of oestradiol-17. The consequences may be an impairment of lactation and a consequent reduction in calf survival. Moreover, the treated cows remained in a continuous state of sexual heat. They appear to have been evicted from their breeding groups and were often harassed by bulls (Whyte & Grobler, 1997).

Considering the influence of sexually associated aggression in bulls on calves, the high incidence of cows in heat, may also have major consequences for the unexpected tourist. One should consider that at any given time at least some 2000 cows will be experiencing this condition (see below). In addition, we cannot discount the potential for continued high levels of estrogens to induce the carcinomic growths that have developed in other species (Li, Li *et al.*, 1983; Li, Oberley *et al.*, 1988).

Information from the group of scientists recently involved in immunizing 21 elephant cows with porcine zona pellucida antibody (pZP) suggests that animals will have to be given a booster at yearly intervals to ensure effectiveness of this antibody as a contraceptive (H. J. Bertschinger, pers. comm.). Apparently, immunocontraception is effective in several free-ranging mammal species. The method's protagonists (see Bertschinger *et al.*, 1996) claim minimal effects and even reversibility (Kirkpatrick, Liu *et al.*, 1992; Turner, Liu & Kirkpatrick, 1992; Kirkpatrick, Turner & Liu, 1996). Others claim evidence to the contrary (see Mahi-Brown *et al.* 1989; Paterson, Koothan *et al.*, 1992; Paterson, Wilson *et al.*, 1996). Active immunization with the zona glycoprotein induces infertility. It also causes ovarian dysfunction and ovarian pathology characterized by a lack of folliculogenesis and depletion of the primordial follicle population (Paterson, Wilson *et al.*, 1996). If this proves to be the case for elephants, such sterilized individuals would be removed permanently from the gene pool – an effect similar to that achieved through culling.

In summary, all of the methods currently under test have known or predicted serious consequences to the health of the cows, their behaviour, and those animals around them. This is not the only problem with contraceptives.

CONTRACEPTIVE OPTIONS FOR THE ELEPHANTS OF KRUGER NATIONAL PARK

Contraceptives alter the inter-calving interval and so offer a potentially effective way of controlling population numbers. Using the demographic model introduced above, we can perform a straightforward calculation of how many of KNP's roughly 3000 reproductively active female elephants would need to be administered contraceptives to ensure zero population growth. The bad news is that the answer is about 75% – reducing the average calving interval to about 12 years.

The worse news is that zero population growth rate only kicks in after 11 years. In that 11-year interval, females born before the use of the contraceptives are steadily recruited into the breeding population. Indeed, 11-year-olds are the largest breeding class, since there cannot be more 12-year-olds than 11-year-olds, 13-year-olds than 12-year-olds, and so on. Consequently, the breeding population increases at about 4% per year to over 5000 adult females before zero population growth is attained. Thus, the final effort requires ~4000 animals to have contraceptives – not the initial number of 2250 (= 75% of 3000).

The parameter for which we have the least confidence is the annual survival. It is a back calculation that assumes a particular growth model and further assumes how the population would have grown without the cull. If we increase the annual mortality from the 1·5% employed in the previous paragraph to 2·5%, then the required fraction of females treated with contraceptives declines only from 75% to 61%. Simply, it is the very short inter-calving interval of KNP's elephants that makes the problem a difficult one.

Our model also confirms Dobson's result that using contraceptives to delay the age at first calving is an even less effective strategy than changing the inter-calving interval.

OTHER MANAGEMENT OPTIONS

The model permits a numerically simple solution to the park's problems. Rather than kill from hundreds to thousands of elephants each year, or put contraceptives in several thousand females, the killing of a much smaller number of female elephants just prior their first pregnancy would achieve the same aim. Killing a mere 300 of such carefully selected animals each year would drive the population to extinction, for no breeding females would enter the population. Killing 250 would stabilize the population.

The word 'sterilize' can be substituted for 'kill' in the previous paragraph and its conclusions be unchanged. Contraception and sterilization are not usually considered to be synonyms. Indeed, the efforts discussed above aim to find reversible contraceptives and to avoid sterilization as the unintended consequence of our ignorance of how the contraceptives function. If sterilization, and not contraception, is the *intended* objective, then it should be stated as such. The ethical issues this raises should be brought into the open and the research programme focused on deliberate sterilization.

CONCLUSIONS

KNP has four management options. It has chosen the option of killing from hundreds to thousands of elephants each year for decades to protect its woodland ecosystems. The other three options are to let elephants increase and lose its woodland, kill or sterilize 250 prebreeding females, or administer contraceptives to 75% of all the breeding females.

There is nothing sacrosanct about keeping the elephant population at its current level, of course. One might choose any mix of the four options, including higher elephant numbers, likely higher inter-calving intervals and so a proportionately smaller number of animals killed, contracepted or sterilized, and more damage to the woodlands. The optimal balance between elephant numbers and woodland is not easy to determine without long-term, large-scale experiments. Moreover, with larger numbers of elephants, the absolute numbers to be killed, contracepted or sterilized will also be larger.

There is still a debate about whether or not woodland – and the low elephant numbers that permit its existence – was naturally the permanent or even an episodic state of this region. What is certainly not natural is the small fraction of protected land in Africa (and elsewhere), the consequent rates of global extinction, and the loss of ecological processes across the landscape. Protecting woodland may be essential to preserve for the future a representative sample of species and processes, whatever the past may have been.

If there were few elephants in the past, then the first question is why? The second is how do we keep elephant numbers low? The numerical targets required for zero growth range from selectively killing or sterilizing a few hundred 11-year-old females to indiscriminately killing many hundreds of animals, to using contraceptives on several thousand adult females. There will also be some individuals who find killing any elephants an anathema. Unfortunately, the use of contraceptives on this scale is completely impractical and they are likely to have severe behavioural and physiological side-effects. Should one unnaturally shoot or sterilize female elephants prior to calving for the first time or let them die naturally of thirst in dry years? This is an ethical issue we are not equipped to judge. Nature is not likely to be so squeamish.

Identifying the smallest numerical target for controlling elephant numbers is not just a practical convenience. It is the most likely target for how the vagaries of nature limit elephant numbers. The high mortality of juvenile elephants may explain why some populations have remained at numbers that do not lead to their destroying woodlands. In this sense, the smallest target for control is also likely to be the most natural one. Whatever the ethical issues of sterilizing female elephants, it does provide the smallest numerical target and it avoids killing animals.

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