
The Relative Effects of Hunting and Habitat Destruction on Elephant Population Dynamics over Time

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INTRODUCTION

Over the last two hundred 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, due to 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; Parker & Graham 1989a&b), 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.

A MODEL OF ELEPHANT NUMBERS

A non-linear Leslie matrix is needed fully to describe elephant population dynamics under harvesting,

because 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 non-linear Leslie matrix formulations. The population size each year is calculated as:

1.

$$N(t+1) = (N(t)1e^{-m(t)} + R(t)) - [1 + i]H(t+1)$$

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 mortality
 $H(t)$ = 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.

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):

2a

$$P = P_{ma} (P_{max} - P_{min}) (1 - (N_t/L)^{\beta})$$

2b

$$P = p_{min} + (P_{max} - P_{min}) [1 - (N_t/L)^{\beta}]$$

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

β = 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 β determines the degree of nonlinearity in the density dependence. If $\beta=1$, the density dependent response is linearly related to population size, while 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. β 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 near zero is less likely than a β 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, 1989a; 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 due to 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 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 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 vegetation type. The estimate of carrying capacity in 1979 is 11 million, 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 civilisation (Bourgoin 1956, Bryden 1903). 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 relatively stable throughout the colonial period due to 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 either decline because total range area declines or because of changes in the proportions of different vegetation types. Savanna 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/km² as opposed to 2/km² in savanna.

c. Volume of the ivory trade 1814 to 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, like the vegetation pattern and mean tusk weight, 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.

1915 to 1950

Data for this period are sketchy due to the two World Wars. Parker (1979) gives import and export data for East African countries for the period 1925-1977, while

Table 1. Maximum elephant carrying capacity (K) in 1814, using 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 (km ²)	Density (km ⁻²)	K
Guineo-Congolian (forest)	2,800,000	0.5	1,400,000
Guineo-Congolian/Zambeian	705,000	2	1,410,000
Zambeian (woodland)	3,770,000	2	7,540,000
Guineo-Congolian/Sudanian	1,165,000	2	2,330,000
Sudanian (wood/grass)	3,731,000	2	7,462,000
Somalia-Masal (bush/grass)	1,873,000	2	3,746,200
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 range	19,243,000 km ²		
Total carrying capacity			26,913,000

Douglas-Hamilton (1979) gives data for West Africa, Central 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 re-moved. A total for the period was then obtained by adding together the data from Parker (1979) and the modified Douglas-Hamilton (1979) data.

1950 to 1987

The data derived from Parker (1979) and Douglas-Hamilton (1979) for 1925-77 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 to 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 1950-79 was used.

Table 2. Elephant ring. In 1987, using Douglas-Hamilton's (1988) vegetation categories and areas, which are based on White's. 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 to 1814.

Zone	Area(km ²)	Density(km ⁻²)			K
		1979	1987	Max	
Forest	1,166,000	0.3	0.33	0.5	583,000
Swamp forest	334,000	0.5	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	0.02	0.01	1,420
Desert	16,000	0.01	0.01	0.01	160
Total range	5,904,000k ²				
Total carrying capacity					8,985,000

Figure 1A. All available data on total ex-Africa ivory trade, 1814-1987. Data, as discussed in the text, are from Parker (1979) [1814-1914, labeled 'customs to 1914'; 1915-1977, labeled 'customs 1915-1977'; 1950-1979, labeled 'Parker MWI']; Douglas-Hamilton (1979) (1915-1977, labeled 'customs 1915-1977'); Pearce (1989) [1950-1979, labeled 'Pearce']; and Luxmoore, Caldwell and Hithersay (1989) (1979-1987, labeled 'WTMU'). Parker's guess at the pre-1914 volume of trade is also shown.

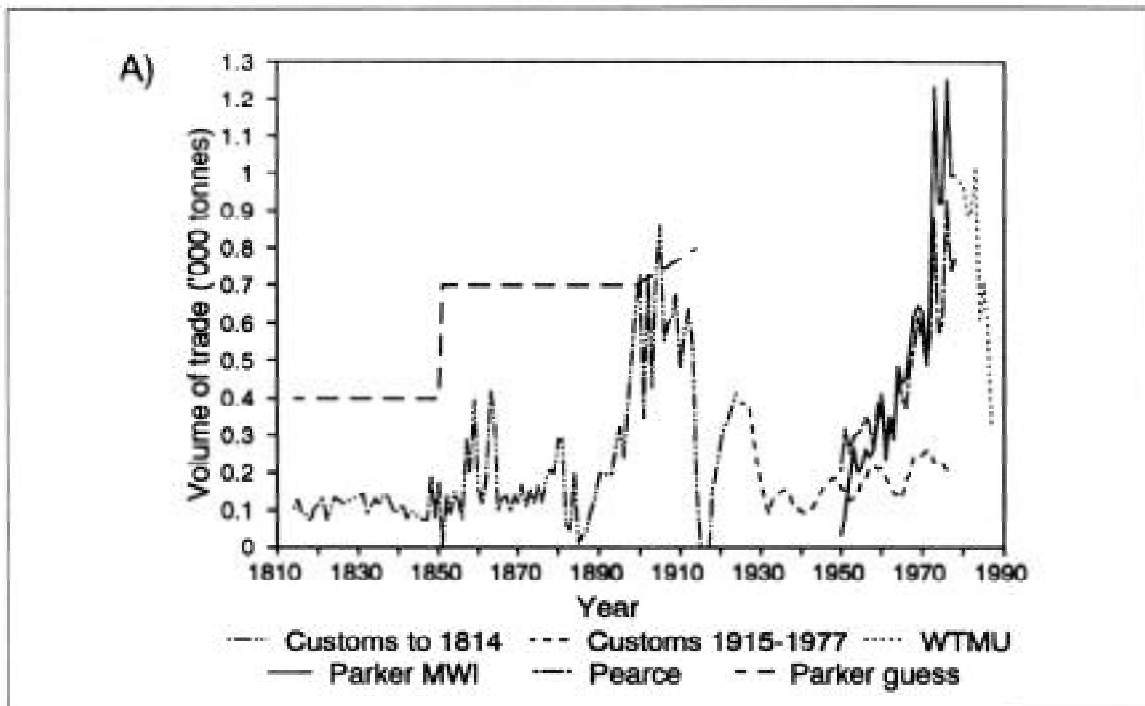


Figure 1B. Estimate of the volume of ivory leaving Africa 1814-1987, using the above data and smoothed using 5 year running means.

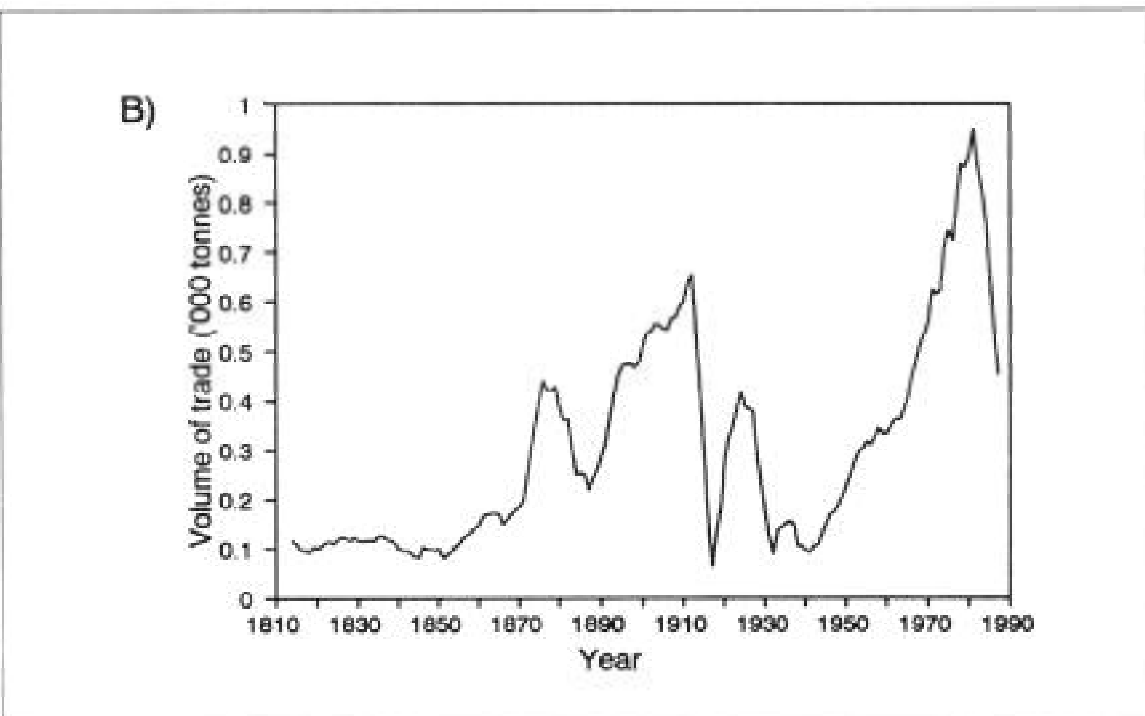


Table 3. A. Values for recruitment rate and adult natural mortality used in the population model, where P_{max} and P_{min} are as defined in equation 2.

Parameter	Recruitment		Mortality	
	Max	Min	Max	Min
Pmax	0.11	0.01	0.10	0.04
Pmin	0.06	0.02	0.04	0.01

B. The sources of the parameter values.

Source	Recruitment	Mortality
Douglas-Hamilton (1972)		0.02-0.04
Hanks (1972)	0.06	
Jachmann (1986)	0.09	0.08
Laws (1969)		0.02-0.1
Laws, Parker, Johnstone (1975)		0.02-0.08
Leuthold (1976)	0.05-0.11	
Ottichiko (1986)	0.06	
Owen-Smith (1988)	0.02-0.1	
Sherry (1975)	0.07	
Smuts (1976)	0.07	
Williamson (1976)	0,09	

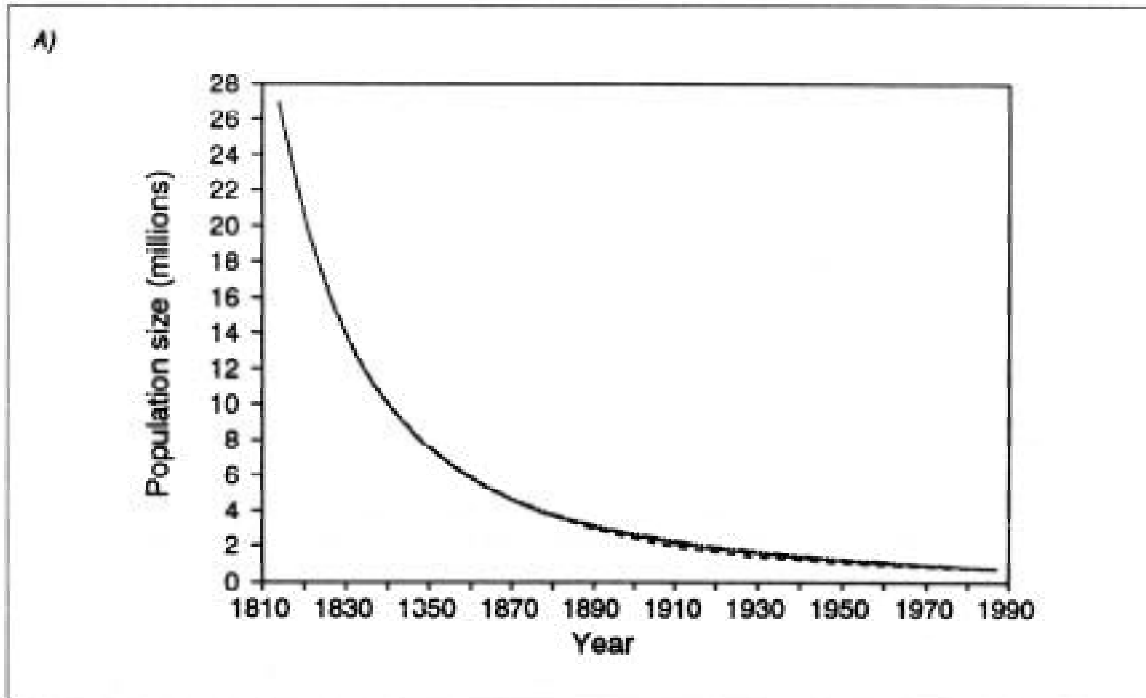
After 1979, the estimates of the Wildlife Trade Monitoring Unit (WTMU) of IUCN were used (Luxmoore, Caldwell & Hithersay 1989). These were compiled from customs data and Convention on International Trade in Endangered Species (CITES) data. CITES has controlled and monitored trade in ivory among member countries since 1981, introducing a system of quotas in 1985 and a moratorium on international trade in 1989, which was reaffirmed in 1992. Using these data, WTMU traced individual ivory shipments from country to country, practically eliminating double-counting. The smuggling and under-reporting of ivory shipments undoubtedly increases at times of high ivory value and trade restrictions, in order to evade taxes or quotas. Since CITES quotas were introduced, and especially since the 1989 international 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 under-

reporting 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 1).

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 rates and β were varied systematically between runs, so that the full range of parameter values was covered.

Figure 2. The mean population size and mean rate of population change over the study period, 1814-1987, when carrying capacity change 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, slow-fast and linear. A) Population size



B) Rate of population change

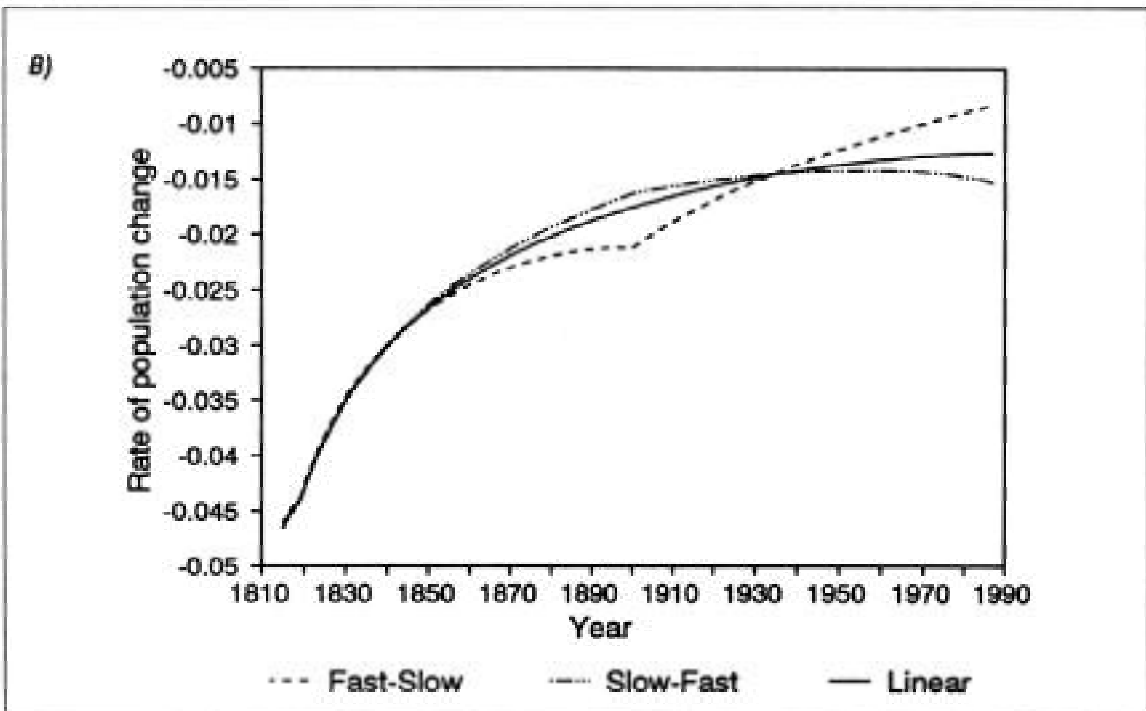


Figure 3. The mean rate of population change over time when hunting alone is assumed responsible for population decline, compared to the results when carrying capacity alone is assumed responsible. The fast-slow carrying capacity trajectory is used, and both populations start from carrying capacity. 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.

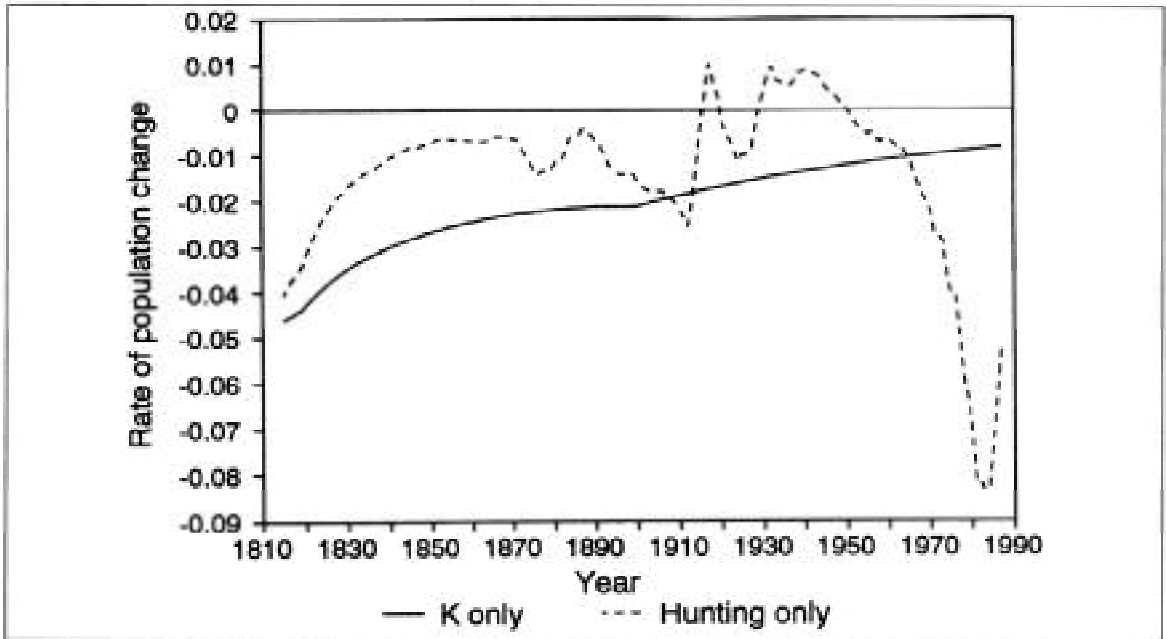
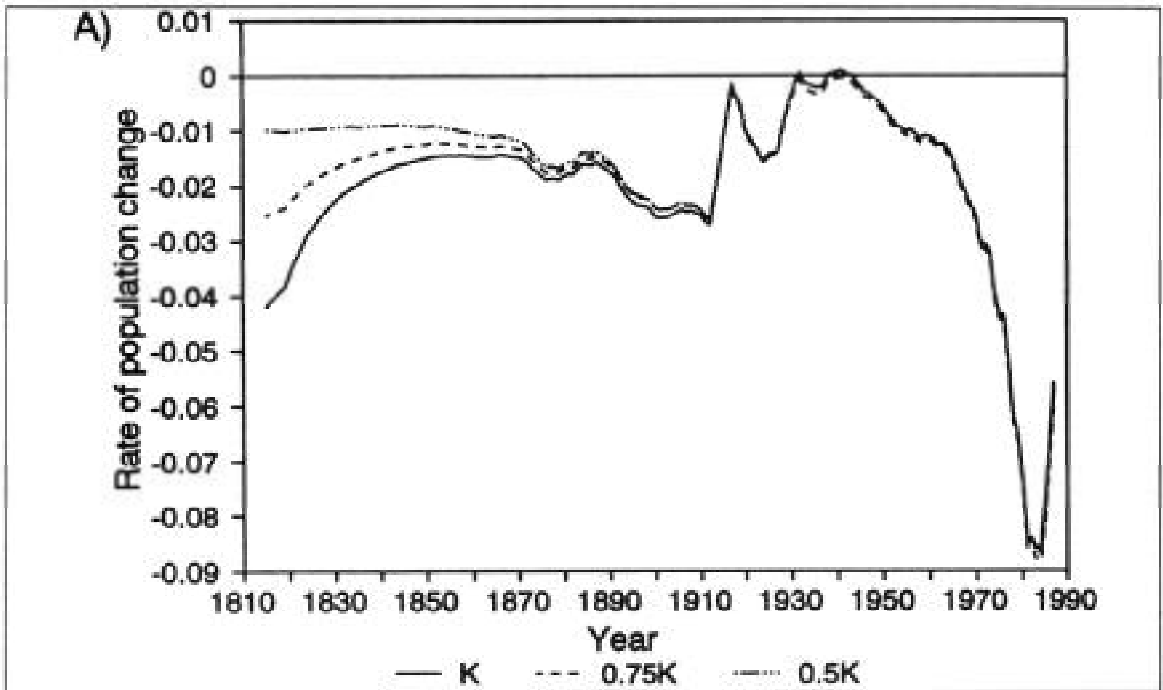


Table 4. Results of the simulation runs, showing the number of trajectories fulfilling the constraints for various population sizes in 1814 and carrying capacity trajectories. The average and maximum values of B and the range of the 1979 population size (in millions) in the trajectories fulfilling the constraints are also shown. The total number of trajectories investigated was 17,640.

1. Fast-slow trajectory					
1814 population	Mean β	Max β	Trajectories	1979 population	
				Max	Mn
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
2. Linear trajectory					
1814 population	Mean β	Max β	Trajectories	1979 population	
				Max	Min
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
3. Slow.fast trajectory					
1814 population	Mean β	Max β	Trajectories	1979 population	
				Max	Min
K	0.37	1.0	183	1.81	1.22
0.75K	0.33	1.0	211	1.78	1.21
0.5K	0.4	1.0	150	1.76	1.22

Figure 4A. 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.



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.

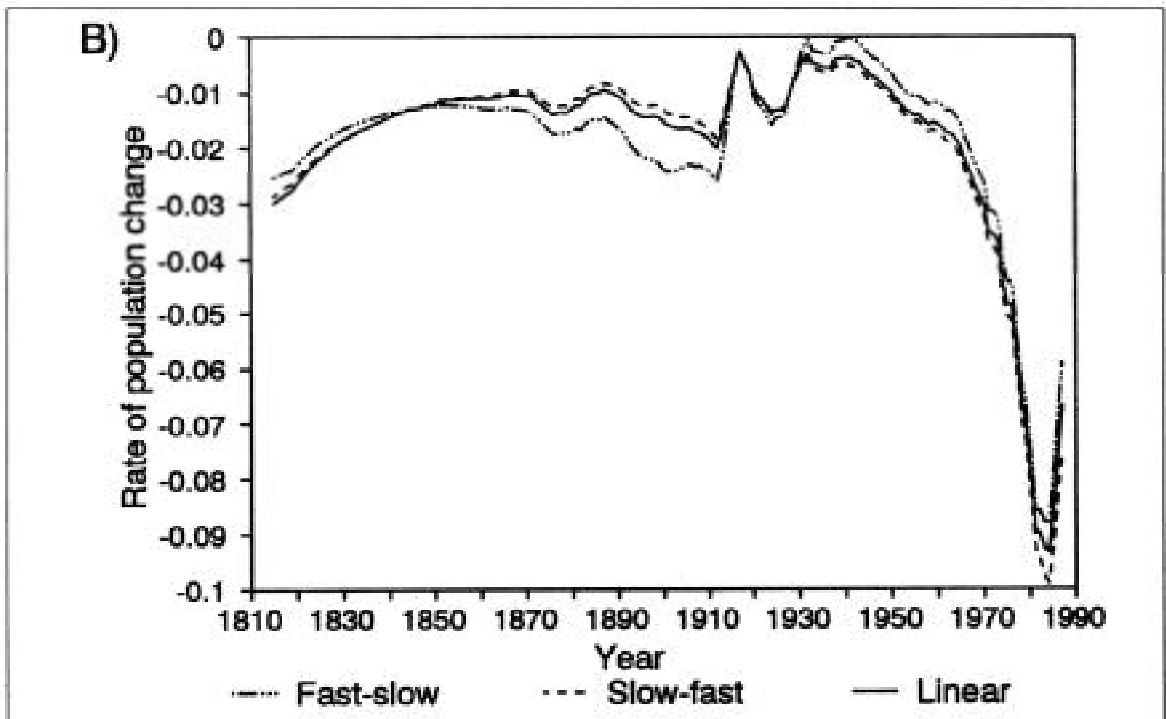


Figure 5A. The population trajectory for the fast-slow scenario starting from 75% of carrying capacity. The mean of the trajectories passing through the 1987 window is shown, together with the maximum and minimum values of population size for those trajectories passing through the window (dashed lines).

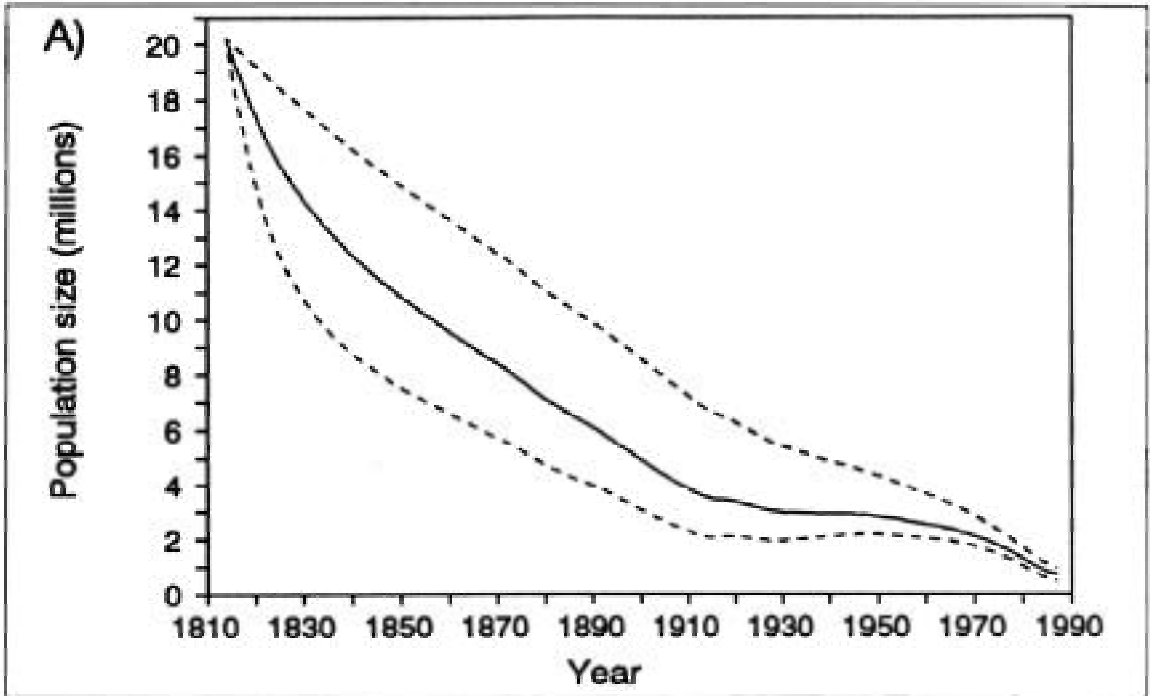


Figure 5B. The rate of population change represented by A), with the maximum and minimum trajectories again shown as dashed lines.

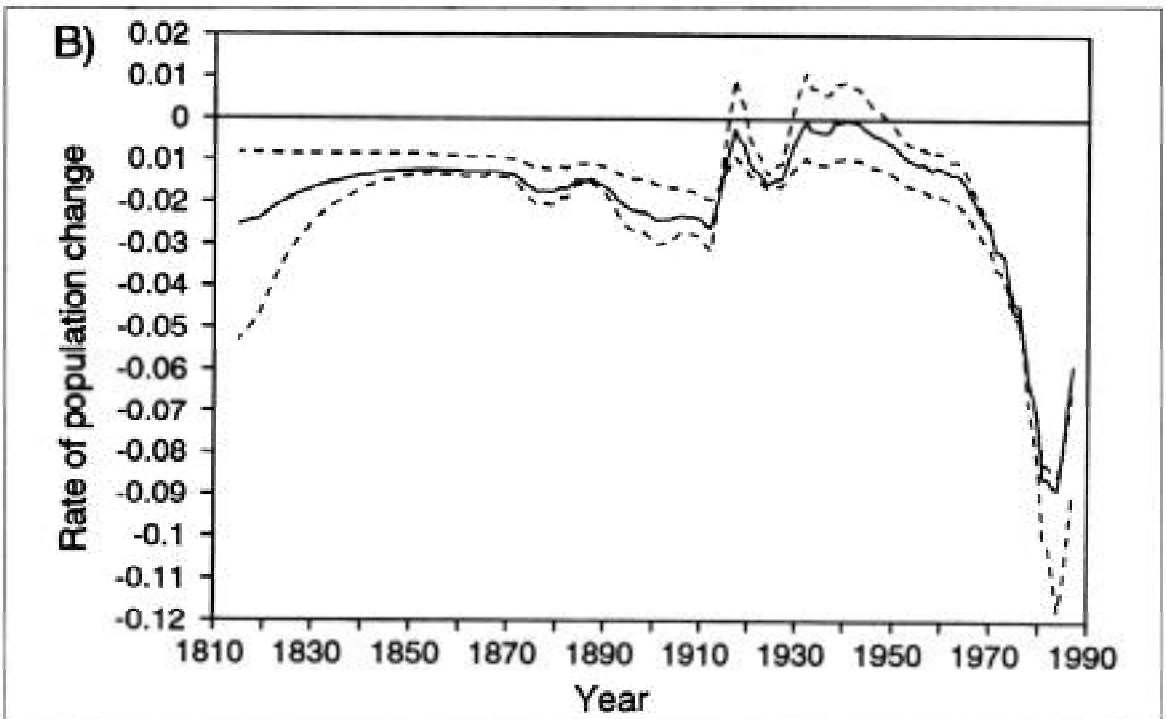
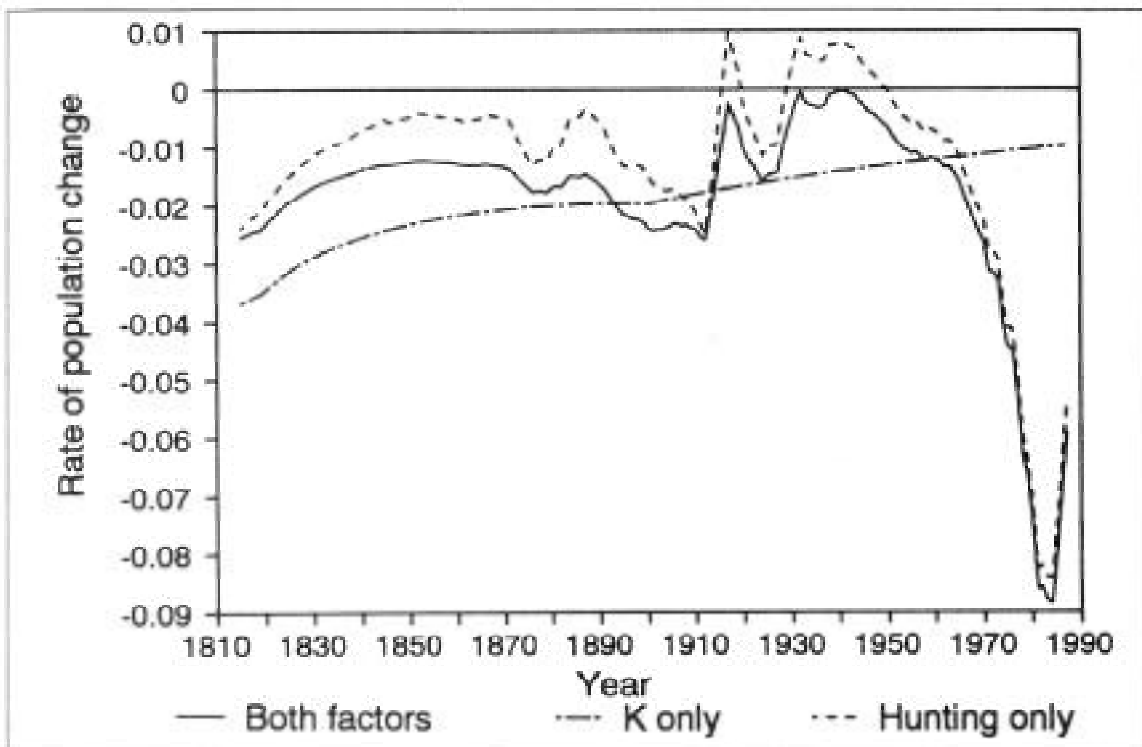


Figure 6. A comparison of the mean rate of population change when hunting alone, carrying capacity alone, and both factors are assumed responsible for population decline. All trajectories start from 75% of carrying capacity, and the scenario assumed is fast-slow. Until around 1970, the trajectory where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



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 $\pm 33\%$ of the estimated value of 720,000 (Douglas-Hamilton 1989) were accepted.

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 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, since 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).

THE MEAN TUSK WEIGHT IN THE TRADE

In order 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 weight in the trade at a particular time, assuming that each elephant killed contributes 1.88 tusks (Parker 1979). The mean tusk weight 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 non-linear Leslie matrix is used to represent elephant population dynamics, the mean tusk weight 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 weight declines exponentially with

time, is (Basson, Beddington & May 1991):

3.
 $w = A + a(Nt)z$

where

- A = mean tusk weight at end of period
- a = scaling constant for mean tusk weight at beginning of period
- z = exponential rate of decline of mean tusk weight

In this case, A and a are scaled so that the mean tusk weight in the trade at the beginning of the period is 15kg, and that at the end is 5kg. The former is reasonable given the data presented in Parker (1979), while the latter is the mean tusk weight observed over the last decade (Milner-Gulland & Mace 1991, data from WTMU). If $z=0$, the mean tusk weight remains constant at the 1987 level throughout the period, while at $z=1$ there is a linear decline in mean tusk weight over time. As z increases above 1, the exponential rate of decline in mean tusk weight with time increases. Basson, Beddington and May (1991) put z at 1.7, and in this study it is set at 2. Trade records of mean tusk

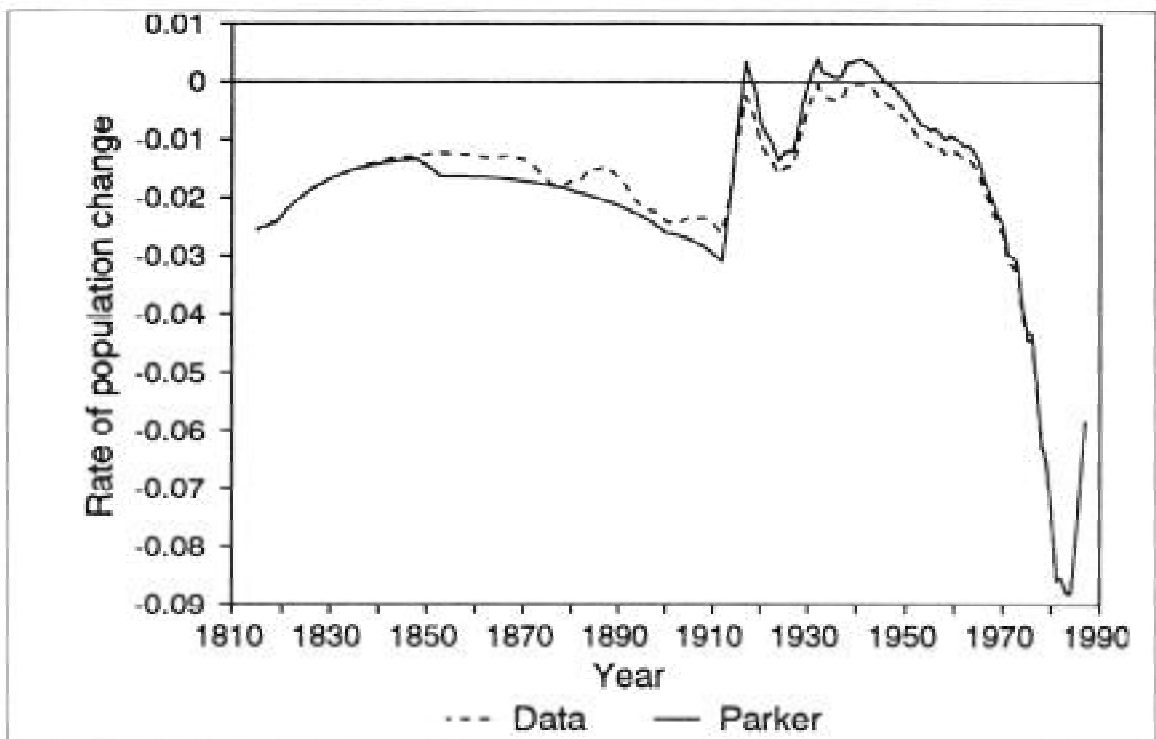
weights are very variable, although the assumption of an overall decline in mean tusk weight over the whole period seems to be supported (Parker 1979).

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 the 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

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 and those using Parker's much higher trade estimates.



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 β , since Fowler (1984) shows that a $13 > 1$ 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 4a). A 0.75K 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 4b). Taking the fast-slow carrying capacity trajectory and a population size of 0.75K 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 5a). 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 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).

SENSITIVITY ANALYSES

The population parameters used are z , which describes the rate of mean tusk weight 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 (Milner-Gulland & Beddington 1993).

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 β 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, using subjective contemporary accounts of the volume of ivory leaving ports. 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 weight assumption also indirectly changes the number of elephants assumed to have been killed for the trade. Changes in these parameters have little effect on the results. 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). This is due mainly 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 under estimation of pre-1914 trade levels.

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-80s, 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 localised, 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 since 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 the 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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REFERENCES

- Barnes, R. (1989). The status of elephants in the forests of central Africa: A reconnaissance survey. In: *The Ivory Trade and the future of the African elephant*. Queen Elizabeth House, Oxford: Ivory Trade Review Group.
- Basson, M., Beddington, J.R. & May, R.M. (1991). An assessment of the maximum sustainable yield of ivory from African elephant populations. *Mathematical Biosciences* 104, 73-95.
- Bourgoin, P. (1956). *Animaux de chasse d'Afrique*. Paris: Le Toison d'Or.
- Bryden, H.A. (1899). *Great and small game of Africa*. London: Roland Ward.
- Bryden, H.A. (1903). The decline and fall of the South African elephant. *Fortnightly Review* 73, 100-108.
- Burrill, A. & Douglas-Hamilton, I. (1987). African Elephant Database project: Final report. *GRID Case study series no. 2*. Nairobi: UNEP.
- Calef, G.W. (1988). Maximum rate of increase in the African elephant. *African Journal of Ecology* 26,323-327.
- Corfield, T.F. (1973). Elephant mortality in Tsavo National Park, Kenya. *East African Wildlife Journal* 11,339-368.

-
- Douglas-Hamilton, I. (1972). *Ecology and behaviour of the African elephant*. D.Phil. Thesis, University of Oxford.
- Douglas-Hamilton, I. (1979). *The Ivory Trade - Final Report*. Washington D.C.: Department of Fisheries & Wildlife.
- Douglas-Hamilton, I. (1988). *African elephant population study - Phase 2*. Nairobi: WWF/UNEP.
- Douglas-Hamilton, I. (1989). Overview of status _ and trends of the African elephant. In: *The Ivory Trade and the future of the African elephant*. Queen Elizabeth House, Oxford: Ivory Trade Review Group.
- Fowler, C.W. (1981). Comparative population dynamics in large mammals. In: *Dynamics of large mammal populations*. ed. by C.W. Fowler & T.D. Smith. New York: Wiley & Sons.
- Fowler, C.W. (1984). Density dependence in cetacean populations. *Report of the International Whaling Commission Special Issue 6*, 373-379.
- Hanks, J. (1972). Reproduction of elephant in the Luangwa Valley, Zambia. *Journal of Reproductive Fertility* 30, 13-26.
- Jachmann, H. (1986). Notes on the population dynamics of the Kasungu elephants. *African Journal of Ecology* 24, 215-226.
- Lankester, K. & Beddington, J.R. (1986). An Age-structured population model applied to the Gray whale. *Report of the International Whaling Commission* 36, 353-358.
- Laws, R.M. (1969). The Tsavo research project. *Journal of Reproductive Fertility*, Supplement 6,495-531.
- Laws, R.M., Parker, I.S.C. & Johnstone, R.C.B. (1975). *Elephants and their habitats*. Oxford: Clarendon Press.
- Leuthold, W. (1976). Age structure of elephants in Tsavo National Park, Kenya. *Journal of Applied Ecology* 13, 435-444.
- Luxmoore, R., Caldwell, J. & Hithersay L. (1989). The volume of raw ivory entering international trade from African producing countries from 1979 to 1988. In: *The Ivory Trade and the future of the African elephant*. Queen Elizabeth House, Oxford: Ivory Trade Review Group.
- Milner-Gulland, E.J. & Mace, R.H. (1991). The impact of the ivory trade on the African Elephant population, as assessed by data from the trade. *Biological Conservation* 55,215-229.
- Milner-Gulland, E.J. & Beddington, J.R. (1993). The exploitation of elephants for the ivory trade: an historical perspective. *Proceedings of the Royal Society B* 252, 29-37.
- Oliver, R. & Atmore, A. (1967). *Africa since 1800*. Cambridge University Press.
- Oliver, R. & Crowder, M. (1981). *Cambridge Encyclopaedia of Africa*. Cambridge University Press.
- Ottichilo, W.K. (1986). Age structure of elephants in Tsavo National Park, Kenya. *African Journal of Ecology* 24, 69-75.
- Owen-Smith, R.N. (1988). *Megaherbivores*. Cambridge University Press.
- Parker, I.S.C. (1979). *The Ivory Trade*. Washington D.C.: Department of Fisheries & Wildlife.
- Parker, I.S.C. & Graham, A.D. (1989a). Elephant decline Part 1: Downward trends in African Elephant Distribution and Numbers. *International Journal of Environmental Studies* 34, 287-305.
- Parker, I.S.C. & Graham, A.D. (1989b). Elephant decline Part 2: Downward trends in African Elephant Distribution and Numbers. *International Journal of Environmental Studies* 35, 13-26.
- Pearce, D. 1989. The Ivory Trade (1950-79). In: *The Ivory Trade and the future of the African elephant*. Queen Elizabeth House, Oxford: Ivory Trade Review Group.
- Poole, J.H. (1989). The effects of poaching on the age structure and social and reproductive patterns of selected East African elephant populations. In: *The ivory trade and the future of the African elephant*. Queen Elizabeth House, Oxford: Ivory Trade Review Group.
- Sherry, B.Y. (1975). Reproduction of elephant in Gonarezhou, South-Eastern Rhodesia. *Arnoldia* 7(29), 1-13.
-

Smuts, G.L. (1976). Reproduction and population characteristics of elephants in the Kruger National Park. *Journal of the South African Wildlife Management Association* 5, 1-10.

White, F. (1983). *The vegetation of Africa: a descriptive memoir to accompany the UNESCOAETFAT-UNSO vegetation map of Africa*. Paris: Unesco.

Williamson, B.R. (1976). Reproduction in female African elephant in the Wankie National Park, Rhodesia. *South African Journal of Wildlife Resources* 6, 89-93.

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