# The Exploitation of Elephants for the Ivory Trade: An Historical Perspective

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## SUMMARY

Two major factors are likely to have caused recent elephant population declines: carrying capacity reductions and hunting for ivory. A model is developed to disentangle the effects of these two factors on elephant population dynamics since 1814. The model suggests that carrying capacity reductions were a major cause of elephant population declines in the 19th Century and first half of the 20th Century, but that, since 1950, hunting for ivory has been the cause of an increasingly rapid population decline. These results are extremely robust to changes in parameter values within a reasonable range.

## 1. INTRODUCTION

Over the last 200 years, the ecology of Africa has changed substantially. One of the best-documented changes has been the decline of the continental population of the African elephant (*Loxodonta africana*) (Burrill & Douglas-Hamilton 1987; Douglas-Hamilton 1988). Two major factors are likely to have contributed to this decline: reductions in the carrying capacity of Africa for elephants, resulting from habitat change, and hunting for ivory. The relative importance of hunting and habitat loss in driving population decline has been at issue for several years (Parker 1979; Douglas-Hamilton 1979), although there is evidence that the population decline since 1979 can be explained solely by hunting for the ivory trade (Milner-Gulland & Mace 1991). In this study, we attempt to tease out the effects of the two factors on the elephant population over the last two centuries, and discuss the likely effects of each in the future.

Although ivory exports from Africa are well documented from 1979 onwards, only one study has attempted to put the ivory trade into an historical context (Parker 1979). That study brought together many of the available data on the volume of ivory leaving Africa, from the 16th Century onwards. However, the data were not used to relate the documented ivory trade to changes in the elephant population size. In this paper, the data compiled by Parker (1979) and others are used to give an estimate of the volume of trade leaving Africa from 1814 to 1987. This estimate is used in a model of elephant population dynamics, from which the relative effects of carrying capacity changes and the ivory trade on population decline can be deduced.

## 2. A MODEL OF ELEPHANT NUMBERS

A nonlinear Leslie matrix is needed to describe fully elephant population dynamics under harvesting, be-

cause it is a long-lived species and hunter selectivity for large tusks has a profound effect on population structure (Milner-Gulland & mace 1991; Wu & Botkin 1980). However, the formulation used in this paper is extremely flexible, allowing many combinations of maximum and minimum parameter values. This approach is thus a robust simplification of more complex nonlinear Leslie matrix formulations. The population size each year is calculated as:

$$N_{t+1} = N_t(e^{-m_t} + R_t) - (1+i) H_{t+1}, \qquad (1)$$

where $N_t$ = population size, after harvest, at time $t$; $m_t$ = adult natural mortality rate at time $t$; $R_t$ = recruitment rate at time $t$; $i$ = incidental hunting morality; and $H_t$ = number of elephants killed at time $t$.

The recruitment rate represents the ratio of young:adult individuals in the population, and is therefore easily measured in the field. The adult natural mortality rate has also been extensively measured, although less easily. The incidental mortality represents the calves that die when their mothers are killed, which are not recorded in the trade statistics because their tusks are too small or they die undetected later. About one calf dies for each adult female killed (Poole 1989), so the incidental mortality rate is approximately equal to the proportion of adult females in the population.

## 3. ASSUMPTIONS AND PARAMETER VALUES

### (a) Density dependence

Two parameters are varied with population size to simulate density dependence: adult natural mortality (equation 2a) and recruitment (equation 2b). The density dependent response is (Lankester & Beddington 1986):

$$P = P_{max} - (P_{max} - P_{min}) [1 - (N_{t-L}/K)^\beta], \qquad (2a)$$

$$P = P_{min} + (P_{max} - P_{min}) [1 - (N_{t-L}/K)^\beta], \qquad (2b)$$

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Table 1. *Maximum elephant carrying capacity (K) in 1814*

(This uses vegetation categories and areas from White (1983) and rough estimates of densities. The forest density is based on Barnes (1989), the Highveld and Sahel densities on contemporary accounts of elephant abundance and data in Burrill & Douglas-Hamilton (1987), and the others on data in Burrill & Douglas-Hamilton (1987). The Karoo–Namib desert zone and the Sahara and Mediterranean zones are non-range.)

| zone (type) | area/km² | density/km⁻² | K |
|---|---|---|---|
| Guineo-Congolian (forest) | 2 800 000 | 0.5 | 1 400 000 |
| Guineo-Congolian/ Zambezian | 705 000 | 2 | 1 410 000 |
| Zambezian (woodland) | 3 770 000 | 2 | 7 540 000 |
| Guineo-Congolian/ Sudanian | 1 165 000 | 2 | 2 330 000 |
| Sudanian (woodland/grass) | 3 731 000 | 2 | 7 462 000 |
| Somalia-Masai (bush/grass) | 1 873 000 | 2 | 3 746 000 |
| Cape (bush) | 71 000 | 2 | 142 000 |
| Afromontane (mountain) | 715 000 | 2 | 1 430 000 |
| Lake Victorian (forest) | 224 000 | 2 | 448 000 |
| Zanzibar-Inhambane (coastal) | 336 000 | 2 | 672 000 |
| Tongaland-Pondoland (bush) | 148 000 | 2 | 296 000 |
| Kalahari-Highveld (grass) | 1 223 000 | 0.01 | 12 230 |
| Sahel (grass) | 2 482 000 | 0.01 | 24 820 |
| total | 19 243 000 | — | 26 913 000 |

where $P_{max}$ = maximum value for recruitment or mortality; $P_{min}$ = minimum value for recruitment or mortality; $N_t$ = population size at time $t$; $L$ = time lag in response; $K$ = carrying capacity; and $\beta$ = exponential response parameter.

The form of the density-dependent response in elephants is not established. Poole (1989) presents evidence for a negative effect at low population sizes which is too anecdotal for inclusion in the model. The recruitment rate is an amalgamation of several fecundity-based factors, including age at sexual maturity, interbirth interval and juvenile survival (Fowler 1981). The elephant's long interbirth interval could lead to a time lag, but juvenile mortality is likely to be one of the first parameters to increase with increased density. Recruitment rate as a whole is known to respond rapidly to changes in vegetation availability, so was assumed not to be lagged (Laws 1969). Adult mortality is likely to have a lagged response to increased density, which is included in the model (Laws 1969; Corfield 1973; Owen-Smith 1988).

The exponential response parameter $\beta$ determines the degree of nonlinearity in the density dependence. If $\beta = 1$, the density dependent response is linearly related to population size, but if $\beta = 0$ there is no density dependence. If $\beta < 1$, density dependence is strongest at low population sizes; if $\beta > 1$ it is strongest near carrying capacity; $\beta$ was varied between 0 and 2 in the model. However, long-lived species tend to

exhibit density dependence most strongly near carrying capacity, so a $\beta$ near zero is less likely than a $\beta$ above 1 (Fowler 1984).

(b) *Carrying capacity*

The area and vegetation of elephant range changed significantly over the period studied, so separate values for carrying capacity in 1814 and 1987 were calculated (Parker 1979; Douglas-Hamilton 1979; Burrill & Douglas-Hamilton 1987). Ecological carrying capacity is the number of elephants that a particular habitat can support indefinitely without degradation. This is an adequate definition on the local scale but not the continental scale, particularly for a species that has disappeared from vegetationally suitable areas as a result of human interference. Climate change can be ignored for the 174 years modelled, but logging, for example, has created large areas of secondary forest, increasing the carrying capacity of the area for elephants (Barnes 1989).

The carrying capacity in 1814 was estimated by using White's (1983) classification of African vegetation types. These were divided into range and non-range, according to contemporary reports of elephants living in the vegetation type (Bryden 1903) and estimates of current elephant densities in the vegetation type (Burrill & Douglas-Hamilton 1987), from which densities at carrying capacity were inferred. The estimate of pristine carrying capacity in 1814 is 27 million elephants (table 1). The 1979 and 1987 carrying capacities were found by using the range areas in Burrill & Douglas-Hamilton (1987) and Douglas-Hamilton (1988). Areas not containing elephants in 1979 and 1987 were thus assumed to be non-range, regardless of vegetational type. The estimate of carrying capacity in 1979 is 11 million elephants and, in 1987, 9 million elephants (table 2). These estimates are crude and subject to unquantifiable error, particularly that for 1814.

An expression for the rate of carrying capacity change over time is needed. Two major factors could have caused a reduction in range: increases in human population size and expansion of agriculture. Contemporary observers state that elephants were driven back by European civilization (Bryden 1903; Bourgoin 1956). The colonial period involved massive agricultural expansion and intensification throughout Africa, so that by 1900 much of the suitable land was cultivated, implying a rapid early carrying capacity decline (Oliver & Atmore 1967). The human population was stable throughout the colonial period because of the slave trade, and only increased rapidly in the 1960s, although much of this increase was in the urban population (Oliver & Crowder 1981).

Carrying capacity can decline either because total range area declines or because of changes in the proportions of different vegetation types. Savannah range, the most suitable for agriculture, declined particularly sharply, so that the proportion of forest increased from 10 % to 25 % of the total range. Forest supports a density of 0.5 elephants km⁻² as opposed to 2 elephants km⁻² in savannah.

Table 2. *Elephant range in 1987*

(This uses Douglas-Hamilton's (1988) vegetation categories and areas, which are based on White's (1983). The estimated average density in each category is given; the variation is due to variations in sampling method as well as genuine change (Douglas-Hamilton 1988). Note the change in range area for different vegetation types compared with 1814.)

| zone | area/km$^2$ | density/km$^{-2}$ | | maximum | $K$ |
| | | 1979 | 1987 | | |
| --- | --- | --- | --- | --- | --- |
| forest | 1 116 000 | 0.30 | 0.33 | 0.5 | 583 000 |
| swamp forest | 334 000 | 0.50 | 0.35 | 0.5 | 167 000 |
| secondary woodland | 71 000 | 0.01 | 0.03 | 1 | 71 000 |
| forest/grassland | 681 000 | 0.21 | 0.08 | 2 | 1 362 000 |
| Miombo woodland | 1 450 000 | 0.28 | 0.17 | 2 | 2 900 000 |
| Sudanian woodland | 479 000 | 0.12 | 0.08 | 2 | 958 000 |
| woodland mosaic | 529 000 | 0.32 | 0.15 | 2 | 1 058 000 |
| coastal mosaic | 154 000 | 0.11 | 0.11 | 2 | 308 000 |
| montane | 95 000 | 0.17 | 0.09 | 2 | 190 000 |
| bushland thicketed | 537 000 | 0.09 | 0.09 | 2 | 1 074 000 |
| grassland | 125 000 | 0.04 | 0.05 | 1 | 125 000 |
| azonal | 125 000 | 0.14 | 0.13 | 1.5 | 187 500 |
| semi-desert | 142 000 | 0.00 | 0.02 | 0.01 | 1 420 |
| desert | 16 000 | 0.01 | 0.01 | 0.01 | 160 |
| total | 5 904 000 | — | — | — | 8 985 000 |

## 4. THE SEPARATE EFFECTS OF HUNTING AND CARRYING CAPACITY

The model was first run using two extreme assumptions: either there was no hunting and changes in carrying capacity alone affected population dynamics, or carrying capacity was constant over the period, and only hunting affected the population. This allows the separate effects of each factor on elephant population dynamics to be assessed. A range of values was used for maximum and minimum recruitment rate and natural mortality, set to reflect the likely range of these parameters found in different habitats and under different population structures (table 3). Values for maximum and minimum recruitment and mortality

Table 3. *Values for recruitment rate and adult natural mortality used in the population model*

($P_{max}$ and $P_{min}$ are as defined in equation (2). The sources of the parameter values are also shown.)

| parameter | recruitment | | mortality | |
| | max | min | max | min |
| --- | --- | --- | --- | --- |
| $P_{max}$ | 0.11 | 0.06 | 0.10 | 0.04 |
| $P_{min}$ | 0.06 | 0.02 | 0.04 | 0.01 |

| source | recruitment | mortality |
| --- | --- | --- |
| Douglas-Hamilton | — | 0.02–0.04 |
| Hanks (1972) | 0.06 | — |
| Jachmann (1986) | 0.09 | 0.08 |
| Laws (1969) | — | 0.02–0.1 |
| Laws *et al.* (1975) | — | 0.02–0.08 |
| Leuthold (1976) | 0.05–0.11 | — |
| Ottichilo (1986) | 0.06 | — |
| Owen-Smith (1988) | 0.02–0.1 | — |
| Sherry (1975) | 0.07 | — |
| Smuts (1976) | 0.07 | — |
| Williamson (1976) | 0.09 | — |

rates and $\beta$ were varied systematically between runs, so that the full range of parameter values was covered. This gave density-dependent values for mortality rate and recruitment (equation (2)), allowing the calculation of a population trajectory (equation (1)). Only trajectories leading to 1987 population sizes within ±33% of the estimated value of 720 000 elephants (Douglas-Hamilton 1989) were accepted. Although the parameter set producing a 1987 population size within these limits could be found analytically, this would be difficult given that five parameters are varied, and so numerical methods were used to find the relevant parameter set.

The parameter set producing a population size within the 1987 window obviously cannot be illustrated in five dimensions, but the intrinsic population growth rate, and the population growth rate at carrying capacity, corresponding to each set of parameter values are shown in figure 1. These are calculated by setting $N_{t-L}/K$ in equation (2) to zero or one, respectively. The intrinsic rate of population growth, $r$, is thought to be around 0.07 in elephants (Calef 1988), and the rate of population growth at carrying capacity should be zero. The results are similar for all the carrying capacity scenarios, with reasonable values for $r$, although the rate of increase at carrying capacity is negative, only taking positive values if a constant carrying capacity at the 1987 level is assumed. This suggests that the pristine carrying capacity may have been overestimated, but the values are not large enough to cause concern.

When investigating the effects of carrying capacity alone, three different carrying capacity trajectories were used: a linear decline from 1814 to 1987 ('linear'); carrying capacity constant for the first half of the period, then declining linearly to the 1987 level ('slow–fast'); and a linear decline to the 1987 level in the first half of the period, then constant in the second half ('fast–slow'). These three scenarios represent the
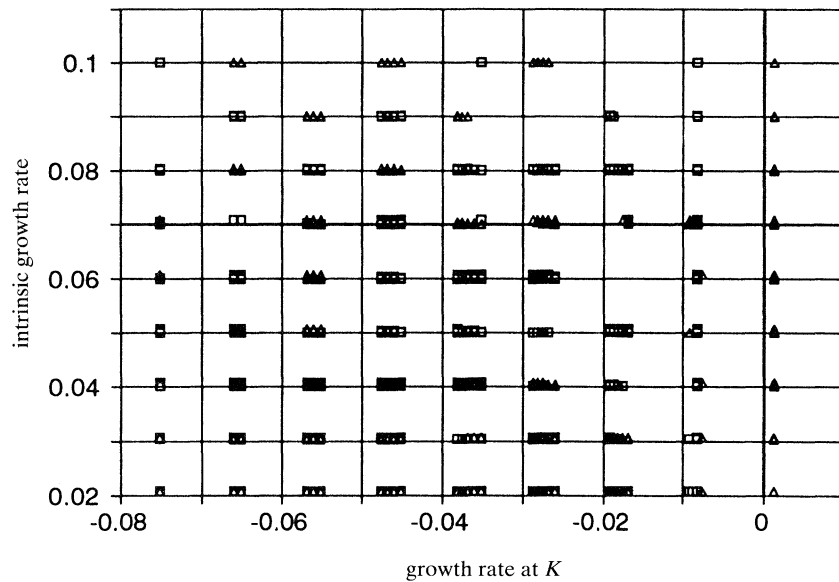
Figure 1. The distribution of the population growth rate at carrying capacity and intrinsic growth rate implied by the demographic parameters of those trajectories passing through the 1987 population window. The expected value of the growth rate at carrying capacity is zero, and of the intrinsic growth rate is 0.07. Results are shown for the fast–slow scenario (squares) starting from 75 % of carrying capacity, and for the scenario when carrying capacity remains constant throughout at the 1987 level (triangles).
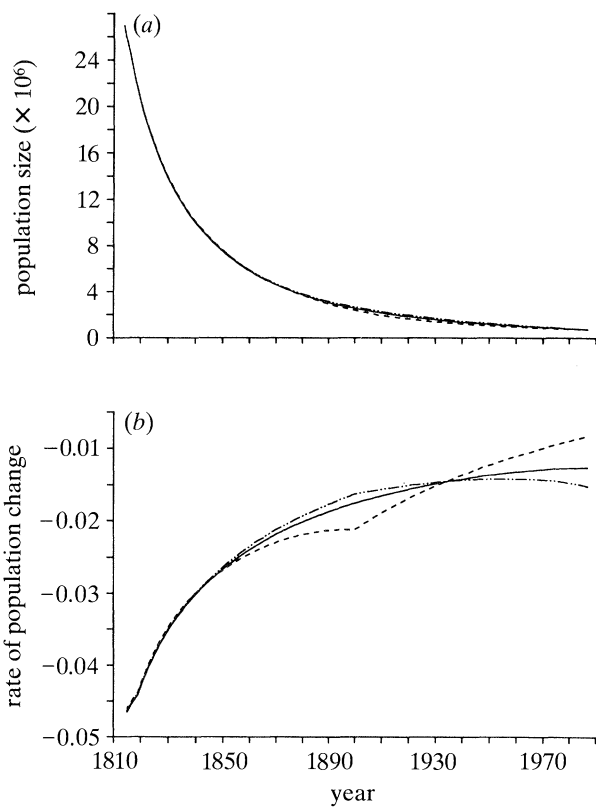


Figure 2. The mean population size and mean rate of population change over the study period, 1814–1987, when carrying capacity changes alone are assumed responsible for population decline. The population is assumed to be at pristine carrying capacity in 1814. The results for three possible carrying capacity trajectories are shown: fast–slow (broken line), slow–fast (dot-dot-dash line) and linear (solid line) (*a*) Population size. (*b*) Rate of population change.
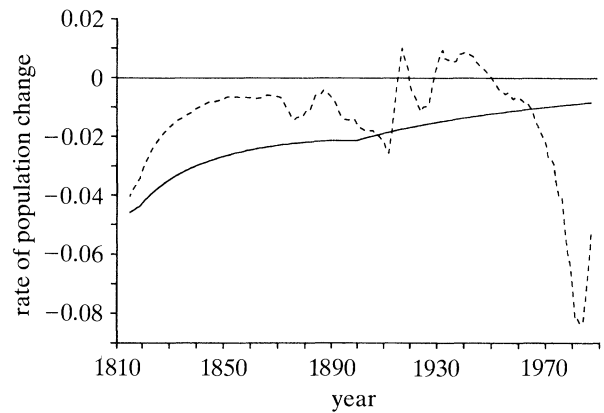


Figure 3. The mean rate of population change over time when hunting alone is assumed responsible for population decline (broken line) compared with the results when carrying capacity *K* alone is assumed responsible (solid line). The fast–slow carrying capacity trajectory is used, and both populations start from carrying capacity. If hunting alone is assumed responsible for population decline, decline is slower than that with carrying capacity changes alone until the 1970s, when decline becomes very rapid.

most likely range of carrying capacity trajectories. The rate of population change varies only slightly with the carrying capacity scenario assumed (figure 2). When

investigating the effects of hunting alone, the carrying capacity was assumed to remain constant at the 1987 level throughout the period, because the evidence is stronger for the 1987 carrying capacity estimate than for the pristine estimate. Hunting alone produces a very different rate of population change to carrying capacity change alone. The rate of population decline is lower for the first 150 years of the simulation, then increases rapidly in the final few years (figure 3).

To include the effects of hunting in the model, the number of elephants killed for trade each year is needed. This is obtained from an estimate of the volume of trade, together with the mean tusk mass in the trade at a particular time, assuming that each elephant killed contributes 1.88 tusks (Parker 1979).

The data used to obtain the estimate of the volume of trade are discussed in Appendix 1.

## 5. THE MEAN TUSK MASS IN THE TRADE

The mean tusk mass determines the number of elephants killed to produce a given volume of ivory. It is influenced by the structure of the hunted population and hunter selectivity for certain tusk sizes. When a nonlinear Leslie matrix is used to represent elephant population dynamics, the mean tusk mass declines rapidly when hunting begins, reaching a stable value which depends on the hunting mortality and hunter selectivity (Milner-Gulland & Mace 1991). A simple representation of this effect, in which the mean tusk mass declines exponentially with time, is (Basson *et al.* 1991):

$$\bar{w} = A + \alpha(N_t)^z, \tag{3}$$

where $A$ = mean tusk mass at end of period; $\alpha$ = scaling constant for mean tusk mass at beginning of period; and $z$ = exponential rate of decline of mean tusk mass.

In this case, $A$ and $\alpha$ are scaled so that the mean tusk mass in the trade at the beginning of the period is 15 kg, and that at the end is 5 kg. The former is reasonable given the data presented in Parker (1979), and the latter is the mean tusk mass observed over the last decade (Milner-Gulland & Mace 1991; data from WTMU). If $z = 0$, the mean tusk mass remains constant at the 1987 level throughout the period, whereas at $z = 1$ there is a linear decline in mean tusk mass over time. As $z$ increases above 1, the exponential rate of decline in mean tusk mass with time increases. Basson *et al.* (1991) put $z$ at 1.7, and in this study it is set at 2. Trade records of mean tusk mass are very variable, although the assumption of an overall decline in mean tusk mass over the whole period seems to be supported (Parker 1979).

## 6. THE EFFECTS OF BOTH HUNTING AND CARRYING CAPACITY

The constraints built into the model determine the basic shape of population trajectories; carrying capacity drops dramatically over the period, and the two population sizes fixed at either end are also very different. The population in 1814 is assumed to vary between 50% and 100% of pristine carrying capacity, but the 1987 population is only 8% of 1987 carrying capacity. However, the assumptions made about hunting mortality and trade levels are likely to interact to determine the shape of the population trajectory. In particular, a number of those individuals killed for trade would have died anyway, so hunting affects the strength with which density dependence acts.

The results of the model are shown in table 4 for starting population sizes varying between 50% and 100% of carrying capacity, and for the three carrying capacity scenarios. The most likely scenario will have the largest number of trajectories through the 1987 population window, the highest mean and maximum

value for $\beta$, as Fowler (1984) shows that $\beta > 1$ is likely for the elephant, and the lowest minimum 1979 population size. The published estimate for the 1979 population size is 1 340 000 (Burrill & Douglas-Hamilton 1987), but the authors say that their figure is likely to be an overestimate. The total number of trajectories passing through the window is shown rather than a mean with confidence limits because the distribution of 1987 populations is non-normal.

The fast–slow scenario is the most likely under the above criteria (table 4). The population size in 1814 makes little difference to the output, only affecting the population trajectory for about 60 years (figure 4*a*). A 0.75*K* population size in 1814 seems the most realistic of the three modelled, given that light exploitation had occurred before 1814. The rate of population change is similar for the three carrying capacity scenarios (figure 4*b*). Taking the fast–slow carrying capacity trajectory and a population size of 0.75*K* in 1814 as fitting the data best, 75 % of the population is lost in the first 100 years, then the rate of decline slows around 1914, increasing again from around 1950 (figure 5*a*). This represents a steady decline of 2–3 % a year until 1914, with some recovery in the war years, and a very rapid increase in the rate of population decline from around
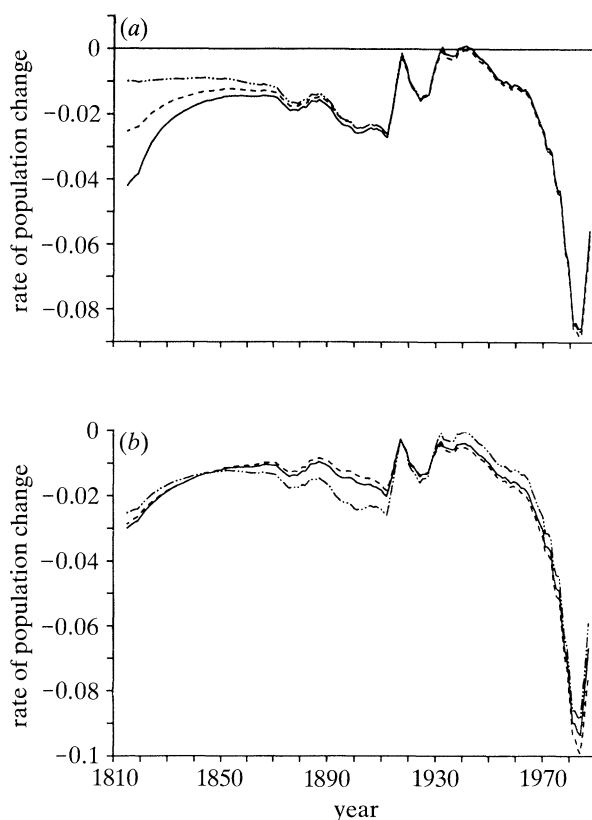




Figure 4. (*a*) The effect of the starting population size assumed as a proportion of pristine carrying capacity on the mean rate of population decline. A fast–slow scenario is assumed. The starting population size makes little difference after the first 60 years. *K* (solid line), 0.75*K* (broken line), 0.5*K* (dot-dot-dash line). (*b*) The mean rate of population decline under three carrying capacity scenarios, starting from 75 % of carrying capacity. Differences between the results for the three scenarios are slight. Linear (solid line), slow–fast (broken line), fast–slow (dot-dot-dash line).

Table 4. *Results of the simulation runs, showing the number of trajectories fulfilling the constraints for various population sizes in 1814 and carrying capacity trajectories*

(The average and maximum values of $\beta$ and the range of the 1979 population size (in millions) in the trajectories fulfilling the constraints are also shown. The total number of trajectories investigated was 17640.)

| 1814 population | mean $\beta$ | mean $\beta$ | trajec-tories | 1979 population | |
|---|---|---|---|---|---|
| | | | | max | min |
| fast–slow trajectory | | | | | |
| K | 0.64 | 1.7 | 333 | 1.66 | 1.12 |
| 0.75K | 0.59 | 1.7 | 369 | 1.83 | 1.12 |
| 0.5K | 0.61 | 1.7 | 375 | 1.76 | 1.12 |
| linear trajectory | | | | | |
| K | 0.48 | 1.2 | 229 | 1.75 | 1.19 |
| 0.75K | 0.45 | 1.2 | 257 | 1.74 | 1.21 |
| 0.5K | 0.50 | 1.2 | 236 | 1.76 | 1.19 |
| slow–fast trajectory | | | | | |
| K | 0.37 | 1.0 | 183 | 1.81 | 1.22 |
| 0.75K | 0.33 | 1.0 | 211 | 1.78 | 1.21 |
| 0.5K | 0.40 | 1.0 | 150 | 1.76 | 1.22 |



Figure 6. A comparison of the mean rate of population change when hunting alone (broken line), carrying capacity alone (dot-dash line) and both factors (solid line) are assumed responsible for population decline. All trajectories start from 75% of carrying capacity, and the scenario assumed is fast–slow. Until around 1970, the trajectory where both factors are involved is between the trajectories of the two extreme assumptions, suggesting that both factors play a part, but after that hunting becomes the major factor involved in population decline.

1970 (figure 5b). The similarity of the maximum and minimum population trajectories shows that results are very similar over the wide range of recruitment rates, mortality rates and density-dependent responses tested in the model. Carrying capacity changes and hunting mortality both affect the rate of population decline in the first 150 years, but hunting clearly causes the sudden rapid decline in population size from around 1970 (figure 6).

### (a) Sensitivity analyses

The population parameters used are: $z$, which describes the rate of mean tusk mass decline over time (equation (3)); the incidental calf mortality; and the lag in the density-dependent response of adult mortality. The effects of changes in these parameters, within reasonable bounds, are not significant (table 5).

Although it is likely that the carrying capacity in 1814 was much higher than in 1987, the 1814 carrying capacity calculated in table 2 could well be an overestimate. The model is not sensitive to relatively small changes in the pristine carrying capacity, and running the model with carrying capacity held constant at the 1987 level sets a lower limit on possible population trajectories. The rate of population change over time is similar whether this extreme assumption or a fast–slow scenario is used, suggesting that it is determined by the ivory trade rather than the carrying capacity trajectory. Fewer trajectories fulfilled the assumptions under the 1987 carrying capacity assumption than when pristine carrying capacity in 1814 is assumed, but the fact that $\beta$ is higher suggests that a lower carrying capacity than that calculated for 1814 might be closer to reality.

Parker (1979) made an informed guess at the maximum likely trade levels before 1914, which are much higher than the documented evidence suggests,
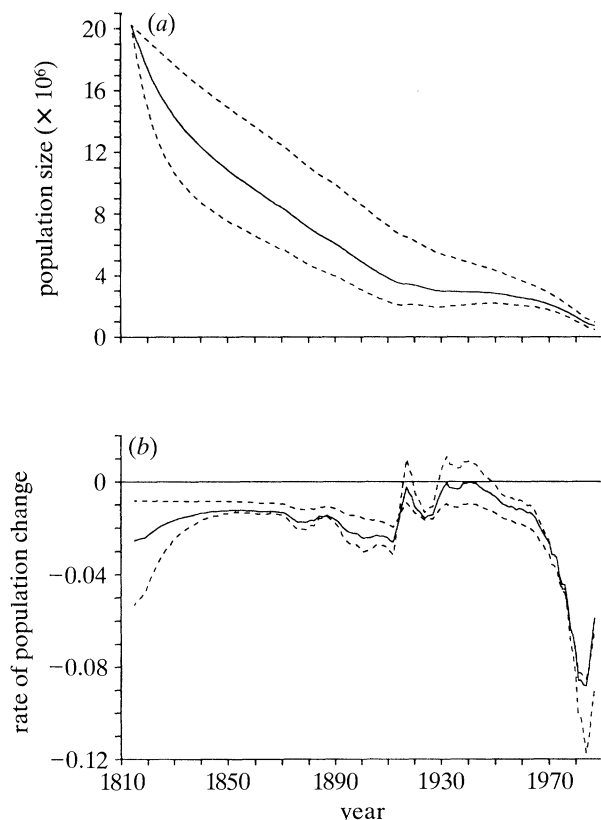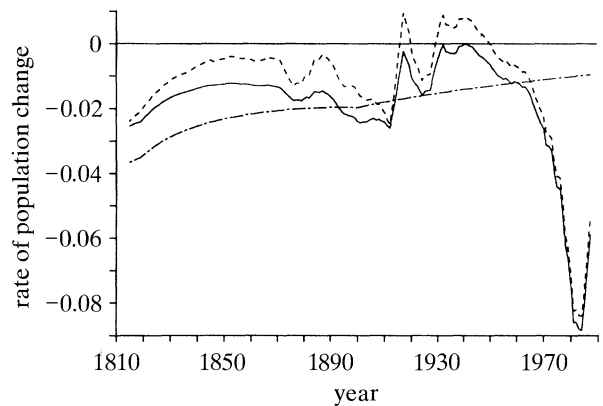




Figure 5. (a) The population trajectory for the fast–slow scenario starting from 75% of carrying capacity. The mean of the trajectories passing through the 1987 window is shown, together with the maximum and minimum values of population size for those trajectories passing through the window (broken lines). (b) The rate of population change represented by (a), with the maximum and minimum trajectories again shown as broken lines.

Table 5. *Results of the sensitivity analyses on the proportion of females in the population, the trade data used in the model, the natural mortality time lag, and the mean tusk mass skew factor*

(The rates of changes of the population under each assumption are not shown, because they are virtually indistinguishable.)

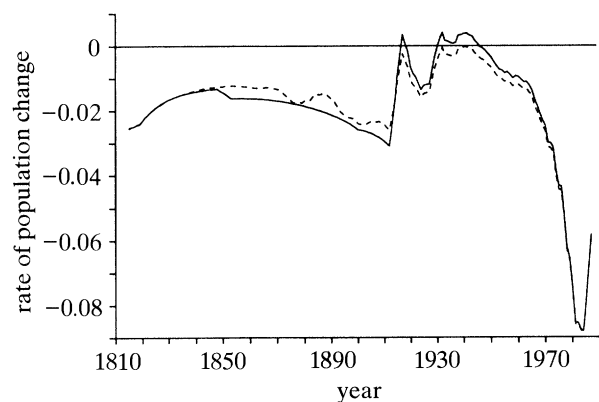| 1814 population | mean $\beta$ | max $\beta$ | trajec-tories | 1979 population | |
| --- | --- | --- | --- | --- | --- |
| | | | | max | min |
| standard | 0.64 | 1.7 | 333 | 1.66 | 1.12 |
| 25% females | 0.56 | 1.6 | 298 | 1.78 | 1.08 |
| 40% females | 0.61 | 1.8 | 377 | 1.86 | 1.17 |
| Parker's guess | 0.64 | 1.8 | 258 | 1.77 | 1.11 |
| no lag | 0.56 | 1.6 | 302 | 1.82 | 1.09 |
| no skew | 0.59 | 1.7 | 407 | 1.81 | 1.11 |
| high skew | 0.60 | 1.7 | 405 | 1.79 | 1.11 |



Figure 7. The effect of using Parker's guess at pre-1914 trade on the mean rate of population change under a fast–slow scenario starting from 75% of carrying capacity. There is little difference between the results using the best estimate of pre-1914 trade (broken line) and those using Parker's much higher trade estimates (solid line).

by using subjective contemporary accounts of the volume of ivory leaving ports (see Appendix 1). By running the model using Parker's guess, the likely range of trade levels before 1914 is covered. Changing the incidental mortality rate and the mean tusk mass assumption also indirectly changes the number of elephants assumed to have been killed for the trade. Previous sensitivity analyses have shown that changes in these parameters have little effect on the results (table 5). However, this systematic increase in numbers killed throughout the simulation is different to Parker's informed guess at the likely maximum trade level in each period. The results using Parker's guess are little different to the previous results, just rather smoother (figure 7, table 5). This is mainly due to the pre-1914 trade not removing a large proportion of the elephant population, even at the high levels guessed at by Parker, and to the action of density dependence. Thus the model is insensitive to the possible underestimation of pre-1914 trade levels.

## 7. DISCUSSION

The model used for this study of the ivory trade since 1814 is simple yet extremely robust. The results strongly suggest that carrying capacity declined rapidly at first, and then more slowly. This is consistent with historical patterns of agricultural expansion. The trade data have given an estimate of the volume of ivory leaving Africa over the period studied, and sensitivity analyses have shown that the results are robust over the likely range of trade volumes. Given a volume of trade and a carrying capacity trajectory, the model results are similar over a wide range of possible recruitment rates, mortality rates and density-dependent responses. The population trajectory produced is insensitive to changes in assumptions about the biological parameters.

The results suggest that African elephant numbers were dramatically reduced during the 19th Century, but only at a rate of about 2% per annum. There was a lull in the first half of the 20th Century, with rates of population change around zero. From 1950 onwards, the population has been declining with increasing rapidity, the rate of decline only dropping in 1987. For the first 150 years, the rate of decline is determined by the interaction between changes in carrying capacity and hunting. However, from around 1970, the hunting mortality rate has increased dramatically, and become the dominant influence on elephant population dynamics.

The elephant population of the whole of Africa is modelled as a single entity in this paper, although local changes in elephant abundance and carrying capacity clearly will not necessarily follow this trend. However, modelling the whole population gives an overall picture of the important factors involved in the determination of elephant numbers. It is unlikely that a dataset exists with which population dynamics and trade data can be coupled at a local level over a long period of time.

The colonial period was thus one of steady decline in elephant numbers, far slower than the dramatic decline in numbers since the second wave of hunting fuelled by the Far Eastern ivory market. Although 19th Century volumes of trade were similar to those of the 1970s and 1980s, they were taken from a larger population and so caused far less population reduction. However, contemporary writers such as Bryden (1899, 1903) saw disastrous reductions in elephant numbers. This suggests either that hunting was localized, not affecting the major elephant populations, or that the massacres which they reported were less severe than they appeared. The former seems more likely, particularly as hunting probably occurred in the same areas as the carrying capacity reductions.

Decreasing carrying capacity is still a threat to the elephant. The population size in 1987 was only 8% of carrying capacity, but 83% of elephant range is completely unprotected (Douglas-Hamilton 1988). If elephant habitat continues to be destroyed, and particularly if ivory continues to be a valuable commodity, elephants will increasingly be confined to protected areas. The carrying capacity of moderately and effectively protected areas is 528 000 animals, 73%

of the 1987 population size. Most protected areas are already becoming crowded as elephant populations in unprotected areas dwindle. Halting the ivory trade will not solve the basic problem of habitat loss. Both the ivory trade and reduced carrying capacity are causing the decline in the continental elephant population, and both must be tackled.

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## APPENDIX 1. Trade data

### (a) 1814–1914

All the data used for the period up to 1914 are in Parker (1979). The records are fragmentary and give a limited picture of the magnitude of the early ivory trade. Parker and contemporary writers have made informed guesses as to the true volume of trade, but this paper keeps as far as possible to documented trade. There are some data on the ivory trade before 1814, going back as far as 1500. However, they are very fragmentary. Other factors, such as the vegetation
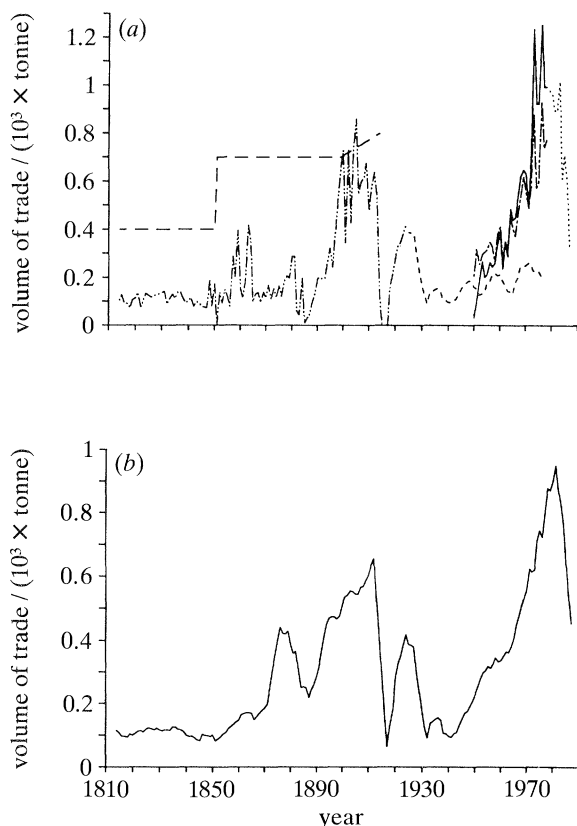
Figure 8. (a) All available data on total ex-Africa ivory trade, 1814–1987. Data, as discussed in the text, are from Parker (1979) (1814–1914 (dot-dot-dash line); 1915–1977 (short dashes); 1950–1979 (solid line)); Douglas-Hamilton (1979) (1915–1977 (short dashes)); Pearce (1989) (1950–1979 (dot-dash line)); and Luxmoore *et al.* (1989) (1979–1987 (dotted line)). Parker's guess at the pre-1914 volume of trade is also shown (long dashes). (b) Estimate of the volume of ivory leaving Africa 1814–1987, using the above data and smoothed using 5-year running means.

pattern and mean tusk mass, are unlikely to have remained constant from 1500 to the present day. The data improve from 1814, and the colonial period of major elephant exploitation starts soon afterwards, so 1814 is taken as the starting point for the population model.

Imports are divided into ivory exported directly from Africa (ex-Africa ivory) and that exported from non-producer countries. For several importers there are long time series of total ivory imports but only a few years of ex-Africa imports. In these cases, the proportion of total imports represented by ex-Africa imports was calculated for the years with data, and applied to the other years. The proportion of imports to Britain that were ex-Africa varied markedly over time, and so, in the absence of data, a linear function was assumed for the period of extrapolation, 1850–1906. In general, if there were no supporting data, point values were not extrapolated to the whole time series. This is likely to have led to an underestimation of the trade between 1850 and 1880. However, sensitivity analyses show that the possible underestimate was insignificant to the results. The final estimate of the volume of ivory traded before 1914 is a mixture of ex-Africa imports when available and exports for the years with no import data.

### (b) 1915–1950

Data for this period are sketchy because of the two World Wars. Parker (1979) gives import and export data for East African countries for the period 1925–1977, and Douglas-Hamilton (1979) gives data for West Africa, Centra Africa, and Somalia for 1915–1977. The data from Douglas-Hamilton (1979) are fragmentary, but again there was no extrapolation between data points. To get total East African exports, trade between the countries themselves was removed. A total for the period was then obtained by adding together the data from Parker (1979) and the modified Douglas-Hamilton (1979) data.

### (c) 1950–1987

The data derived from Parker (1979) and Douglas-Hamilton (1979) for 1925–1977 are very incomplete, but particularly so after 1950, when other countries rose to prominence as ivory exporters. When estimates using these data after 1950 are compared with those of Pearce (1989) and Parker's (1979) estimate of 'minimum world imports', there is no significant correlation. Pearce and Parker worked on the same customs data, but with different aims. Parker wanted a measure of trading activity, arguing that the data were too unreliable, the records too incomplete and the methods too crude to allow an accurate estimate of African exports. Pearce attempted an accurate estimate of the African exports by eliminating double-counting. The two estimates are similar, but Pearce's estimate for 1950–1979 was used because it is more likely to be correct.

After 1979, the estimates of the Wildlife Trade Monitoring Unit (WTMU) of IUCN were used

(Luxmoore *et al.* 1989). These were compiled from customs data and Convention on International Trade in Endangered Species (CITES) data. CITES has controlled and monitored trade in ivory between member countries since 1981, introducing a system of quotas in 1985 and a moratorium on trade in 1989, which was reaffirmed in 1992. By using these data, WTMU traced individual ivory shipments from country to country, practically eliminating double-counting. The smuggling and underreporting of ivory shipments undoubtedly increases at times of high ivory value and trade restrictions, to evade taxes or quotas. Since CITES quotas were introduced, and especially since the 1989 trade ban, there has therefore been little way of estimating the true volume of ivory leaving Africa. This may also have happened in Zanzibar in the early 19th Century, when taxes were imposed on goods entering the island (Oliver & Atmore 1967). Given this problem of underreporting and the incompleteness of the data, the final estimate of the volume of the ivory trade since 1814 must be seen as a minimum (figure 8).

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