POPULATION DYNAMICS OF ELEPHANTS IN
ETOSHA NATIONAL PARK,
S.W.A./NAMIBIA.

by

MALAN LINDEQUE

Dissertation presented for the Degree of Doctor of Philosophy at the University of Stellenbosch.

Promoter : Prof. J.A.J. Nel.

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DECLARATION

I the undersigned hereby declare that the work contained in this dissertation is my own original work and has not previously in its entirity or in part been submitted at any University for a degree.

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ABSTRACT

Elephant numbers in Etosha National Park have increased steadily since the recolonization of the park by elephants in the early 1950's. A period of rapid increase occurred from 1979 to 1983, coinciding with the recent Trans-African drought. The population appeared to have erupted and was culled twice to halt further increases and prevent irreversible changes in plant species diversity due to an over-population of elephants. This study was done to determine fecundity and mortality schedules and the rate of increase of the elephant population, in order to manage the population by artificial control of numbers.

Six aerial censuses at four-month intervals from 1983 to 1985 showed that the number of elephants in the park varied between seasons, and both the dry and wet season populations declined after 1983. The rate of decline, as also the rate of increase from 1973 to 1983, was higher than expected from fecundity and mortality rates. Age structures of herds were determined by aerial photogrammetry and did not change substantially from 1983 to 1987, and from 1977-1987 when using ground observations. Fecundity rates determined from females culled in 1983 and 1985 were higher than in populations elsewhere in Africa, in contrast to the observed decline in population size in Etosha National Park. Survival schedules based on the age distribution of females indicated higher mortality rates than in other populations. The relative importance of mortality factors was determined from carcase records, and anthrax proved to be the single most important cause of death in all age groups except calves, where predation by lions was more important.

Evidence from reproductive parameters, age structures and mortality schedules along with recorded movements of elephants in and out of the park, suggest that changes in abundance were not due to explosive breeding or mortalities before and after the drought respectively, but to immigration and emigration. Elephants moved freely in and out of the park as determined by rainfall and human disturbance, and the Etosha National Park population appears to be part of a regional population of elephants occurring in north-western SWA/Namibia, including parts of the Kaokoveld, Ovambo and Kavango.

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CHAPTER 1 GENERAL INTRODUCTION

The "elephant problem" in Etosha National Park which resulted in this study appears to be similar to elephant problems elsewhere in African conservation areas. Factors other than the usual determinants of gross distributional shifts and population increase have caused a condition regarded as over-population of elephants in virtually all African conservation areas. Over-abundunce of elephants, either as increased local population density or the establishment of resident populations in formerly vacant or seasonally vacant areas, is characterized by habitat modification by elephants, typically a change from woodland to scrubland or grassland and subsequent population responses in other herbivores, as summarized in Laws (1970) and Eltringham (1982).

Human interference in the form of pastoralism and civil-military unrest is possibly the prime cause of elephant range contraction and subsequent concentration in the remaining suitable parts of former ranges (Laws 1969b, 1973, Douglas-Hamilton 1987). Where elephant populations inhabit protected areas but are not confined to them, population characteristics such as the rates of births and deaths often reflect environmental qualities over the total distribution area (Caughley 1977a). This aspect could not be examined in the present study, due to security-imposed limitations on access to the entire distribution range of the population which occurs in Etosha National Park. Historical and recent socio-political trends, human population growth and land use practices are currently significant determinants of the population status of virtually all wildlife in Africa. It is perhaps also significant that recent problems with over-abundance of large mammals owing to loss of former range due to human presence, are unrivalled in terms of gross demographical changes over the past 10 000 years (Laws 1981). Only Pleistocene climatic upheavals could have produced equally severe changes. In a matter of a few decades, representing only a few elephant generations, the African elephant has had to adapt or respond to previously unknown environmental changes. Present concern about the elephant population in Africa has nevertheless shifted from that of over-abundance in conservation areas to rapid decimation through poaching (Douglas-Hamilton 1987).

In a period little longer than the lifetime of one elephant, the widespread distribution of elephants in SWA/Namibia, limited formerly only by the availability of water, has shrunk to a narrow strip along the northern border of the country (Joubert & Mostert 1975, De Villiers & Kok 1984). In an even shorter period of three decades, elephants have increasingly occupied Etosha National Park, formerly devoid of resident herds, until the present where most of the elephants in north-western SWA/Namibia occur in the park for most of the year.

The elephant population in Etosha National Park should be seen against the background of other elephant populations, although it should be recognized that local conditions may produce local results in demographical parameters not comparable to responses elsewhere. Some characteristics of the study population nevertheless render it useful for examining some of the generalizations made for and processes operating in other populations of the African elephant.

The Etosha National Park population is relatively small and at a very low density and is still migratory within a system driven largely by sporadic rainfall and availability of water. Primary production and its availability are strongly affected by the unpredictable features of the environment, such as rain, fire, frost and concommitant unpredictable trends in populations of biota capable of dramatic modifications in plant biomass, such as termites, locusts, pathogenic fungi and perhaps some vertebrates.

The Etosha National Park environment appears to be characterized by upheavals, such as sudden changes in climate, which might be more conducive to an assemblage of r-selected plant and animal species such as is found in some deserts. The position of a K-extreme such as the elephant in an environment closer to the r-end of the spectrum is therefore of great interest. Elephants appear to be unable to track temporal environmental changes, due to built-in delays caused by the long gestation period, mostly single offspring per litter and advanced age at first conception. Elephants might equally not respond to temporal stresses, by using body reserves or moving to alternative parts of the home range. The fact that elephants destroy their own habitat under certain conditions has been ascribed to this inability to respond quickly to changes in resource abundance (Croze, Hillman & Lang 1981, Laws 1981). An elephant population might therefore be limited to responses in births or deaths to the more regular or predictable elements in their environment, such as seasonal rainfall, fires and phenological changes due to photoperiodicity. Access to surface water is probably the most severe limiting factor, as elephants are obligate drinkers. This factor alone represents a major environmental uncertainty for elephants, particularly in semi-arid environments with a paucity of perennial rivers and springs.

Localized changes in the vegetation of Etosha National Park have certainly occurred as the result of elephant utilization. It is inevitable that the introduction of a renowned modifier of habitat to a system would result in changes, as discussed by Owen-Smith (1987). This is indeed the situation in Etosha National Park, where elephants now occupy areas which could not have supported elephants over at least the last few hundred years and possibly longer, due to the absence of perennial springs in large areas with unsuitable topography and geological strata for the development of springs. Previous occupation was limited to wet-season dispersal determined by surface water, when elephants have a predominantly grass diet (De Villiers 1981). Present changes in the woody vegetation are the result of interference by man, who has provided artificial sources of water, and thus removed the impact of limited surface water on the distribution of obligate drinkers such as elephants.

Changes in woody vegetation in conservation areas by elephants, as caused by the artificial provisioning of water, restriction of movements by fences, and the inability of elephant populations to respond quickly to changes in resource abundance, are used by Hanks, Densham, Smuts, Jooste, Joubert, Le Roux & Milstein (1981), Cumming (1981, 1983), Pienaar (1983) and De Vos, Bengis & Coetzee (1983) to justify interference management to stabilize elephant-vegetation interactions at some preconceived or subjective level. In Etosha National Park the effect of elephant density on vegetation is not as clear-cut as in other parks. Early arguments for population reduction by culling in Etosha National Park during the drought years of 1980-1983 were not based on observed structural changes in the vegetation caused by elephants, but on the potential for such changes. Once the worst effects of drought had passed, it became clear that elephants had a minor impact on the vegetation compared to other factors such as fire and frost, except on a few rare and highly susceptible tree species such as Albizia anthelminthica and Moringa ovalifolia (Nott 1986, pers. obs.).

STUDY AREA

The study was conducted from June 1983 to December 1987 in Etosha National Park (hereafter referred to as Etosha N.P. in the text), in South West Africa/Namibia. The park is located in the transition area between three major biotic zones, the South West Arid, Namib Desert and Southern Savanna Woodland (Rautenbach 1978, Smithers 1983), and contains faunal, floristic and physiographic elements of all three zones. The park is within the tropic of Capricorn, with coordinates centering at 19°S 16°E (Fig. 1.1). Etosha N.P. is roughly rectangular and extends about 295 km east-west and 65-110 km north-south, encompassing an area of about 22270 km^2 of which 5140 km^2 are barren salt pans.

Detailed descriptions of the physiography and history of Etosha N.P. are given in Bigalke (1961), Joubert (1971a), Berry (1980) and Le Roux (1980), but the following are of particular relevance to this study. The topography is largely uniform as the park is located on the southern edge of the regional Etosha basin in Kalahari beds of Tertiary to Recent age. Soils are predominantly composed of calcareous sand and calcrete gravel. The south-eastern edge of the park is rimmed by dolomite hills of the Otavi Group of the Damara sequence, which appear also on the western edge as a rim, along with the Khoabendus Group of metamorphic and volcanic series.

The Etosha Pan is the lowest part of an endoreic drainage system, similar to other such systems in the Kalahari such as the Makgadikgadi in Botswana. Previous impressions of the Etosha Pan as a dying system due to stream capture of the Kunene River away from former links with the pan via the Ekuma River, have been refuted by Rust (1985). Any changes were likely due to climatic changes and not the fluvial history of any river. The Etosha Pan receives water from all directions with major drainage channels in the form of omurambas (dry rivers) and oshonas (shallow waterways) from the north and north-east. The pan, however, is usually dry. Minor floods occur during the rainy season, and largely originate from the Cuvelai system draining the highlands of Angola, via a complex series of undefined oshonas and several major omurambas of which the Ekuma River is the most important.

Numerous seasonal and some perennial contact or water-table springs (fountains) occur on the southern edge of the Etosha Pan, as well as artesian springs further south (Fig. 1.2). Contact springs also occur on the western edge of the basin, but only one is perennial at present (Okondethe, Fig. 1.2). The entire northern and central sections of the park and most of the west and south-east are therefore devoid of perennial surface water, but some 40 boreholes currently provide water to game on a rotation system. Etosha N.P. was completely fenced off in 1973, but only a few sections of the fence can be regarded as elephant-proof (Fig. 1.2).

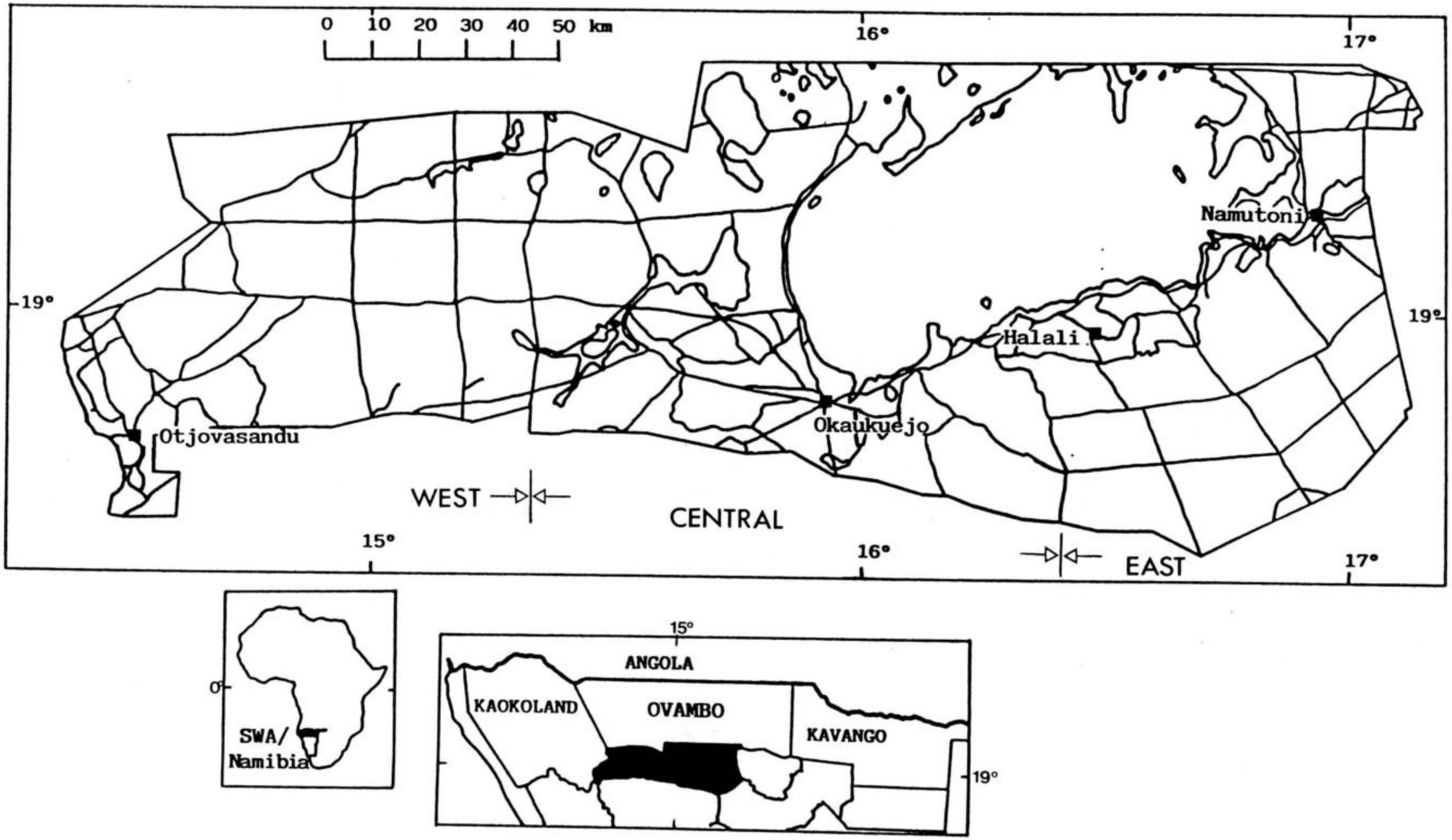
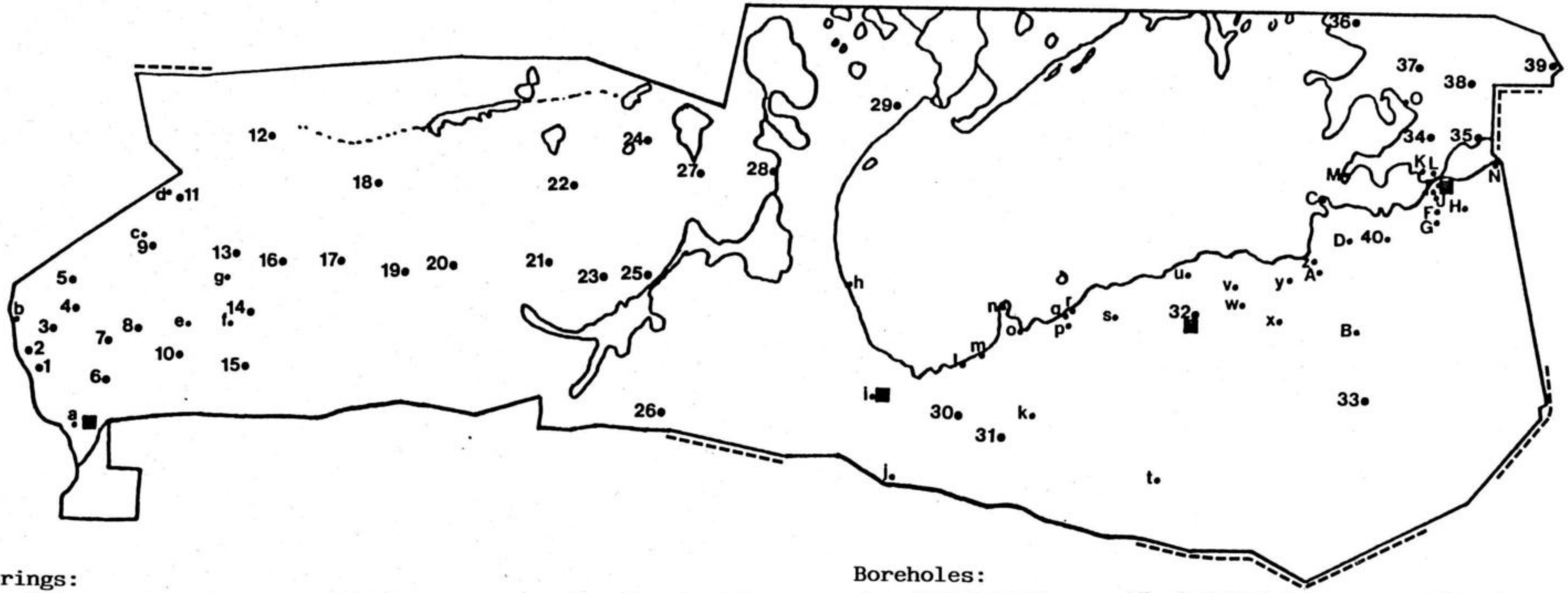


Figure 1.1 Camps (■), roads and firebreaks (—) in Etosha National Park, SWA/Namibia.



Springs:

a. Otjovasandu (s)
b. Okondethe
c. Onautinda (d/s)
d. Onandera (d/s)
e. Otjihaka (d/s)
f. Okawao (d/s)
g. Okatjongeama (d/s)
h. Okondeka
i. Okaukuejo
j. Ombika
k. Aus
l. Kapupuhedi (s)
m. Ondongab (s)
n. Gonob
o. Homob
p. Charitsaub
q. Sueda
r. Salvadora
s. Rietfontein
t. Gobaub
u. Nuamses
v. Goas
w. Noniams
x. Koinseb
y. Agab
z. Springbokfontein
A. Batia
B. Tsam (s)
C. Okerfontein
D. Ngobib
E. Stinkwater (s)
F. Aub
G. Chudop
H. Klein Namutoni
I. Numeros
J. Koinagas
K. Okevis
L. Namutoni
M. Leeunes
N. Twee Palms

Boreholes:

1. Aasvoelbad
2. Luiperdskop
3. Klippan
4. Rateldraf
5. Dolomietpunt
6. Renostervlei
7. Dolomietpoort
8. Kalahari
9. Duineveld
10. Jakkalswater
11. Onangombati
12. Dorsland
13. Nomab
14. Leeukamp
15. Duikerdrink
16. Olifantsrus
17. Tobiroen
18. Nerens
19. Teespoed
20. Bitterwater
21. Sonderkop
22. Good Hope
23. Arendsnes
24. Narawandu
25. Ozonjuitji m'Bari
26. Eindpaal
27. Pan Point
28. Brakwater
29. Okutamare
30. Gemsbokvlakte
31. Olifantsbad
32. Helio
33. Dungaries
34. Tsumcor
35. Aroe
36. Andoni
37. Mushara
38. Kameeldoring
39. Makalane
40. Kalkheuwel

Figure 1.2 Surface water available to game in Etosha National Park during 1983-1988, and elephant-proof sections of the surrounding fence. (Squares denote position of rest camps; --- = elephant-proof cable fences; s = seasonal; d/s = dormant for at least one wet season since 1983).

Accounts of the local climate are available in Bigalke (1961), Berry (1980) and Le Roux, Grunow, Morris, Bredenkamp & Scheepers (1988). Three seasons are evident in Etosha N.P., namely the hot-wet season from January to April, cold-dry season from May to August, and the hot-dry season from September to December. Rainfall is strongly seasonal, with a single peak in February - March. No cyclical pattern is evident in the rainfall, as measured continuously at Okaukuejo since 1934, and over lesser periods at Namutoni, Halali, Ombika (Anderson Gate) and Otjovasandu (Fig. 1.3). There is a rainfall gradient from east to west, with Namutoni receiving an average of 442 mm per rainy season (n=26 years) and Otjovasandu 316 mm (n=20 years).

Rainfall at a given point varies dramatically between years, and also between points within the park, and can best be described as unpredictable. What became known as the Trans-African drought of the eighties had an early manifestation in Etosha N.P. in 1979 and it has been dry ever since.

The vegetation of Etosha N.P. is classified into four major zones: saline deserts with a dwarf savanna fringe, mopane (Colophospermum mopane) savanna, mountain savanna and karstveld, and tree savanna and woodlands (Giess 1971). The greater part of the park is covered by mopane savanna, which has been subdivided by Le Roux et al. (1988) into 16, and the rest of the park in a further 15 communities. Figure 1.4 illustrates a simplified classification of the vegetation of Etosha N.P., based on Le Roux (1980) and Le Roux et al. (1988). Various mopane associations comprise an area of approximately 11800 km^2, or 69% of the total area excluding the saline pans. Mopane woodlands and mixed woodlands are generally tall in the east and in shrub form to the west, which Le Roux et al. (1988) ascribe to the rainfall gradient. Density and biomass of the various mopane associations seem to be strongly influenced by factors such as frost, fire, drought and outbreaks of larvae of the mopane moth Gonimbrasia bellina (pers. obs.).

The only region regarded as over-utilized by ungulates in the 1950's when 50-60 elephants occurred in Etosha National Park, were the open plains on the fringe of the Etosha Pan (Schoeman, in Le Roux 1980). Bigalke (1961) in providing the first general ecological account of the Etosha N.P. made no mention of elephants or elephant-induced changes in the vegetation. Jaeger (1926) and earlier accounts of aspects of the vegetation by Schinz and other 19th century travellers (in Le Roux 1980), confirm that shrub mopane occurred throughout the west of the park, when no elephants were present. Giess (1970) furthermore attributed the height of mopane to the incidence of frosts. Nordenstam

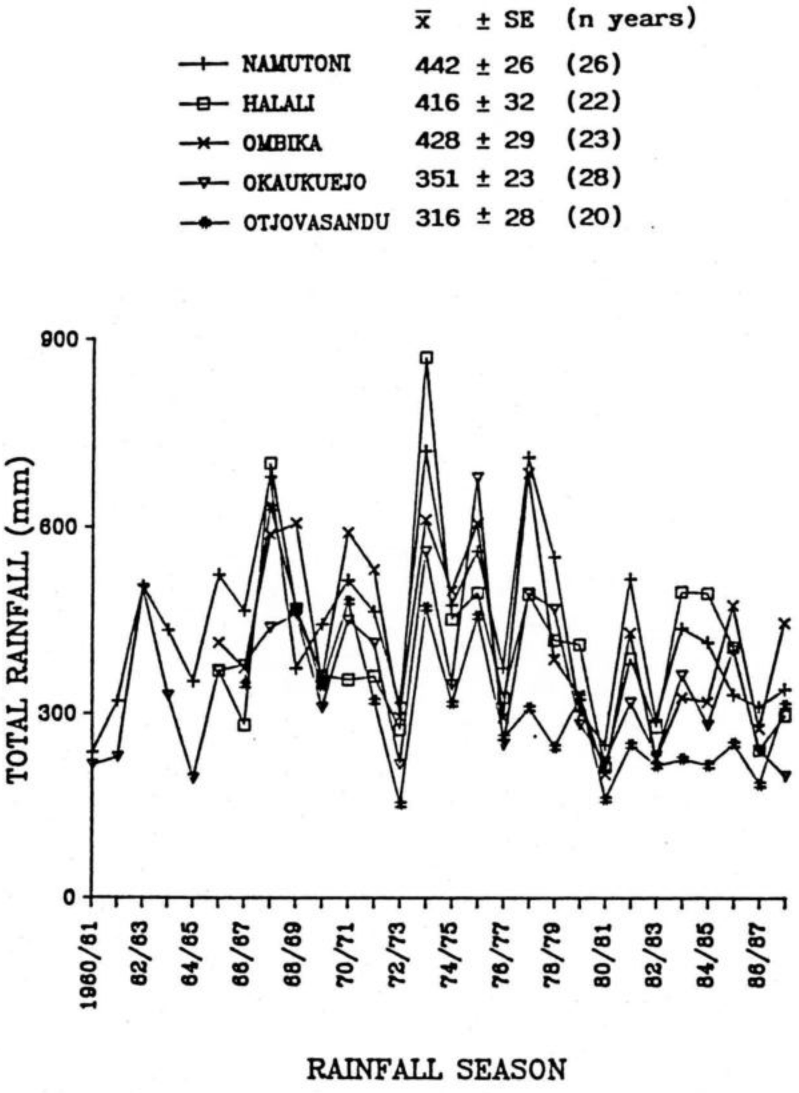


Figure 1.3 Total rainfall per season (mm) and long term mean (± SE) rainfall per season in Etosha National Park measured at five stations on an east-west gradient.

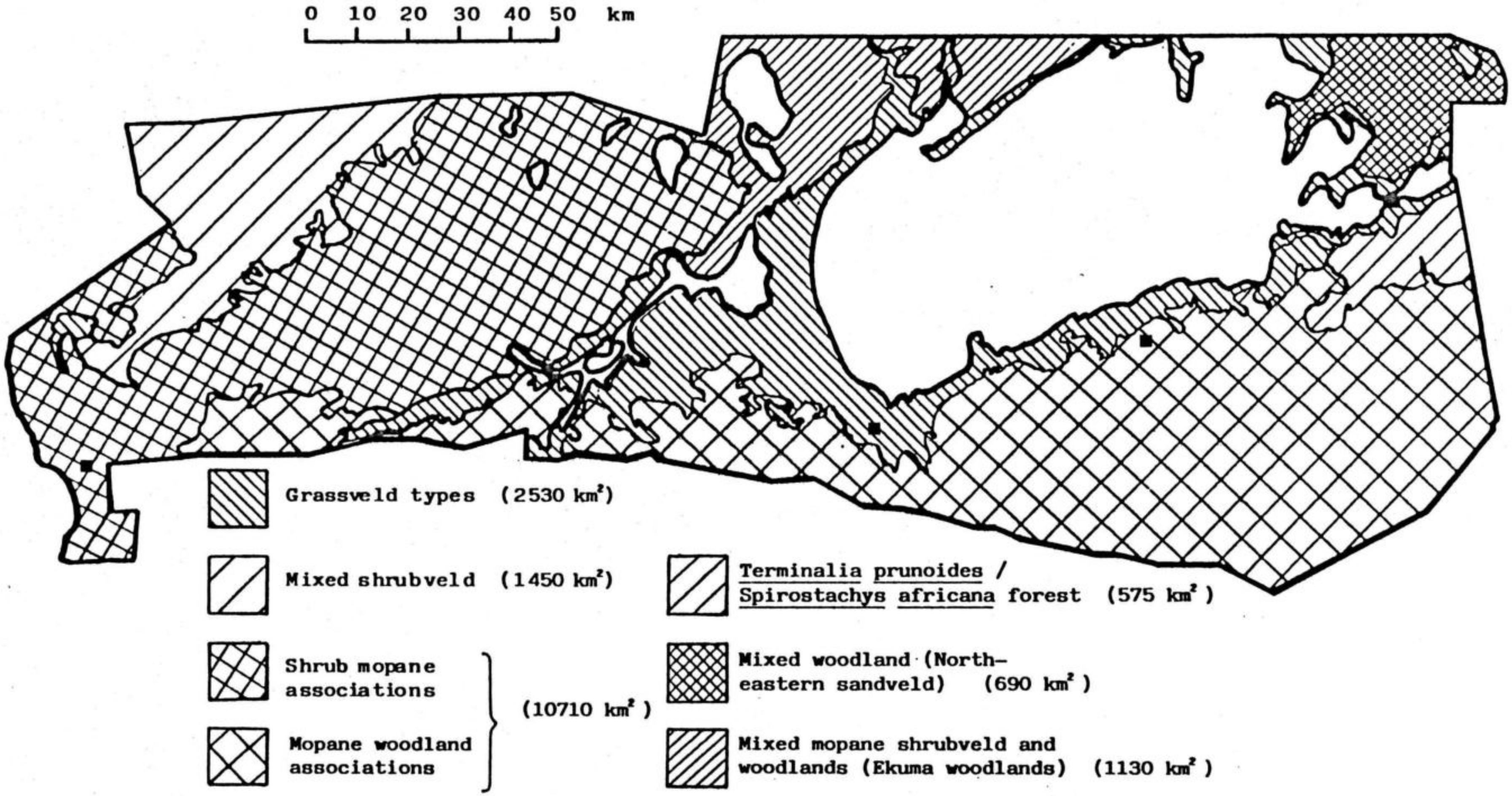


Figure 1.4 Broad vegetation divisions in Etosha National Park, as based on Le Roux et al. (1988). Approximate extent of each zone is given in parenthesis.

(1970) and Joubert (1971a) mentioned the noticeable effects of elephant utilization on woody vegetation, particularly around some watering points. Le Roux (1979, 1980) in the first detailed account of the vegetation of Etosha N.P. attributed the "poor" condition of the plains to overgrazing, absence of fire and the effect of artificial watering points, yet referring only to the plains ungulates. De Villiers (1981) in the first study on elephants in Etosha N.P., found increasing signs of elephant damage throughout the park from 1976-1979. Mostly mopane trees were pushed over, but few trees died as the result. Localized tree damage was ascribed to periodic "over-concentration" of elephants in an area, and the elephant population was said to be below the carrying capacity of the park. De Villiers (1981) suggested that a drought would lead to over-utilization of the vegetation by elephants, but no signs of excessive utilization of any height class of mopane could be found in the area of the park with the highest concentration of elephants throughout the drought (Nott 1986).

The only evidence of serious modifications in the woody vegetation by elephants in the period 1983-1988 was found around springs and boreholes throughout the park, in most cases restricted to a radius of about 2 km around each watering point (Nott 1986). Other far more significant changes in the vegetation were caused by fire, frost and drought, notably the change from a perennial to an annual grass cover in the extreme west of the park, and large-scale mortalities of several Acacia species (pers. obs.).

In the colonization sequence of elephants in Etosha N.P., something intervened before modifications of the vegetation by elephants could spread beyond the immediate vicinity of watering points. The elephant population in Etosha N.P. is thus probably well below the ecological carrying capacity as determined by vegetation only, if subjectively indicated by the appearance of the woody stratum in the park.

A complete survey of the mammals of Etosha N.P. has not been done, but regular censuses and distribution surveys of the larger herbivores have been undertaken since the late 1960's. Long-term declines in Burchell's zebra (Equus burchelli, following Meester, Rautenbach, Dippenaar & Baker 1986) and blue wildebeest (Connochaetes taurinus) have been ascribed to the effects of fencing, anthrax and predation, as summarized in Berry (1982a, b). Current studies are in progress on aspects of the ecology of black rhinoceros (Diceros bicornis), giraffe (Giraffa camelopardalis), black-faced impala (Aepyceros melampus petersi), lion (Panthera leo), kudu (Tragelaphus strepciseros), springbok (Antidorcas marsupialis), gemsbok (Oryx gazella) following earlier studies on black rhinoceros (Joubert 1971b) and blue wildebeest (Berry 1980).

HISTORY OF ELEPHANTS IN ETOSHA NATIONAL PARK

Elephants occurred throughout SWA/Namibia north of the 20th parallel before the turn of the century, based on accounts of the 19th century travellers, but limited surface water and extensive hunting for ivory accounted for the impression that elephants were regionally uncommon (De Villiers & Kok 1984, Viljoen 1987). By 1900 elephants were already regarded as very scarce south of the Kunene River in Ovambo (Moeller 1899, Bryden 1903), and the last herd of elephants within the confines of the present day Etosha N.P. was exterminated in 1881 (Fischer 1914). Elephants were regarded as absent from Etosha N.P. in a game survey by the game warden of the Namutoni Game Reserve in 1926, and Shortridge (1934) only encountered elephants in the Kaokoveld (600-1000) and reported small numbers in isolated parts of the Kavango, Outjo district and Ovambo.

Apart from occasional vagrants visiting springs in the south (Gobaub and Ombika) (Anon. 1946, Heck 1955), and west of the dolomite range near Otjovasandu, elephants were apparently absent from the park, and rare in Ovambo (Bigalke 1958) for about 70 years. The now invalid <u>Loxodonta</u> <u>africana</u> <u>zukowski</u> Strand 1924, or the Kaokoveld elephant, was described from Qoabendus (Khoabendus) about 5 km from Otjovasandu and inside the present Etosha N.P. (Shortridge 1934). Several bulls and small herds first recolonized the Halali and Namutoni areas in the 1950's, presumably from the Gobaub area, and subsequently also the rest of the park. During the 1960's, boreholes were developed in the dry west of the park, specifically to attract elephants into the park and solve elephant-farming conflicts in the Kamanjab and Outjo districts. This plan was successful, but almost two hundred elephants have been shot on border farms since the 1970's.

Elephants also recolonized the park from the east, possibly from the Mangetti region and Kavango, but it is not possible to identify discrete sub-populations in Etosha N.P. today, and recorded movements indicate the mixing of elephants from eastern and western origins (De Villiers 1981). The sub-populations defined in De Villiers (1981) were arbitrarily demarcated. Little has been recorded about the early years of recolonization, but elephants were less sedentary than at present, and only occurred in the park during the wet season. Tinley (1971) reported that large numbers of elephant moved between the Kaokoveld and Etosha N.P., but Owen-Smith (1972) found no evidence of annual migrations between the two regions. Elephants nevertheless move freely between Etosha N.P. and eastern Kaokoveld (Viljoen 1980, 1982a, 1987). Dispersal during the rainy season occurred towards the north-east, north, and west, much the same as at present (Bigalke 1964, De Villiers 1981). The number of elephants remaining in the park during the wet season, however, gradually increased from year to year. Estimates of the number of elephants in Etosha N.P. based on aerial surveys indicate that the population present during the dry season increased from about 500 in 1967 to an estimated maximum of 2800 elephants in 1983 (further detail in Chapter 2). The number of elephants present in the park during the wet season increased from 480 in 1973 to 1880 in 1979. In 30 years, the occupation of Etosha N.P. by elephants therefore changed from a small number of vagrants present during the wet season to a residential population numbering up to 1900, and a further 900 elephants present in the park during the dry season only.

Elephants can still move freely between Etosha N.P., Ovambo, the Kaokoveld (a bioclimatic region comprising Kaokoland and Damaraland) and parts of Kavango (pers. obs.). The elephant population in Etosha N.P. is therefore best regarded as part of a larger population occurring throughout north-western SWA/Namibia, hereafter referred to as the regional population. The distribution of this regional population is not continuous and particularly the eastern and western limits are still uncertain. Only one group of elephants in north-western SWA/Namibia appear to be sufficiently isolated from the rest to warrant sub-population status, namely the "western population" of Viljoen (1980, 1982a, 1987) occurring west of the 150 mm rainfall isohyet in the northern Namib desert. (The collective term used for elephants present in Etosha N.P. at any given time in this study is the population, an arbitrary delimitation following Caughley (1977a), without implying genetic integrity).

Apart from a general description of the ecology of elephants in Etosha N.P. by De Villiers (1981) and De Villiers & Kok (1984), and brief summaries of distribution and status of elephants in Etosha N.P. by Bigalke (1958) and Joubert & Mostert (1975), only two publications deal specifically with elephants in Etosha N.P. Ebedes (1975) described the immobilization of elephants and Super (1975) conducted optometric examinations on elephants. Unpublished departmental reports on elephants prior to 1981 are summarized in De Villiers (1981), and with the reports from 1981 to 1988, are referred to in the appropriate section of this thesis.

OBJECTIVES OF STUDY

The management of the elephant "problem" in Etosha N.P. during the drought of 1980-1983 was based on the following perceptions:

- elephants (and other herbivores) would accelerate the desertification of western Etosha N.P. by denudation of the ground cover.
- elephants outcompete other species for the dwindling water supplies, which could stress the black rhinoceros and roan antelope (Hippotragus equinus) populations in particular.
- elephants outcompete other species for food, presumably the other bulk removers such as Burchell's zebra and black rhinoceros.

After the first temporary relief in the drought in 1984, no evidence for these effects could be found, and the resilience of the system was amply demonstrated by the rate of recovery of the vegetation in response to rain (pers. obs.). Furthermore, it has appeared since that:

- denudation of the mostly annual grass stratum in the sandy soils of western Etosha N.P. was an inevitable outcome of the drought and that some other bulk removers such as termites, Hartmann's (Equus zebra hartmannae) and Burchell's zebras were responsible along with elephants.
- elephants dominate water supplies, potentially to the detriment of other species, although not a single mortality of any large herbivore species through lack of water was recorded inside Etosha N.P. during the drought. The water provisioning facilities in Etosha N.P. are currently being extended, which will eliminate this potential threat in future.
- other than interference competition at watering points, elephants probably do not compete directly with other species, which all probably benefit from elephant feeding activities at current levels. During the drought springbok, gemsbok and the two zebra species fed almost exclusively on the principal food of elephants, namely shrub mopane (pers.obs.). Elephants could conceivably benefit other herbivores by reducing the height of mopane shrub.

The recovery of the vegetation in 1984 and the absence of regional changes in the tree and shrub strata which could be ascribed to elephant over-abundance, suggested that the elephant population is in relative harmony with the vegetation in Etosha N.P. The subsequent decline in elephant numbers after the drought was therefore interpreted as being independent of carrying capacity considerations and caused by other factors. As the decline was contrary to predictions by local staff, and changes in abundance are difficult to describe in a small population dispersed over such a large area, this study was designed to:

- determine the trend in population size , and
- determine the causes of this trend, including an assessment of the possible explanation of rapid breeding and decline after the carrying capacity had apparently been exceeded.

This should be seen against the wider framework of a long-term project on aspects of the ecology of elephants in Etosha N.P. such as movements and vegetation interactions, in order to establish a management scheme that facilitates the attainment of the objectives set for the park. This study was originally planned to have a complement in a study on present trends in the woody vegetation in the park, with reference to the effect of elephants, fire and provisioning of water on plant species diversity. The latter is still outstanding, but remains a priority, as the present apparently stable elephant-vegetation system might be affected by radical and inescapable socio-political events. The trends in poaching of black rhinoceros in Etosha N.P. may well force the erection of elephant-proof fencing on the northern boundary, with predictable consequences. This thesis can nevertheless be condensed to a single question

- what is, and which factors determine, the rate of increase of the elephant population?

The description of the dynamics of a population can be found in a single equation. The quality of information used in the final synthesis, is however of absolute significance, and directly correlated with the accuracy of conclusions and predictions.

This report therefore consists of two chapters examining the methodology of two crucial assessments in the demography of elephant populations, namely the estimation of population size and trend (Chapter 2), and age of individuals and age structure of the population (Chapter 3). Two subsequent chapters deal with evidence collected which describe additions and subtractions to population size through reproduction (Chapter 4) and mortalities (Chapter 5). The final chapter (Chapter 6) is an attempt to synthesize the preceding work into a unified and interactive format culminating in the modelling of population response to specific changes in key features.

Implications for management of the Etosha N.P. elephant population based on this study are presented in Appendix 5.

CHAPTER 2 POPULATION SIZE AND CENSUS METHODS

INTRODUCTION

The general perception of elephant numbers in Etosha N.P. prior to this study was based on the study by De Villiers (1981, De Villiers & Kok 1984), aerial census estimates and unpublished departmental reports by Ebedes (1970), Joubert (1973), De Villiers (1978, 1979), Berry (1980, 1982a, 1984a, b) and others. Three important findings applicable to the period 1970-1983 were that:

- Elephants were not evenly distributed throughout the park and equally abundant throughout the year. Concentrations of elephants occurred during the dry season around the perennial watering points along the 19th latitude area west of the Etosha Pan (Fig. 2.1) and the southern fringe of the Etosha Pan. From December each year, elephants dispersed away from the dry season concentration areas to the northern and southern parts of the park, depending on where it had rained first and the availability of ephemeral pools of water. Most elephants apparently dispersed northwards, even as far as the southern part of Ovambo, and the eastern part of Kaokoland (Viljoen 1982a, 1987).

- More elephants occurred in Etosha N.P. during the dry season than during the wet season. From the high incidence of fence crossings in November-December and again in May-June, it appeared as if the movements of elephants out of the park early in the rainy season, and back into the park at the start of the dry season, accounted for the observed difference in seasonal elephant densities.

- The number of elephants present in the park in both the wet and dry seasons increased from the 1950's to 1983. Census estimates of population size were available from 1973, but were too infrequently done and based on different methods of censusing to allow inferences from the data other than a general population increase over this period.

This increase was ascribed to the breeding rate (Berry & Nott 1983), although it was known that elephants in Etosha N.P. were not confined to the park. Some 2000 Hartmann's zebra moved into the park during 1980-1982 (Berry 1982a), but a similar influx of elephants accounting for the sudden increase in numbers from 1979 to 1983 was not considered possible. If large numbers of elephants had moved into the park during the drought, they would have occurred somewhere outside the park during the dry seasons of the previous few years. Less than 500 elephants were known to occur in the Kaokoveld by 1979 (Viljoen 1980, 1982b, 1987) and could not have been the source of the approximately 1500 elephants which were added to the Etosha N.P. population from 1979 to 1983. Estimates of elephant numbers in 1978 and 1983 respectively were 1300 and 2390-2800 (De Villiers 1978, Berry & Nott 1983).

The maximum estimate of the number of elephants elsewhere in SWA/Namibia in the late 1970's was 900, in the immediate vicinity of the Kunene River (Ruacana Falls area) in Ovambo, and the Okavango, Cuando, Zambezi, Linyanti and Chobe Rivers in Kavango and Caprivi (De Villiers 1981, De Villiers & Kok 1984). Virtually no surface water accessible to game occur away from these rivers in Kavango and Ovambo.

The highest density of the human population in SWA/Namibia is found along the northern border of Ovambo and the Okavango River in Kavango (Van der Merwe 1983), in some of the most suitable parts of the region for elephants. The relict populations in Ovambo and Kavango could not have accounted for the increment of 1500 in the number of elephants in Etosha N.P. during the drought. No information was available on the number of elephants in war-torn southern Angola, or the movements of elephants across the Caprivi to and from Zambia and Botswana.

The failure to account for the increase in numbers of elephants in Etosha N.P. from 1979 to 1983 by comparing estimates from different regions is probably the result of inaccurate estimates of the number of elephants outside the park. Only the estimates from the Kaokoveld were based on aerial censuses (Viljoen 1980, 1982b). Access to large parts of Kaokoveld, Ovambo, Kavango and Caprivi was highly restricted due to the war against insurgents. It is also probable that the increase in the number of elephants in Etosha N.P. was exaggerated as the result of increasingly more efficient counting techniques used in the park.

Elephants are one of the least problematic species to count, owing to their size, and only Eltringham (1972) attempted to determine the confidence that can be placed in aerial censuses of elephants. Caughley (1974), however, shows that apparently satisfactory results can be interpreted quite differently, and identified major counting biases in Eltringham's (1972) data.

The almost continuous increase in the number of elephants counted in Etosha N.P. from the first survey in 1967 until 1983, was the prime motivation for this study. I have undertaken six aerial censuses specifically designed to count elephants since 1983, each yielding consistently lower estimates of elephant numbers than other recent censuses in 1982 and 1983. It was therefore necessary to determine the validity of the methods used in this study, as the same methods employed in earlier counts could not be used for logistical reasons. None of the aerial censuses in Etosha N.P. prior to this study were exactly similar, and no standard method has been adopted yet.

The first census covering the entire Etosha N.P. was done in 1982 (Berry 1982a), but this census was so costly that it could only be repeated at two or three year intervals. Annual estimates and preferably seasonal estimates of population size were required from 1983 onwards, as the elephant population was regarded as over-abundant and a policy of population control was adopted. A quick, cheap but nevertheless reliable method of counting elephants therefore had to be found.

It is impossible to adjust previous census results for variation in the main sources of bias, such as transect width, altitude, time of day and area coverage, due to a lack of information on the methods followed in each census. The trend in elephant population growth described by censuses prior to this study therefore has to be accepted. The aim of this chapter is to test the validity of my own censuses and therefore the description of a general decline in elephant population size after 1983, which has important management implications. Rates of increase and decrease in population size are discussed in the final chapter.

METHODS

Aerial censuses in Etosha N.P. prior to this study were not standardized with regard to area covered, aircraft used, timing, orientation of transects and counting blocks, due to mostly logistical problems. Censuses had to be done whenever an aircraft and funds were available simultaneously, and were as intensive as available time and funds allowed. Berry (1982a) proposed a standard census design, including the systematic coverage of the entire park using a helicopter and fixed-wing aircraft. Three such total counts have been done, in 1982, 1984 and 1987. Even these three censuses could not be done in exactly the same way, as for example, different aircraft were used each time and were more or less suitable for census work than others (Berry 1982a, 1984b, Lindeque & Lindeque 1987). These censuses cost approximately R63 600, R74 300 and R53 500 respectively. The last one was cheaper due to the fact that the Directorate of Nature Conservation had by then obtained its own fixed-wing aircraft and did not have to hire one.

A twin-seater fixed-wing aircraft (Piper Supercub) was available for this study and was used to obtain more frequent estimates of elephant numbers in Etosha N.P. Six censuses, referred to as the elephant censuses, were done at approximately four-month intervals, each costing approximately R8 000 for 90 hours of flying over 15 days. The duration of censuses was limited to 15 days to prevent counting any group more than once, due to local movements. The series of elephant censuses at four-month intervals was scheduled to continue until 1987, but could not be maintained after December 1985 as no pilot or aircraft was available. In the absence of an aircraft, rough estimates of elephant numbers were obtained from counts at waterholes, spoor and reports from rangers.

The park was divided in two broad strata of shrubland and woodland, based on the structure and density of woody vegetation. Transect widths used were 2 km and 4 km in woodland and shrubland respectively, double the widths used in previous censuses. Transect widths were demarcated by strut markers and streamers, as described by Pennycuick & Western (1972). Woodland and shrubland were flown over at an altitude of 90 m and 120 m respectively, conforming to previous censuses in Etosha N.P. and as used in East Africa (Norton-Griffiths 1978). Altitude was measured at the start of each transect, using a calibrated barometric aircraft altimeter and Pennycuick's (1973) shadowmeter.

Elephants not in line with the predetermined flight path, but within the limits of the transect, were counted by flying towards them and circling overhead for as long as necessary. Transect lines were interrupted when such a herd was perpendicular to the transect line, and after the pilot had located a ground feature to relocate the point where the transect was deviated from. This approach ensured that all elephants sighted were counted accurately. Total group sizes, numbers of adult bulls, adult cows, and calves less than approximately two years old were recorded, and the position of each herd plotted on a 1:100 000 map. Each breeding herd was photographed vertically at the designated transect altitude.

Censuses in December 1983 and May and December 1984 were undertaken in blocks demarcated by distinct ground features (Fig. 2.1 A). Transects were flown across the long axis of a block, parallel to a conveniently staight side. In order to investigate census bias and a sample instead of a total type census, the flight pattern was modified in subsequent censuses. A double set of North-South transects were flown throughout the park (Fig. 2.1 B) in three elephant censuses in 1985.

The last census done in September 1987 was part of the regular monitoring program of all large mammals in Etosha N.P., and known concentration areas of plains ungulates were counted by helicopter (Bell Jet Ranger) and using 1km transect widths as indicated in Fig. 2.1 C. The rest of the park was counted by fixed-wing aircraft (Maule Lunar Rocket), using the same altitude and transect orientation as in the elephant censuses in 1985, and transect widths as shown in Fig. 2.1 C.

A series of experimental transects of variable width and altitude were used in the May and August 1985 elephant censuses to determine the effect of these variables on apparent elephant density.

RESULTS AND DISCUSSION

Elephant numbers in Etosha National Park.

Table 2.1 presents estimates of the number of elephants in Etosha N.P. from aerial game distribution surveys by Tinley (1966), Ebedes (1970) and Joubert (1973). These surveys were not intended as censuses and did not cover the entire distribution area of elephants in the park. The first total aerial census of elephants and other large mammals in September 1973 (Joubert 1973) when 1293 elephants were counted, can be regarded as the first accurate estimate of population size. From 1973 the number of elephants in Etosha N.P. in the dry season increased from about 1300 to 2800 in 1983 (Table 2.2). The next scheduled total census after the start of the present study would have been done in either September 1984 or 1985, but more frequent estimates of population size were

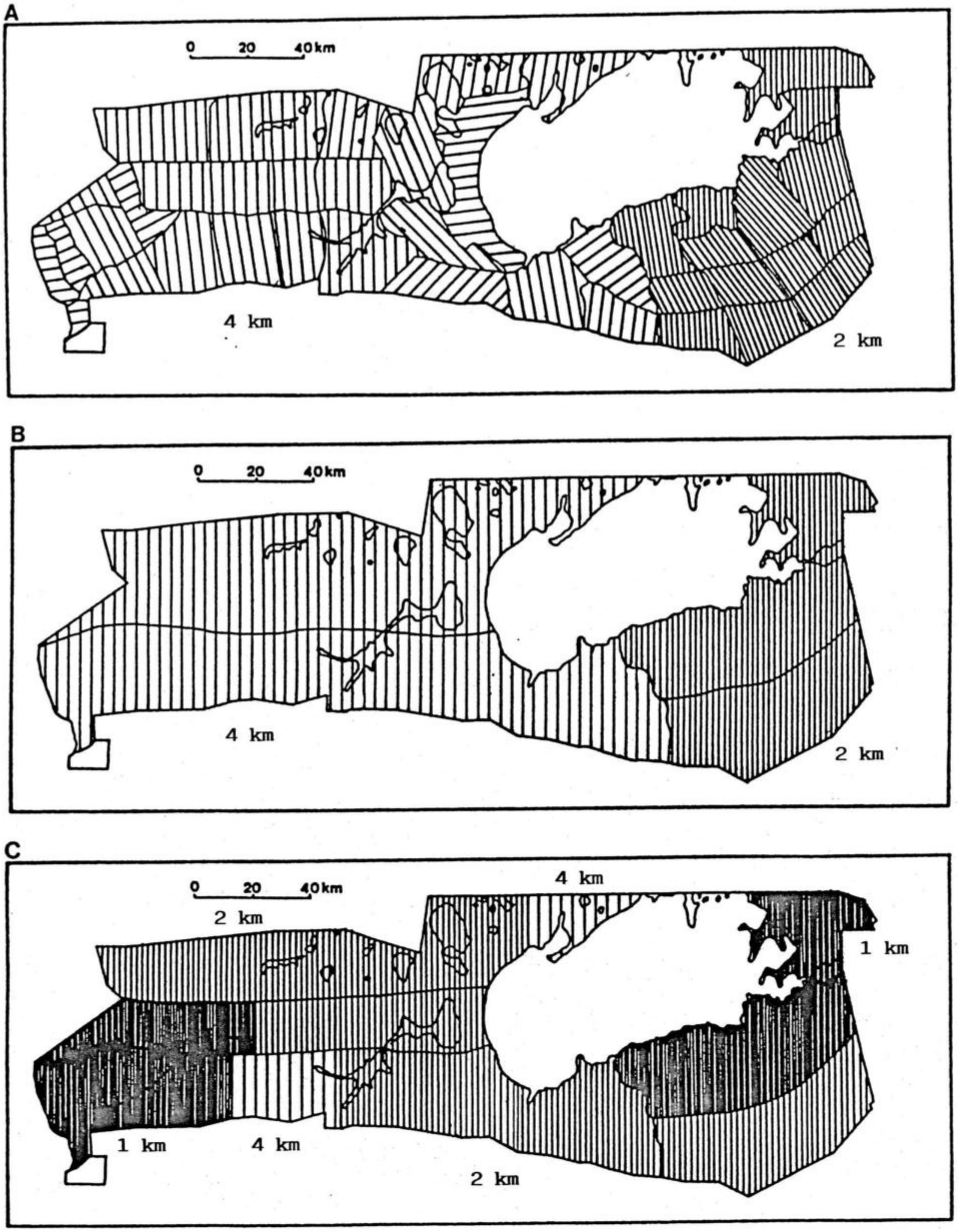


Figure 2.1 Census blocks in Etosha National Park illustrating the approximate orientation and number of transects in aerial censuses of elephants done in 1983 and 1984 in A; a double set of North-South transects used in censuses in 1985 in B; and transects used in the 1987 census in C. (Transect widths are given in km; 1 km transects were flown by helicopter, all others by fixed-wing aircraft).

Table 2.1 Estimates of the number of elephants in Etosha National Park from aerial game distribution surveys of known concentration areas. Data from Tinley (1966), Ebedes (1970) and Joubert (1973).

YEAR	MONTH	AREA OF PARK COVERED	NO. OF ELEPHANTS COUNTED
1966	March	Central, East	1
1967	March	Central	123
1968	September	8km radius around all waterholes	301
1969	April	Concentrations in Central, East	64
1970	February	Central, East	494
1970	November	Central	116
1971	February	Central	124
1972	March	Central	447
1972	April	Central	547
1972	June	Central	433
1972	July	Central, East, West	419
1972	September	Central, East, West	863
1972	October	Central, East, West	686
1973	February	Central, East, West	292
1973	March	Central, East, West	477
1973	April	Central, East	81
1973	June	Central, West	715

Table 2.2 Estimates of the number of elephants in Etosha National Park from aerial censuses using helicopters (H) in concentration areas and fixed-wing aircraft (FW) in the remainder, from 1973 to 1983.

YEAR	MONTH	AREA OF PARK COVERED	REFERENCE	NO. OF ELEPHANTS COUNTED
1973	Sept	Conc. areas H, FW rest	Joubert (1973)	1293
1974	Feb	Conc. areas H, FW rest	Berry & Hofmeyr (1974)	904
	July	Conc. areas H, FW rest	Berry & Hofmeyr (1974)	835
1976	July	Conc. areas H, FW rest	Berry, Hofmeyr & De Villiers (1976)	1170
1977	Mar	Conc. areas H, FW rest	Berry (1977)	836
1978	Mar	Conc. areas H, FW rest	De Villiers (1978)	826
	Sept	Conc. areas H, FW rest	De Villiers (1978)	1298
1979	Mar	40% Random block sample FW	De Villiers (1979)	1876
1982	July	Total count H, FW	Berry (1982a)	2202
1983	May	West only FW	Berry & Nott (1983)	2389 (2800) *

* 1819 elephants counted in west, + 570 counted in 3 days in random flights over rest of park, 2800 estimated for total area of park.

required to determine seasonal fluctuations in the number of elephants in the park in view of the policy of population control adopted in 1983.

Aerial censuses at four-month-intervals were used to determine the number of elephants in Etosha N.P. during the dry season, the number remaining in the park after dispersal in the wet season, and population size at the end of the rainy season prior to the annual return of elephants to the dry season concentration areas. Table 2.3 presents estimates of the number of elephants in Etosha N.P. or parts thereof after the start of this study, including the routine multi-species aerial censuses in September 1984 and August 1987, and estimates based on ground observations when an aircraft was not available in 1986 and 1987.

Figure 2.2 A illustrates an increase in the number of elephants counted in January-May, June-September and October-December since 1973. The same trend is illustrated in Fig. 2.2 B & C when estimates made in the wet season and dry season are graphed separately.

Precision and accuracy of elephant census estimates.

Bias in estimates of animal numbers can be divided into errors resulting from imprecise or from inaccurate counts. Precision is a measure of the variation in the sources of error, and not a reflection on the true numbers of objects to be counted. Accuracy is a measure of how close the census estimate is to the true but unknown total population size.

Precision

Table 2.4 presents estimates of precision in counting elephants in Etosha N.P. using the standard counting methods as described, during the elephant censuses of the present study, as the percentage change in the number of groups and individuals in two counts of the same census block. Six arbitrary census blocks totalling 2600 km^2 were counted twice in quick succession. This experiment was done in December 1984 in the woodland area at a time when most trees had produced new leaves, and represent the worst conditions for visibility during the year anywhere in Etosha N.P.

The number of groups varied between the first and second counts, with more groups

Table 2.3 Estimates of the number of elephants in Etosha National Park since 1983 (H= helicopter, FW = fixed-wing aircraft). Estimates in parenthesis are based on ground surveys.

YEAR	MONTH	AREA OF PARK COVERED	REFERENCE	NO. OF ELEPHANTS COUNTED
1983	Dec.	Total count FW	This study	1437
1984	May	Total count FW (+ H in extreme west)	This study	1158
1984	Sept.	Total count H, FW	Berry 1984b	2464
1984	Dec.	Total count FW	This study	2081
1985	May	Total count FW	This study	1244
1985	Aug.-Sept.	Total count FW	This study	1186
1985	Dec.	40% stratified random transect sample count	This study	702 ± 18
1986	May	West only H	Scheepers 1986	(650) *
1986	Aug.	Ground survey	This study	(1400)
1986	Dec.	Ground survey	This study	(1200)
1987	May	Ground survey	This study	(1500)
1987	Aug.	Total count H, FW	This study	2021
1987	Dec.	Ground survey	This study	(1100)

* 196 elephants counted by H, ground estimate for rest of park.

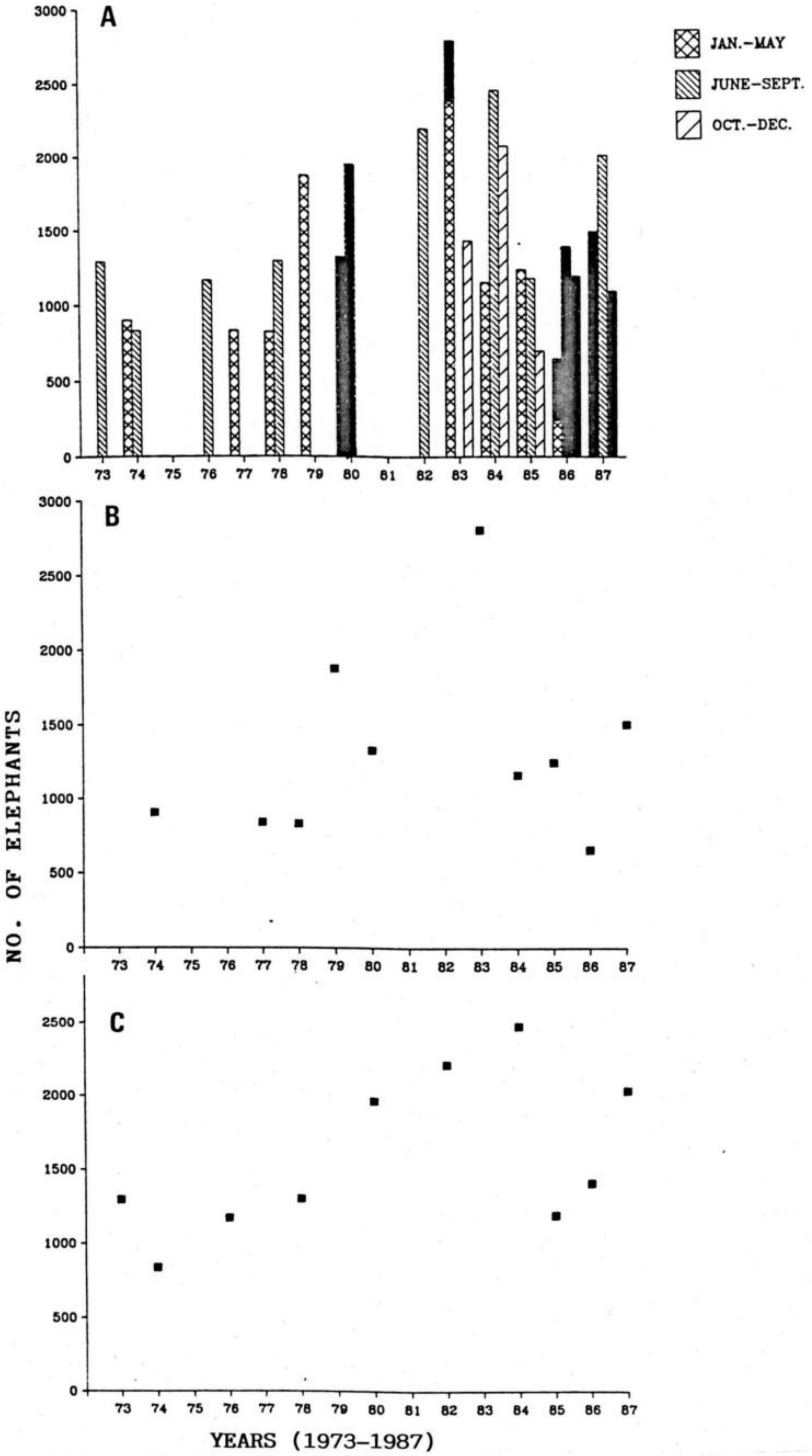


Figure 2.2 Estimates of elephant abundance in Etosha National Park from 1973-1987 based on aerial censuses and ground surveys (black columns) in A, and dry and wet season estimates separately in B and C respectively, including estimates for 1980 in De Villiers (1981).

Table 2.4 Mean (± Standard Error) percentage change in the number of groups of elephants and the number of individuals in first and second counts in six census blocks in Etosha National Park.

Number of groups in first and second counts		Time lapse between counts (min)	% change
12	20	30	+ 66.7
7	9	25	+ 28.6
17	22	45	+ 29.4
9	12	60	+ 33.3
2	2	15	0
5	6	20	+ 20.0

Number of elephants in first and second counts		Time lapse between counts (min)	% change
139	145	30	+ 4.1
89	94	25	+ 5.6
121	118	45	- 2.5
93	90	60	+ 3.3
17	17	15	0
9	9	20	0

recorded in second than in first counts. The total number of elephants in each block remained similar, however, indicating that disturbance by the aircraft caused herds to split up into smaller groups. It thus seems that estimates of elephant numbers can be very precise, as long as methods are rigidly standardized.

Caughley (1974) used the difference in the number of groups of elephants in a series of counts of elephants in Eltringham (1972) to estimate the true population size using a binomial model. The estimate thus obtained was larger than the total number of elephants counted in any one survey done by Eltringham (1972), which Caughley (1974) ascribed to counting bias. This may be unfounded, if elephants elsewhere react to aircraft in a similar way as in Etosha N.P.

Accuracy

The accuracy of estimates of population size is dependent on two types of errors. Some animals will never be seen, and some of those seen will not be counted accurately. Photographing herds, and the use of aircraft with several observers, are used to limit counting errors. In the elephant censuses in Etosha N.P. accurate counts of all groups seen were obtained by flying towards each herd and counting at close range. Counts of herds on the outer edge of the counting strip were up to 25% higher than the real number recorded at close range, as shown by trial counts. Small calves are underestimated when counted from far away, but the number of adults is overestimated, the same type of error as in the classification of elephants into age groups from the ground (Chapter 3).

The number of groups that are not spotted at all due to inadequate time available for searching the entire width of the transect, or the distance between animal and observer, is possibly a more serious source of error. The number of groups that are missed can be minimized by flying lower, slower and narrower transects, using experienced observers and aircraft offering good visibility. Counting is also limited to early morning and late afternoon. These options result in an increase in the cost and duration of a census, which may not be acceptable. Norton-Griffiths (1978) advocates the opposite approach of quantifying the bias associated with an aerial census and correcting estimates of population size accordingly.

A model describing some major sources of variance in an aerial census was developed by Caughley (1974) and tested by Caughley, Sinclair & Scott-Kemmis (1976) and Bayliss &

Giles (1985). This model, with minor modifications, was applied to a series of transects in the August 1985 elephant census. Of the dozens of variables encountered during a census, transect width, altitude and airspeed are regarded as major sources of error. Two of these, namely transect width and altitude were investigated in this analysis, while airspeed, if not always constant, could not be measured. Airspeed was nevertheless always lower than or within the limits recommended for East Africa (100-150 km/h) (Norton-Griffiths 1978).

An area with a relatively high density of elephants was chosen, and six treatment combinations of strip width (1km, 2km, 4km) and altitude (100m, 130m) were randomly allocated to a series of North-South transects covering the whole area (Table 2.5). The number of elephants counted was expressed as a density ($Y=N/km^2$). Areas of transects were calculated using designated strip width and lengths measured from a 1:100 000 map. Partial regressions of apparent density (Y) on strip width (X_1) and altitude (X_2) were calculated, using a polynomial multivariate regression method following Caughley (1974) and Steel & Torrie (1980). The analysis of variance in apparent elephant density due to the individual and combined effects of changes in transect width and altitude is presented in Table 2.6. Elephant density was not significantly related to changes in both altitude or transect width, within the limits of those variables tested.

The perpendicular distance between objects to be counted and the transect line followed by the observer has also been used to estimate accuracy of counts by Anderson & Posphala (1970), Pollock (1978) and Burnham, Anderson & Laake (1980, 1985). It was not possible to measure distances accurately from the air in the present study, but distances could be estimated using streamers normally used for demarcating transect widths. Additional streamers were used in the August 1985 elephant census, indicating distances on either side of the aircraft of 500 m, 1000 m, 1500 m and 2000 m at altitudes of 100 m and 130 m. A further category was used, namely greater than 2000 m classed as 2500 m.

Figure 2.3 illustrates the number of groups and individuals counted at increasing distances away from the aircraft in 980 km^2 of the woodland stratum and 1460 km^2 of the shrubland stratum in the August 1985 elephant census. There was no significant decline in the number of groups or individuals over the distances used in elephant censuses, namely 1000 m in woodlands (1000 m on each side of the transect line), and 2000 m in shrubland.

Table 2.5 Random sequence of treatment combinations of transect width and altitude used in an experimental count of elephants in Etosha National Park to estimate bias.

TOTAL ELEPHANTS COUNTED	TRANSECT AREA (km^2)	APPARENT ELEPHANT DENSITY NO./km^2 (Y)	DESIGNATED TRANSECT WIDTH (X_1) km	DESIGNATED ALTITUDE (X_2) m
6	9	0.70	2	91
3	6	0.48	1	122
6	23	0.26	2	122
12	50	0.24	4	122
0	40	0.00	2	91
15	100	0.15	4	91
0	100	0.00	4	91
4	26	0.16	1	91
18	27	0.68	1	91
56	120	0.47	4	91
46	32	1.44	1	91
41	64	0.64	2	122
22	49	0.45	2	91
50	78	0.64	4	122
5	64	0.08	4	122
284	788			

TOTALS

Table 2.6 Summary of analysis of variance in apparent elephant density (Y) in the experimental census of elephants in Etosha National Park.

SOURCE OF VARIANCE	SS	df	MS	F
Main effect:				
Transect width X_1	0.382	1	0.382	2.913 NS *
Altitude X_2	0.012	1	0.012	0.092 NS
Interaction:				
$Y/X_1;X_2$	0.370	1	0.370	2.822 NS
$Y/X_2;X_1$	0.001	1	0.001	0.001 NS
Residual	1.572	12	0.131	
TOTAL	1.953	14		

* Not Significant, F < p 0.05

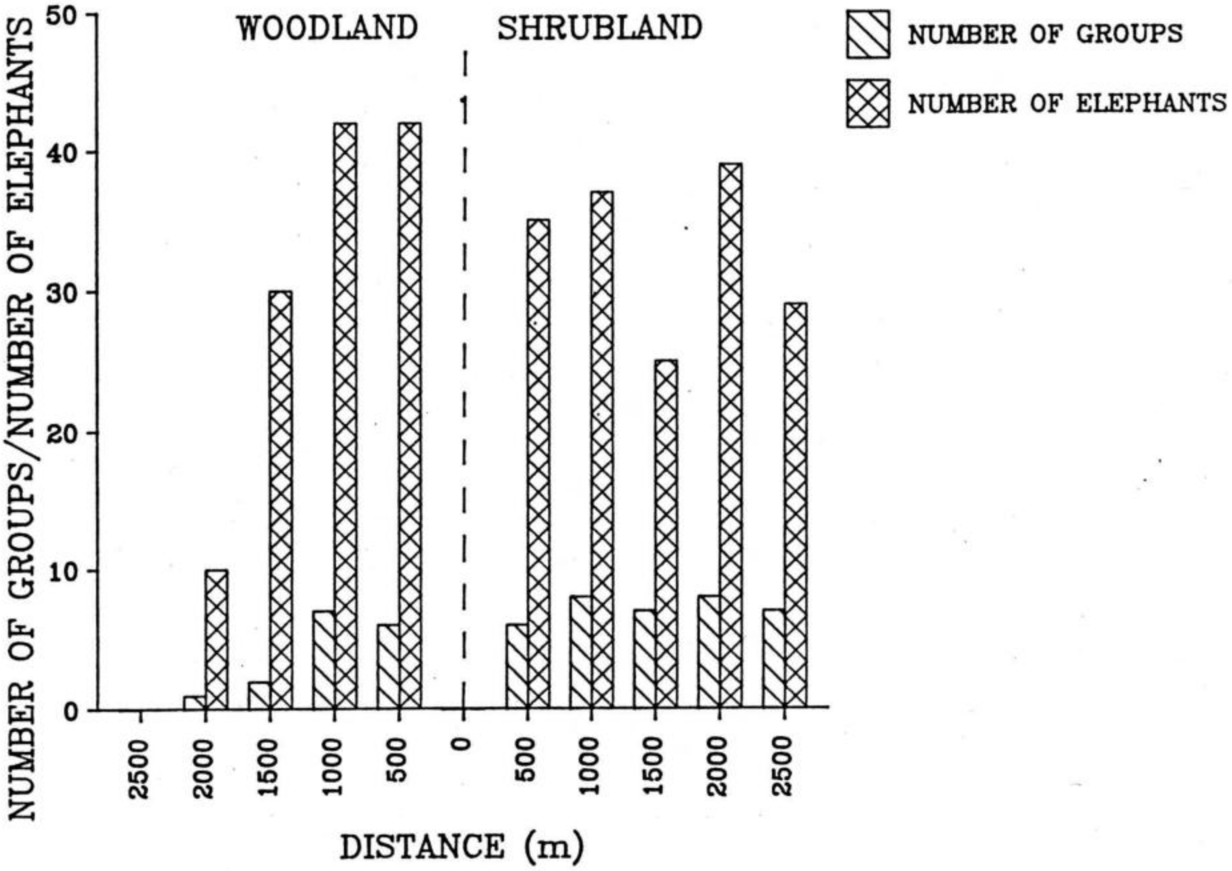


Figure 2.3 The number of groups and the number of elephants counted at increasing distance from the aircraft in the woodland and shrubland strata in a census experiment in Etosha National Park.

The number of known individuals in an area has been used to estimate bias in aerial surveys (Rice & Harder 1977, Gasaway, Dubois & Harbo 1985, Packard, Summers & Barnes 1985, Crete, Rivest, Jolicoeur, Brassard & Messier 1986). This is done by radio-telemetry or the use of conspicuously marked individuals. The proportion of known individuals to unknown ones is, however, an important consideration, and can be determinded for specific sampling intensities following the usual Peterson estimation procedures, as described by Rice & Harder (1977). Where marked or known animals are present, the fraction of those seen during a total count may therefore be used to estimate bias in counting. The one proviso is that marked individuals should not be more visible than unmarked ones, which may complicate the use of this method.

Elephants marked during July 1984 and July 1985 were observed in later censuses, and resightings are presented in Table 2.7. All those marked in July 1984 were present in the park and resighted in September 1984, the latter no doubt aided by the conspicuous painted numbers on their backs. By December 1984, most painted numbers were no longer conspicuous, but this is also the time when herds leave the park, which may account for the one herd missed. By August 1985, all herds had to be scrutinized to detect any faded collars, and the two herds not seen do not necessarily represent counting bias. If only those censuses are used where marked elephants could definitely be recognized, namely September 1984 and August 1985, the fractions not resighted were 8.3% and 7.1% respectively.

Counting animals from photographs taken while doing a census has been used successfully to counteract observer bias (Sinclair 1973, Watson, Parker & Allan 1969, Norton-Griffiths 1973, 1974, 1978). This technique appears to be most useful when counting large aggregations of species like wildebeest or buffalo. Photographs nevertheless introduce a new set of biases different from observer bias. An attempt to count elephants from transparencies taken in censuses in Etosha N.P. resulted in lower counts as compared to direct observations. Calves are not easily seen on photographs, and this method was discontinued. The practice of circling over each herd and observing all members from all angles ensured that herds were counted accurately. Herds were always counted twice, and if different totals were found, two further counts were done. Photography has no use in the one possibly major source of error, namely herds that are not seen at all.

Various methods based on double counts, binomial and parabolic estimates, have been used to estimate the number of animals missed or counting bias and thus to correct census

Table 2.7 Radio-collared elephants resighted during censuses of elephants in Etosha National Park.

		RESIGHTINGS IN CENSUSES			
Marked:	July 1984:	Sept 1984	Dec 1984	May 1985	Aug 1985
Breeding herd members	12	12	11; 1M/A	12	10; 2M/A
Bulls	1	1	1	1 A	1 A
Marked:	July 1985:				
Breeding herd members	3	-	-	-	2; 1A
Bulls	14	-	-	-	11;2A;1M
no. (%) present		13 (100)	13(92.3)	12(92.3)	26 (86.7)
no. (%) seen of those present		13 (100)	12(91.7)	12 (100)	23 (88.5)
no. (% of total) known to be absent		-	-	1 (7.7)	4 (13.3)
no. (%) possibly absent or missed		-	1 (8.3)	-	3 (11.5)

M : missed
A : absent from Etosha

results (Caughley 1974, Magnusson, Caughley & Grigg 1978, Caughley & Goddard 1972). Routledge (1981) and Pollock & Kendall (1987) regard these methods as flawed by invalid assumptions. All methods using mark-resighting or replicate counts are fraught with technical problems, and may be more useful with stationary objects or larger samples. The utility of these methods lies in the ability to detect gross inaccuracy but does not extend to the calculation of the number of individuals missed. It is also possible that estimations of bias are more effective the greater the variance is between surveys or within a multiple sampling method.

The method used to count elephants in this study could not be shown to be less accurate than previous and more intensive methods used in Etosha N.P. By using wider transects, and eventually a standard orientation of transect lines, flying time and costs could be reduced without affecting the quality of estimates of population size. The method used could be useful in future when frequent counts of elephants are required, such as in a harvesting or culling program.

Further reductions in the intensity of surveys can be achieved by doing a sample count instead of a total count. Such a sample count as based on the elephant censuses in this study was developed through simulations, and is presented in Appendix 2. As long as total censuses can be afforded, these should be used as the systematic coverage of the park facilitates the collection of additional information on animal distribution, phenology, distribution of surface water, extent of veld fires and veld condition. There are nevertheless alternative methods for obtaining quick but reliable estimates of elephant numbers at relatively low cost (see Appendix 2).

The decline in elephant abundance in Etosha N.P. after 1983 and the seasonal fluctuations in numbers, as shown by the elephant censuses done in this study, cannot be regarded as artifacts of less intensive census techniques. Highly variable numbers of elephants do occur in Etosha N.P. from season to season and between years. Preliminary findings from a long-term study on elephant movements and distribution in Etosha N.P. and adjacent regions indicate that elephants concentrated around perennial watering points during the dry season and dispersed during the wet season in 1983-1988, as also described by De Villiers & Kok (1984) for the period 1976-1979. This pattern also occurs in Kruger N.P. (Smuts 1974), northern Botswana (Melton 1985), the Zambezi Valley and Hwange N.P. in Zimbabwe (Kerr & Frazer 1975, Williamson 1975, Martin 1983, Taylor 1983), the Luangwa

Valley in Zambia (Caughley & Goddard 1975, Rodgers & Elder 1977), Ruaha N.P. in Tanzania (Norton-Griffiths 1975, Barnes & Douglas-Hamilton 1982), Amboseli N.P. and Tsavo N.P. in Kenya (Laws 1969b, 1981, Leuthold & Sale 1973, Leuthold 1977, Western & Lindsay 1984, Ottichilo 1986a), and Rwenzori N.P. in Uganda (Eltringham 1977).

The availability of water seems to be the prime determinant of elephant movements and distribution in Etosha N.P. Secondary influences appear to be human disturbance (such as culling operations, illegal hunting, harassment and military presence) and the quality of water. These factors, along with the availability of food have been implicated in all studies on elephant distribution and abundance (references as above, and Weir 1972, 1973). Elephants were probably absent from present-day Etosha N.P. for about 70 years (1880-1950, Chapter 1), but occurred all around the park. It seems that the park could not have been a preferred part of elephant distribution range in north-western SWA/Namibia, or recolonization by elephants would perhaps have occurred sooner. A possible explanation may be the quality of water available at the perennial springs and later also the boreholes. Weir (1972, 1973) found that elephant distribution in an environment deficient in soluble minerals was closely correlated with sodium gradients. Almost all water sources in Etosha N.P. contain sodium-rich water (Winter 1985) and elephants compete to drink from eyes and outlets at springs and boreholes rather than the main body of a pool or trough, where salinity is even higher due to evaporative concentration (mean total annual evaporation at Okaukuejo is 3500 cm, or about ten times the average rainfall, Berry 1980). The quality and quantity of water available at each watering point generally decreases during the dry season (Winter 1985) which possibly explains the rapid movements away from perennial watering points at the start of the rainy season. Elephants would likewise have avoided Etosha N.P. as long as more palatable water was available in other areas, as is found in the Outjo and Kamanjab districts and parts of the Kaokoveld (De Villiers 1981, pers. obs.).

Elephants in Etosha N.P. are highly mobile and capable of rapid displacement from one part of their range to another (pers. obs.), similar to elephants in northern Botswana (Melton 1985), Kruger N.P. (Smuts 1974) and Tsavo N.P. (Leuthold 1977). Exceptional daily movements recorded for both bulls and breeding herds in Etosha N.P. include straight line distances of 90-180 km (pers. obs.). Initial dispersal at the start of the rainy season occurred in a synchronized fashion throughout the park in 1984-1987, and within one week most elephants had vacated the dry season concentration areas. Elephants in Etosha N.P. apparently also responded to signs of imminent rain, perhaps thunder or atmospheric changes, as movements started a day or two before it rained (pers. obs.).

The pattern of range contraction and expansion during the dry and wet seasons respectively, as well as the variable spatial distribution of rainfall and consequently surface water, as recorded since 1983, almost certainly account for changes in seasonal and annual abundance of elephants in Etosha N.P. It seems likely that elephants from the Kaokoveld, Ovambo and Kavango moved into the park during the severe drought when surface water outside the park must have been very limited (pers. obs.). The decline in elephant abundance in Etosha N.P. after 1983 and an increase in 1987 could be due to movements of elephants in and out of the park as determined by rainfall in the north-western part of the country.

Harassment by humans and the occupation or domination of the limited perennial watering points for game in the Kaokoveld, Ovambo and Kavango, through the rapidly expanding human and livestock populations, also have forced elephants to occupy Etosha N.P. This compression effect probably operated throughout the 1970's, and is very similar to events in other parts of Africa. Populations of elephants were re-established after absences of several decades in Kruger N.P. (Smuts 1974) and Serengeti N.P. (Lamprey, Glover, Turner & Bell 1967, Watson & Bell 1969, Dublin & Douglas-Hamilton 1987). Other populations showed rapid increases due to immigration as the result of compression, notably Lake Manyara N.P. (Douglas-Hamilton 1987), Tsavo N.P. (Laws 1969b, Ottichilo 1986a), Kabalega Falls N.P. (Buechner, Buss, Longhurst & Brooks 1963, Laws, Parker & Johnstone 1975), Ruaha N.P. (Norton-Griffiths 1975) and the Luangwa Valley (Caughley 1976, Hanks 1979, Lewis 1986).

The effect of human disturbance on the distribution of elephants can be illustrated by the effects of the two culls in Etosha N.P. In 1983, about 1820 elephants occurred in the western half of the park prior to the cull, but after 220 elephants were culled, only about 300 were left in the area (pers. obs.). In 1985, 350 elephants were removed out of a total of 800 in western Etosha N.P., and less than 150 elephants remained in the area by the end of the cull (pers. obs.). In both years, culling temporarily reduced the elephant population not by the intended 10% and 15% (actual removals were 8% and 14% - 220 out of 2800 in 1983 and 350 out of the 2464 counted in the previous dry season in 1984), but by 54% and 52% in 1983 and 1985 respectively. In 1983 and 1985 an estimated 1300 and 300 elephants respectively moved out of the culling area and out of the park three to four months before such movements usually occur. Long-distance communication by elephants, as suggested by Payne, Langbauer & Thomas (1986) and Poole, Payne, Langbauer & Moss (1988), might well be responsible for such an effect.

As the result of these changes in elephant distribution after the two culls in Etosha N.P. and the variable numbers present in the park from one dry season (culling time) to the next, it was decided to suspend further culling as long as the elephants in Etosha N.P. are not confined to the park, or elephant-induced changes in the vegetation remain at current levels.

The compression of elephants into Etosha N.P. was apparently accentuated during the Trans-African drought and some 1500 elephants moved into the park. Culling operations, harassment and perhaps the brackish perennial waters of the park were responsible for dispersal away from concentration areas and out of the park as soon as alternative water supplies were available through rainfall. Elephants present in Etosha N.P. at any one time therefore represent a fraction of the regional population occurring in Ovambo, Kavango, and parts of the Kaokoveld. The portion of this population that is present in Etosha N.P. varies from year to year, as the result of rainfall patterns and human activities. If previous trends in human population growth and land use continue, the potential range of the regional population will be further reduced and Etosha N.P. will become even more important as a dry and wet season distribution area, and particularly during periods of drought, for the regional elephant population. It is possible that elephants in Etosha N.P. might be ultimately isolated from relict groups elsewhere, at which point it will be more appropriate to regard elephants in Etosha N.P. as a discrete unit.

This perhaps simplistic explanation of changes in elephant abundance in Etosha N.P. over the previous decade cannot be substantiated in all respects, as vital evidence regarding the movements of elephants in and out of the park could not be collected due to logistical and political problems. Supporting evidence of changes in abundance through movements, rather than explosive breeding and a population crash after the recent drought, can be found in the age structure of the population, breeding rate, mortality record, and survival-fecundity rates of increase presented in subsequent chapters.

CHAPTER 3 AGE ESTIMATION AND AGE STRUCTURE

INTRODUCTION

The estimation of the age of individuals and population size are fundamental to any demographic analysis. Where possible, aspects of breeding and mortality should be qualified by reference to age and numbers. Broad distinctions between adults and juveniles may be sufficient in some instances, but finer resolution of the age of individuals opens new pathways in analysis and comprehension of mechanisms operating in a population. Changes in some threshold ages, such as the age at first reproduction, are seen as indicators of change in population status, and might therefore be useful in monitoring the consequences of a management policy. Present management schemes on elephants in southern Africa aim to control numbers without causing a change in the age structure of populations (Cumming 1981, 1983, Hanks et al. 1981, De Vos et al. 1983, Pienaar 1983). This implies that age structures should be determined, and the objective of this section is therefore to evaluate methods used to classify elephants into intervals of age.

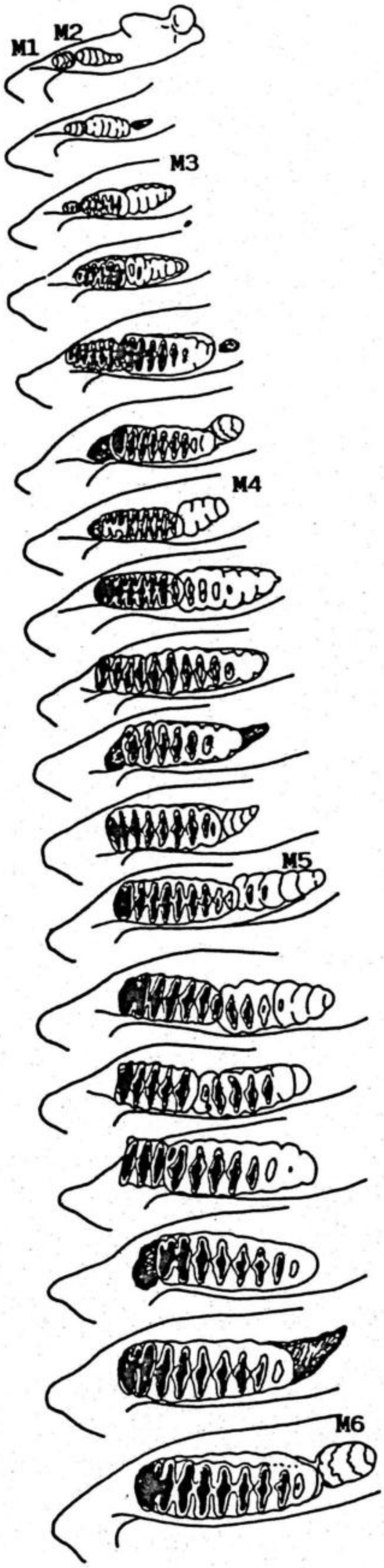
Both recent methods of estimating ages of elephants rely on the forward progression of the six molars in each half of the upper or lower jaw. Laws (1966) and Sikes (1966, 1968) provide detailed descriptions of the dentition of elephants in East Africa and both propose methods of age estimation based on the earlier work of Morrison-Scott (1947), Perry(1954), Bourliere & Verschuren (1960 in Laws 1966) and Johnson & Buss (1965). Briefly, this entails the classification of relative position, development and attrition of the molar series into discrete categories related to chronological age. A scarcity of known-age individuals, however, left many assumptions and approximations made by Laws (1966) and Sikes (1968) unconfirmed. Subsequent use of their methods on other populations showed several inconsistencies and both methods are currently regarded as suspect (Croze, Hillman & Lang 1981, Eltringham 1982, Jachmann 1985, 1988).

At least three major processes combine to produce the appearance of the molar complement in a given mandible. Forward movement, resorption of roots of functional molars and eruption of a newly consolidated molar should be coordinated to some degree for the jaw to function properly. Minor variation in the rate of appearance and disappearance of a molar should, however, not adversely affect mastication. Small variations in either eruption, forward movement or attrition could nevertheless result in misclassification of a mandible in both the methods of Laws and of Sikes.

Laws (1966), Sikes (1968) and Hanks (1972a, b) show that several methodological errors may influence age estimation, notably in the correct identification of molars and laminae which are crucial to either age estimation method. Hanks (1972a) suggested that cycles of recruitment in populations, as indicated by age distributions, were artifacts of the age estimation method of Laws (1966), and he was supported, if indirectly, by Sherry (1975), Smuts (1975), Williamson (1976) and Kerr (1978). "Cycles of recruitment" or peaks in the age distributions occurred at more or less the same ages in the populations they studied and the five studied by Laws (1969a, Laws & Parker 1969), although this was obviously not correlated to rainfall prior to conception or birth. Fatti, Smuts, Starfield & Spurdle (1980) suggest that misclassification accounts for the peak in 2-4 year-olds, while misclassification of completely different age groups accounts for two peaks, at 12-16 years and 20-28 years respectively. All three peaks coincide with the actual loss of a molar, M2, M3 and M4 respectively. The loss of M2 may be variable and therefore not accurately represented in Laws' (1966) system (see age classes V - VII in Fig. 3.1). The identification of and thus distinction between M4 and M5 are not foolproof, the more so in the absence of a preceeding tooth such as in age classes XI and XVI (Fig. 3.1), and may result in the allocation of jaws of completely different ages to these classes. The other alternative cause of misclassification of 12-16 and 20-28 year-olds could be that incorrect intervals are allocated to the various stages of loss of M3 and M4, thereby making age classes IX-XI and XV-XVIII not accurate.

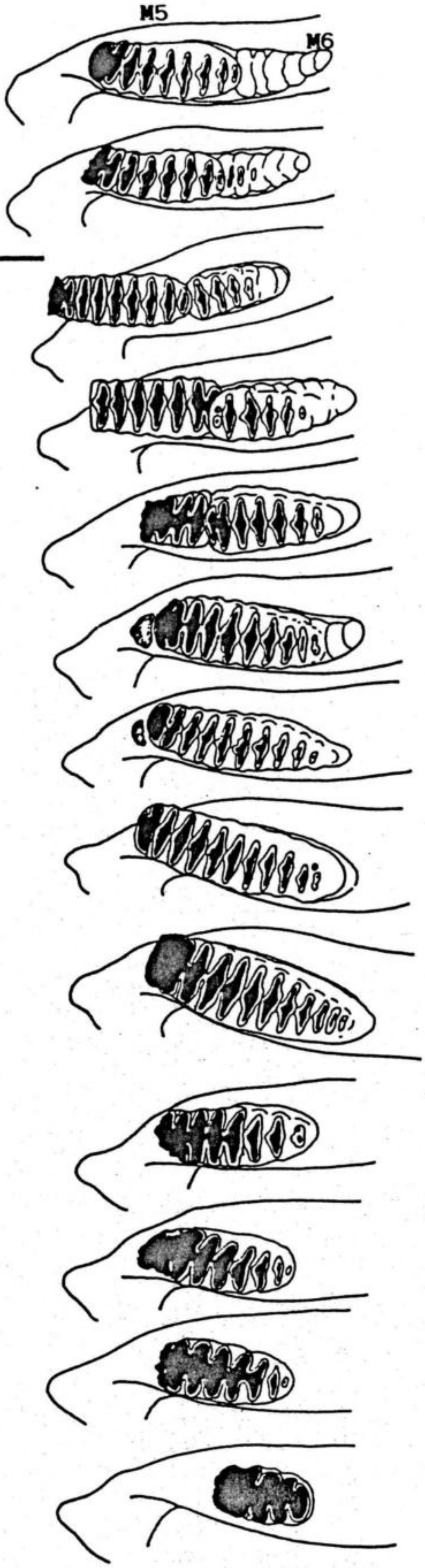
Jachmann (1985) has suggested that the method of Laws (1966) overestimates the age of individual elephants over the range 10-30 years of age, based on photographs of the mandibles of three known-age elephants in Lang (1980) and one in Laws et al. (1975). Jachmann (1988) therefore proposed a tentative revision of the age estimation method of Laws (1966) over the range 10-30 years of age (Fig. 3.1), based on molar replacement and growth in shoulder height of six captive elephants (Lang 1980), and photographs of the mandibles of the four known-age elephants mentioned.

Jachmann (1988)	
ix	10 ± 1
x	12 ± 1
xi	14 ± 1
xii	16 ± 1
xiii	18 ± 1
xiv	20 ± 1
xv	22 ± 1
xvi	24 ± 2



Laws (1966)		(Laws 1967a)
I	0 –	(± ½)
II	½ –	(± ½)
III	1 –	(± ½)
IV	2 ± <½	(± ½)
V	3 ± <½	(± 1)
VI	4 ± < 1	(± 1)
VII	6 ± 1	(± 2)
VIII	8 ± 1	(± 2)
IX	10 ± 1	(± 2)
X	13 ± 1	(± 2)
XI	15 ± 1	(± 2)
XII	18 ± 1	(± 2)
XIII	20 ± 2	(± 2)
XIV	22 ± 2	(± 3)
XV	24 ± 2	(± 3)
XVI	26 ± 2	(± 3)
XVII	28 ± 2	(± 3)

Figure 3.1 Molar replacement sequences in right mandibles of elephants, redrawn from Laws (1966) and Jachmann (1988). Molars are indicated by M1-6, age classes of Laws (1966) by I-XXX, and the revised age classes of Jachmann (1988) by ix-xviii. Chronological age in years ± probable range of each age class was taken from Laws (1966, 1967a) and Jachmann (1988) for age classes ix-xviii.



Jachmann (1988)	Laws (1966)	(Laws 1967a)
xvii 26 ± 2	XVIII 30 ± 2	(± 3)
xviii 30 ± 2	XIX 32 ± 2	(± 3)
	XX 34 ± 2	(± 3)
	XXI 36 ± 2	(± 3)
	XXII 39 ± 2	(± 3)
	XXIII 43 ± 2	(± 6)
	XXIV 45 ± 2	(± 6)
	XXV 47 ± 2	(± 6)
	XXVI 49 ± 2	(± 6)
	XXVII 53 ± 2	(± 6)
	XXVIII 55 ± 4	(± 6)
	XXIX 57 ± 4	(± 6)
	XXX 60 ± 4	(± 6)

Figure 3.1 Continued.

All studies of the demography of African elephants, including Jachmann's own study in Malawi (Jachmann 1980, 1988), have relied on the age estimation method of Laws (1966). The original method of Laws (1966) was used in this study in favour of the tentative revisions by Jachmann (1988), to facilitate comparison with previous studies, and also because the revision is not final (Jachmann 1988).

METHODS

The mandibles of 525 elephants were collected during culling operations in the western part of Etosha N.P. in 1983 (219) and 1985 (306). Additional mandibles were collected from elephants shot on farms bordering on the park and natural mortalities. Mandibles were individually marked with a numbered metal tag and painted with polyester resin after the soft tissue had been removed by scavengers. Standard body measurements following Laws (1966) were recorded for all culled individuals, but only used as a direct indication of age in 44 juveniles captured live during the 1985 cull.

Mandibular molars were identified by their relative sizes (Laws 1966, Hanks 1972b). Maximum widths and lengths of intact and incomplete molars were measured as in Laws (1966). The full laminary complement was recorded in intact molars, as well as the number of laminae posterior to a vertical line through the foramen mentale, i.e. the laminary index of Sikes (1968). The incidence of incompletely developed first and last laminae (Fig. 3.2) was recorded, as well as the number of functional laminae in each molar. Alveolar sockets were classed as open (molar lost recently), semi-filled, closed but visible with some small cavities, and closed entirely, grading into matrix (longest interval since molar was lost) (Fig. 3.3). The number and relative position of the foramina mentale were recorded for both sides of each mandible.

All mandibles were allocated to the 30 age classes of Laws (1966), as based on the characteristic stage of molar progression shown in Fig. 3.1, as well as the revised age schedule of Jachmann (1988). Only right halves were used as is conventional. As a test for personal subjectivity, all mandibles were furthermore reclassified twice, based on the appearance of the anterior and posterior molars independently. Chronological age

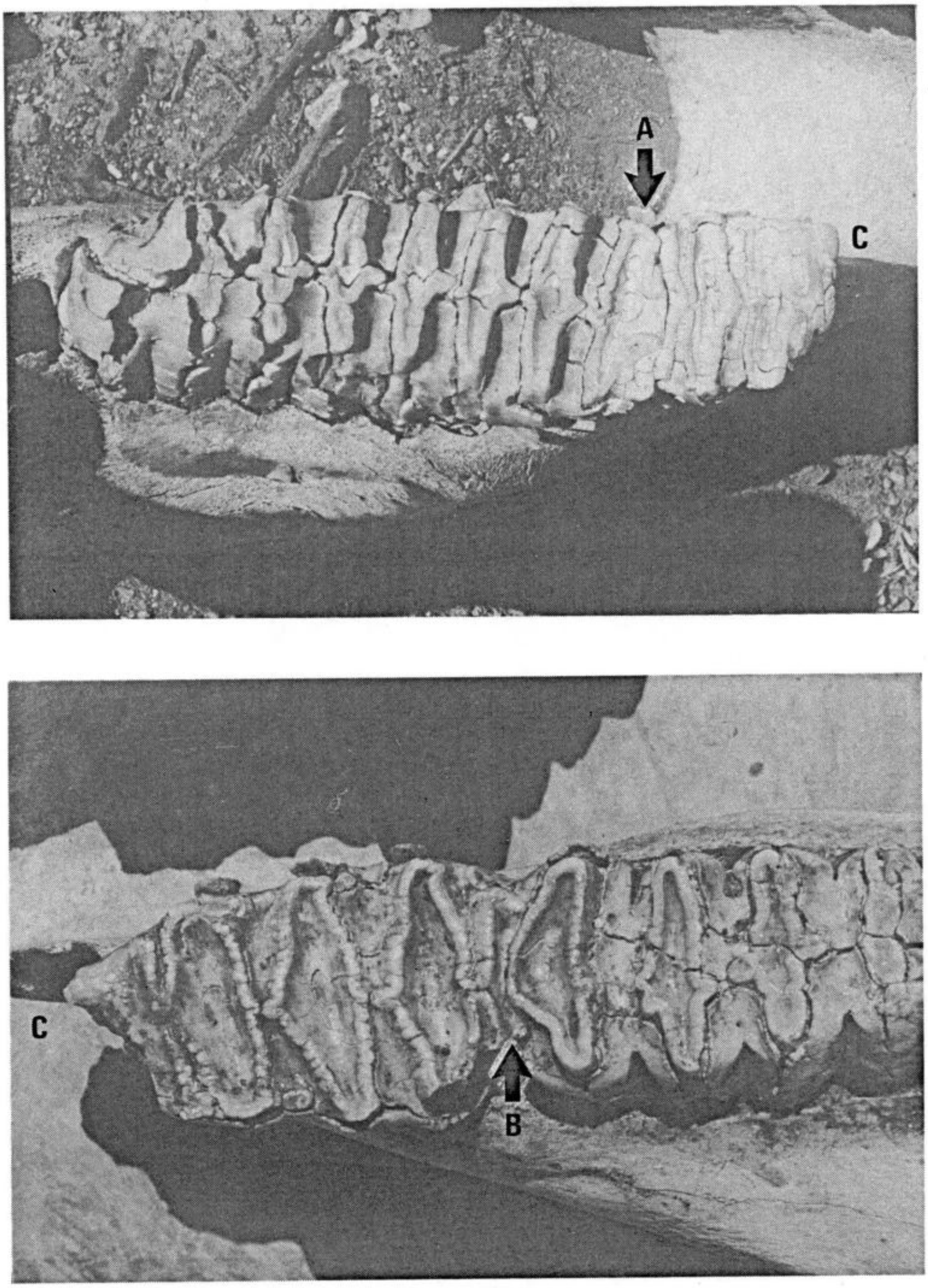
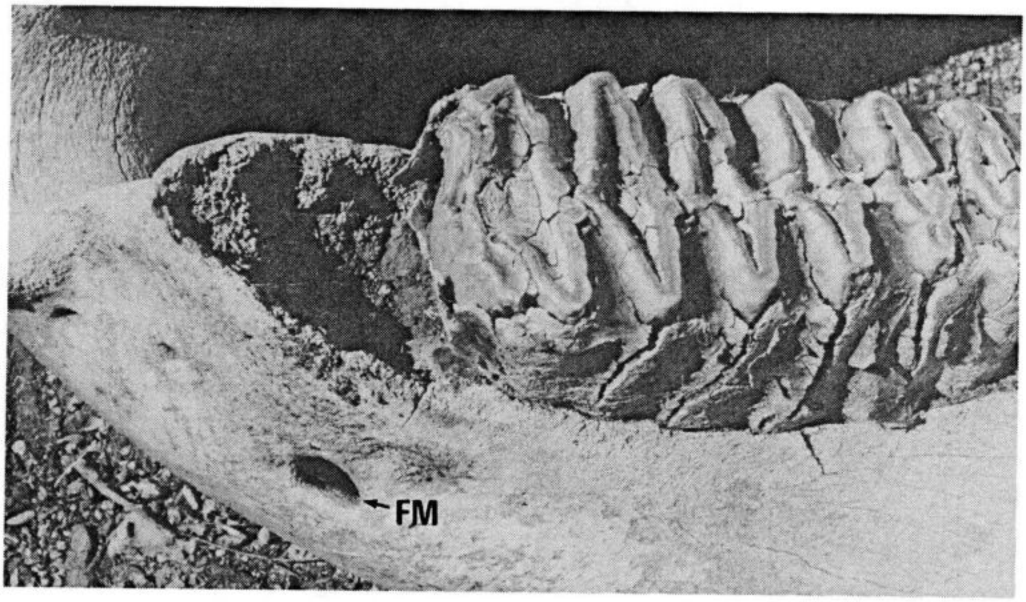


Figure 3.2 Examples of incompletely developed first (anterior) and last (posterior) laminae of molars from elephants culled in Etosha National Park. Arrows indicate an incomplete first lamina (A) and last lamina (B), and C denotes the anterior edge of the molar series in each mandible.



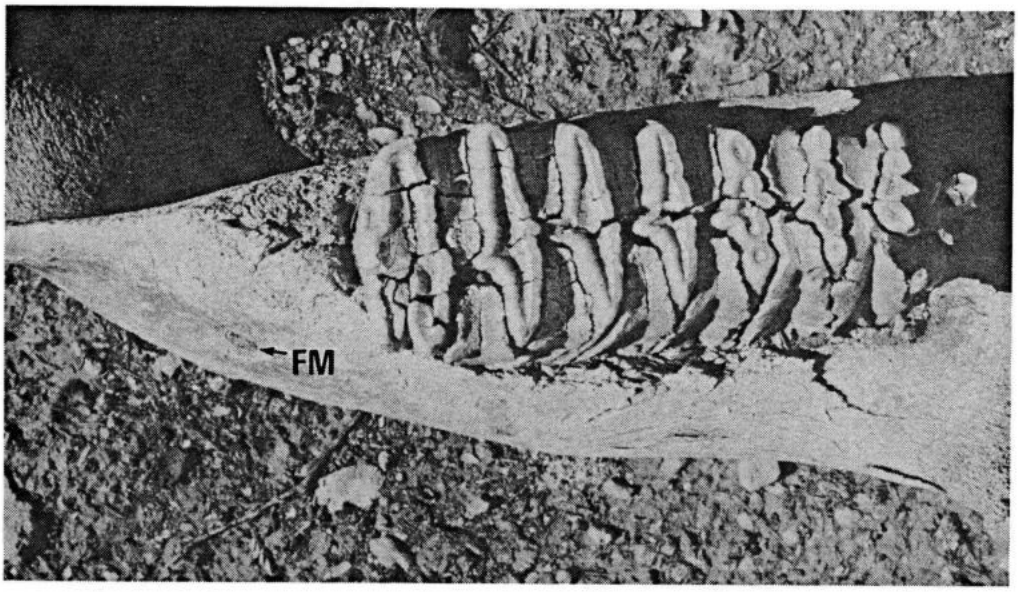


Figure 3.3 Variable degree of filling of the alveolus after the loss of molar fragments from left mandibles of elephants culled in Etosha National Park. FM denotes the foramen mentale.

limits were assigned to age classes by Laws (1966) later refined by Laws (1967a) and modified by Jachmann (1988). The frequency of individuals in year groups were calculated using equal representation of the number of individuals in each age class over the number of years represented by each age class, or by using three-year running averages.

After identification of molars situated above the foramen mentale, the laminary index, or "FM formula" of Sikes (1968), was identified by counting the number of laminae posterior to the imaginary vertical line passing through the foramen mentale, of the molar above the foramen. Chronological ages were assigned to six of the 57 possible molar age groups of Sikes (1968).

Vertical colour transparencies were taken of all breeding herds seen during aerial censuses after December 1983, as described by Glover (1963), Laws (1969b) and Croze (1972). The relative age of individual elephants was estimated from the relative size of each elephant compared to the largest individuals in each group, following Croze (1972).

The most precise measurement that can be recorded from a vertical view of an elephant is the distance between the apex of the anal flap and the junction of the ears with the head (hereafter referred to as back length). Laws (1969b) found that the proportional increase in body length with age is nearly identical to the proportional increase in shoulder height. The distance between the base of the tail and the junction of the ears and head is also nearly identical to shoulder height. The base of the tail is nevertheless less accurately determined on aerial photographs than the apex of the anal flap. Croze (1972) used Von Bertalanffy growth curves for shoulder height derived by Laws et al. (1975), to construct a weighted mean breeding herd growth curve. This is necessary as sexes cannot be distinguished in aerial photographs, except perhaps adult males. The curve is weighted according to the sex ratio at age, as males and females grow at different rates (Hanks 1972c, Laws et al. 1975, Sherry 1978).

Formal growth models were not used to construct an age-length key in this study, in view of the variable quality of measurements taken from elephants and unsubstantiated method of age estimation. An unsexed weighted mean distribution of back lengths over age was therefore constructed using the 1985 culled sample from Etosha N.P. Back lengths were measured over the curves, as it is difficult to adjust the posture of a recumbent dead elephant to measure a straight distance as though the elephant was standing upright. Mean back lengths were calculated for each age class using all males and females culled, assuming that the culled sample represents the sex ratio of the population. Mean back lengths were regressed using a third degree polynomial equation of $y = 131.30-14.33x-0.59x^2-0.01x^3$ ($r^2 = 0.891$), which yielded a good fit to the data over the first age classes, but is otherwise biologically meaningless. Mean back lengths for age intervals up to 30 years were found by interpolation.

Growth appears to slow down in females by 30 years of age in Etosha N.P., at an asymptotic back length of 280 cm (median of back lengths of females $\geq$ 30 years). Adult females with asymptotic back lengths are used as the reference measurement in herds, and all other elephants are measured as the ratio of back length : asymptote (Table 3.1). This approach obviates the measurement of the distance between camera and elephant, which is very difficult to determine and not worth standardizing in practice. In the 1985 sample, 12% of individuals were adult females at the asymptotic growth phase, and 12% of individuals in each group in a photograph were used to calculate a mean asymptotic back length for each photograph individually. The problem of scaling is thus circumvented. In practise, as also reported by Leuthold (1976), a fixed proportion of adults to calculate the asymptote is not practical, as the herds in Etosha N.P. and Tsavo N.P. are generally much smaller than in Croze's (1972) study, where he recommends 10% as a fixed proportion. Some groups contain adult bulls which might or might not be identified as such, especially in small groups. A reverse approach was therefore used where the ratio of the smallest individual to the asymptote was used. When this ratio was less than 0.4, the photograph was discarded as biased by the presence of undetected adult bulls. Photographs containing adult females not facing the same general direction as the rest of the group also produced a biased asymptote, and were discarded.

Correction factors to counter parallax errors, as described by Croze (1972) were not used. Photogrammetrical errors probably cancel out over large samples, and are minor compared to inaccuracies in age-length keys, as suggested by Leuthold (1976).

Elephants were also classed into six age intervals following diagrams in Laws (1966) and Hanks (1979) during ground-based observations by all staff members in Etosha N.P. Classes used were 0-1 year-old calves, calves, juveniles, intermediates, sub-adults and adults, which represent chronological intervals similar to the intervals 0-5 years (including 0-1), 6-10, 11-15, 16-20 and older than 20 years, used in photogrammetrical age structures (Leuthold 1976).

Table 3.1 Back length-age key and ratios of back lengths at age:asymptote of elephants in Etosha National Park.

AGE (years)	BACK LENGTH A (cm)	A/280 * = B	UPPER LIMIT PER AGE GROUP **
1	145.04	0.518	0.541
2	157.66	0.563	0.584
3	169.19	0.604	0.623
4	179.70	0.642	0.659
5	189.24	0.676	0.692
6	197.86	0.707	0.721
7	205.62	0.734	0.747
8	212.58	0.759	0.770
9	218.79	0.781	0.791
10	224.30	0.801	0.818
12	233.44	0.834	0.847
14	240.46	0.859	0.869
16	245.78	0.878	0.885
18	249.83	0.892	0.898
20	253.07	0.904	0.909
22	255.92	0.914	0.919
24	258.82	0.924	0.930
26	262.21	0.936	0.944
28	266.52	0.952	0.962
30	272.19	0.972	0.986

* Asymptotic back length : 280 cm

** Determined as $\frac{(B_{x+1} - B_x)}{2} + B_x$

Regression slopes were compared using a Student's t- and an F-test procedure given in Steel & Torrie (1980). Correllation coefficients were checked for significance against tabled values in Clarke (1969). Sample means were compared using Student's t- and chi-square tests. Polynomial regressions were calculated using a computer package. Age (frequency) distributions were compared using a contingency analysis (χ^2) following Caughley (1966).

RESULTS

Identification of molars

Figure 3.4 illustrates the sizes of molars of males (A) and females (B) from Etosha N.P. M1, M2 and M3 showed no overlap in size, while M6 could be identified by the absence of an alveolus posterior to it. M4 and M5 were distinguished by their relative sizes and the presence or absence of a preceding M3. Molars of males were generally more massive than those in females, but sizes overlapped as is shown in Hanks (1972b). This overlap was only in part due to the inclusion of partially worn or incompletely developed teeth in the series (Fig. 3.4 A-'A', B-'B'). Mean sizes of fully developed molars are presented in Table 3.2. One supernumerary molar (M7) (Fig. 3.5) was found, giving an incidence of 0.2% in the total sample. One mandible in the 1985 sample was abscessed and had a fractured M4, possibly as the result of a gunshot wound, while one mandible in the 1983 sample showed the loss of an entire M5 soon after complete eruption with no further development of M6. The other half was normal (Fig. 3.6).

Number of laminae

Frequency distributions of the number of laminae in each molar are shown in Fig. 3.7. Variation in the number of laminae per molar occurred in all molars, with overlapping numbers from M3 to M6. Apart from the number of rudimental laminae described by Sikes

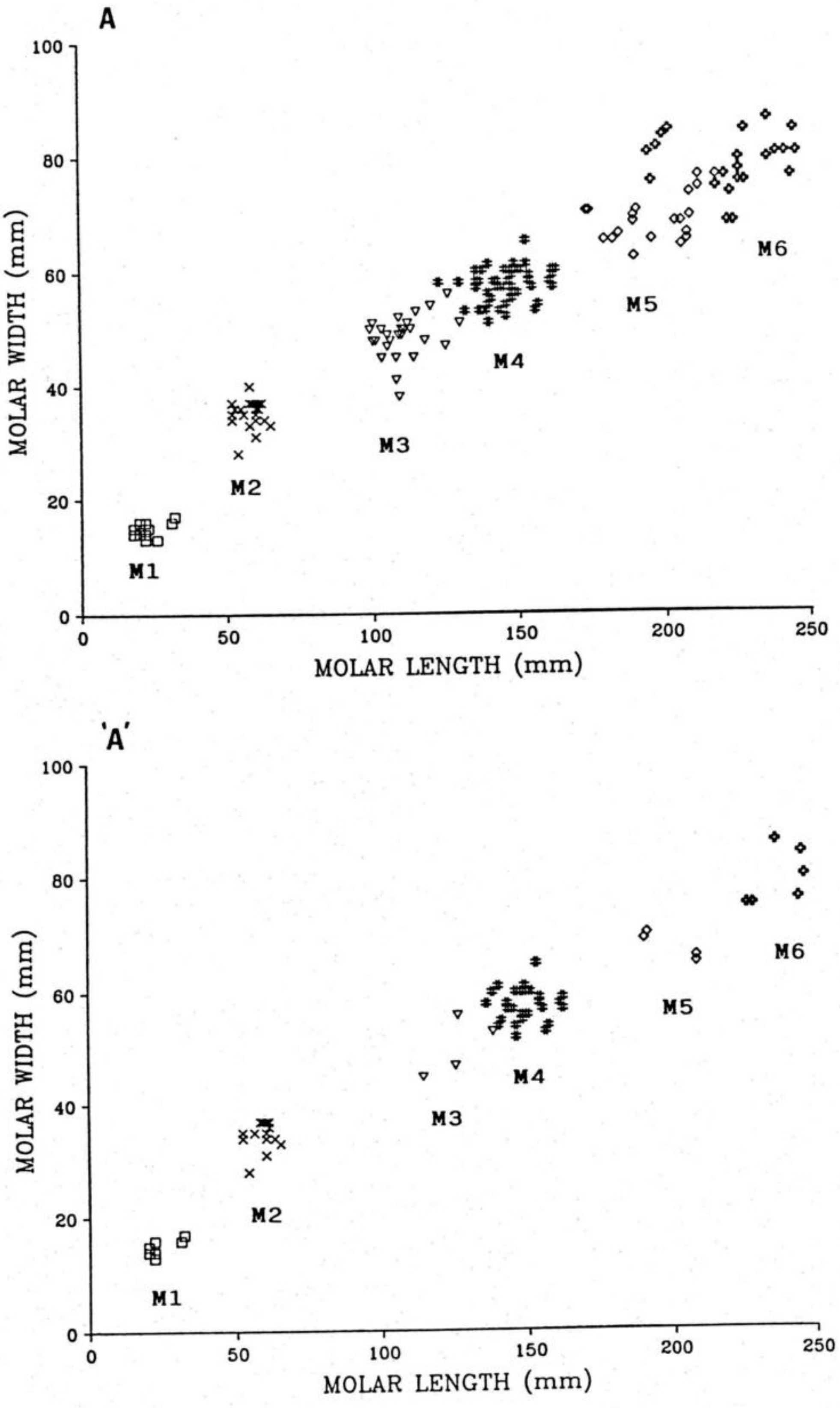
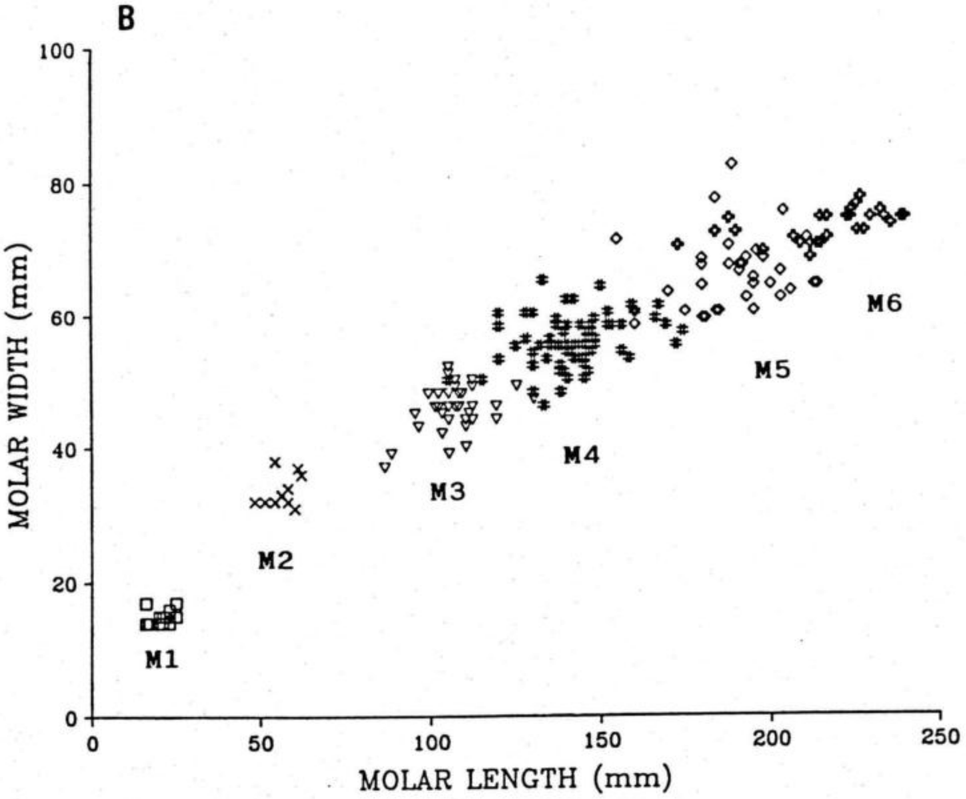


Figure 3.4 A Widths and lengths of M1-M6 in the total sample of males (A) and of intact molars only ('A') of elephants culled in Etosha National Park.



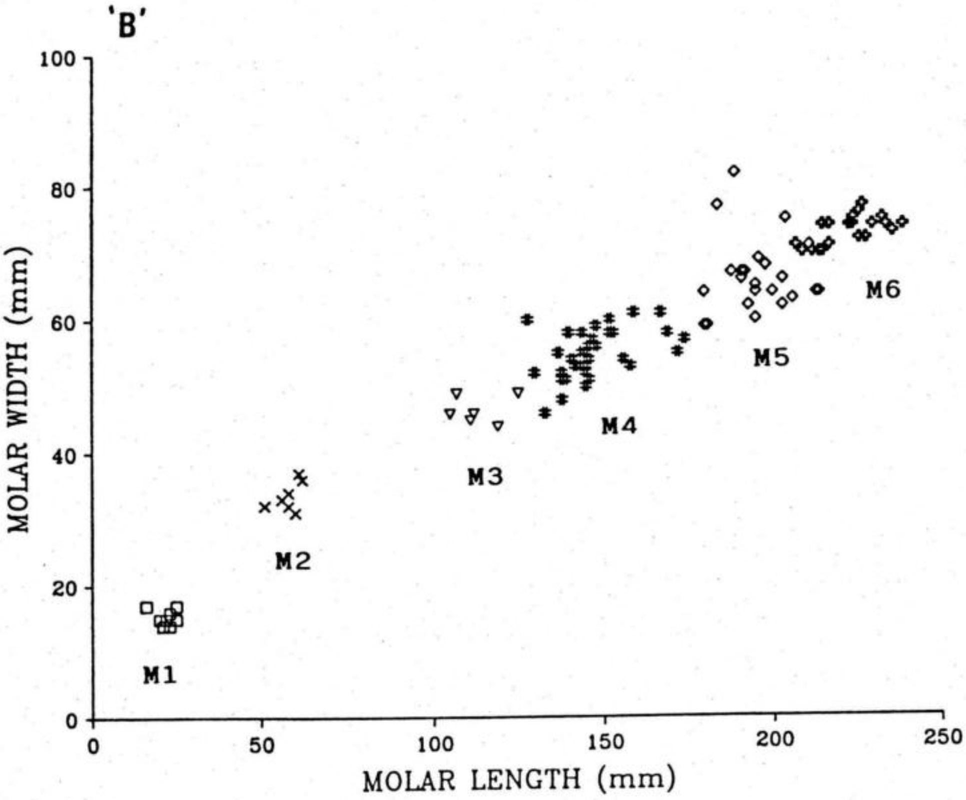


Figure 3.4 B Widths and lengths of M1-M6 in the total sample of females (B) and of intact molars only ('B') of elephants culled in Etosha National Park.

Table 3.2 Mean (± SE) width (w) and length (l) in mm of fully erupted intact molars and partially eroded or erupted molars of male and female elephants in Etosha National Park.

FEMALES

Molar		Fully erupted intact molars only	n	All molars	n
M1	w	15.6 ± 0.4	9	15.1 ± 0.3	14
	l	22.2 ± 1.0		21.2 ± 0.8	
M2	w	33.4 ± 0.7	9	33.6 ± 0.7	11
	l	56.8 ± 1.4		55.7 ± 1.4	
M3	w	46.0 ± 0.8	5	45.8 ± 0.6	35
	l	110.8 ± 2.4		106.9 ± 1.5	
M4	w	54.7 ± 0.6	37	55.5 ± 0.4	76
	l	146.9 ± 1.8		142.3 ± 1.5	
M5	w	66.5 ± 1.1	25	65.9 ± 0.9	38
	l	196.5 ± 2.0		189.6 ± 2.3	
M6	w	73.1 ± 0.5	21	72.6 ± 0.4	29
	l	224.4 ± 2.5		217.7 ± 3.4	

MALES

Molar		Fully erupted intact molars only	n	All molars	n
M1	w	15.0 ± 0.5	7	14.8 ± 0.3	13
	l	24.1 ± 1.9		22.8 ± 1.2	
M2	w	34.7 ± 0.7	15	35.3 ± 0.5	23
	l	58.8 ± 1.0		58.3 ± 0.8	
M3	w	50.3 ± 2.6	4	48.6 ± 0.7	31
	l	125.8 ± 4.9		110.9 ± 1.6	
M4	w	57.6 ± 0.6	27	57.4 ± 0.4	51
	l	148.9 ± 1.4		146.1 ± 1.3	
M5	w	67.5 ± 1.2	4	68.1 ± 0.9	21
	l	199.3 ± 5.1		197.0 ± 2.9	
M6	w	79.3 ± 2.0	6	78.0 ± 1.0	22
	l	237.5 ± 3.6		223.7 ± 3.5	

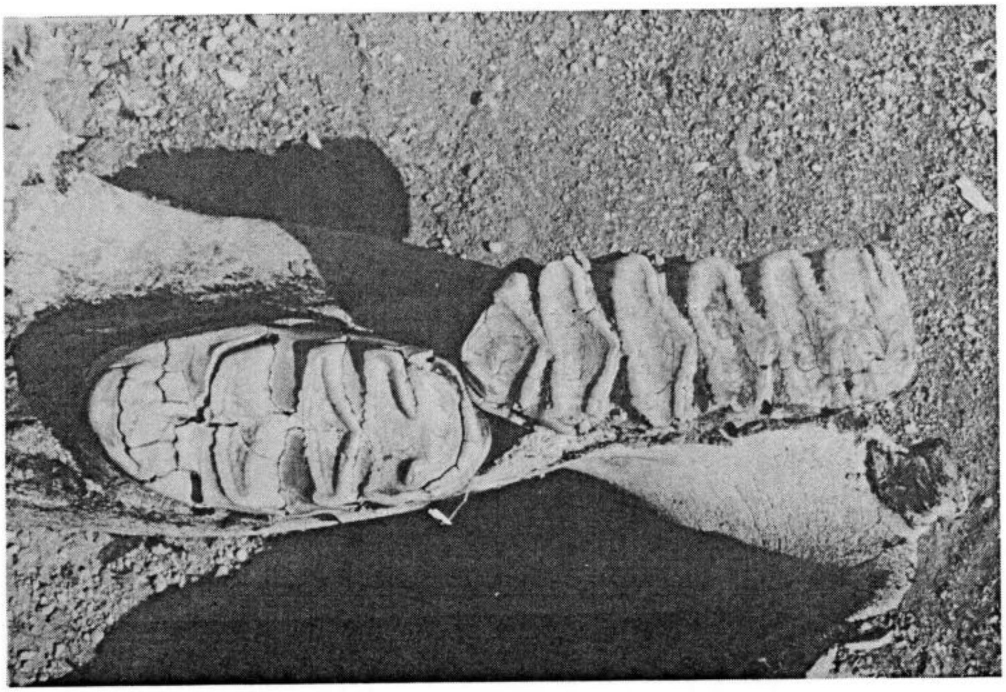


Figure 3.5 The only supernumerary M7 found (on the left), in the mandible of a 60 year-old female elephant from Etosha National Park.

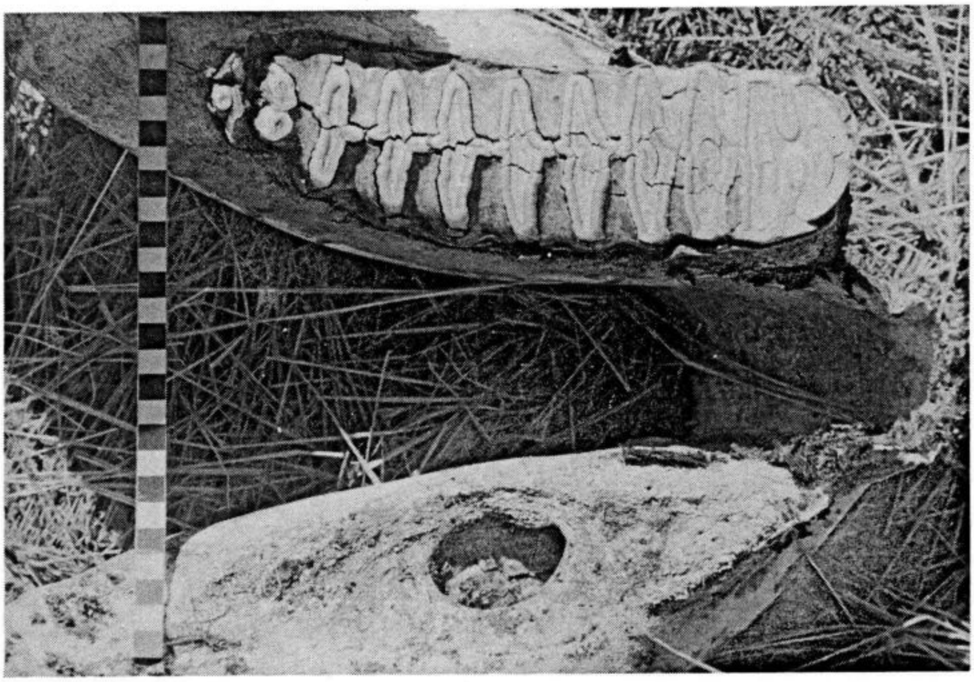


Figure 3.6 Abnormal dentition in an adult female elephant from Etosha National Park, with M5 absent in the right mandible (scale in cm).

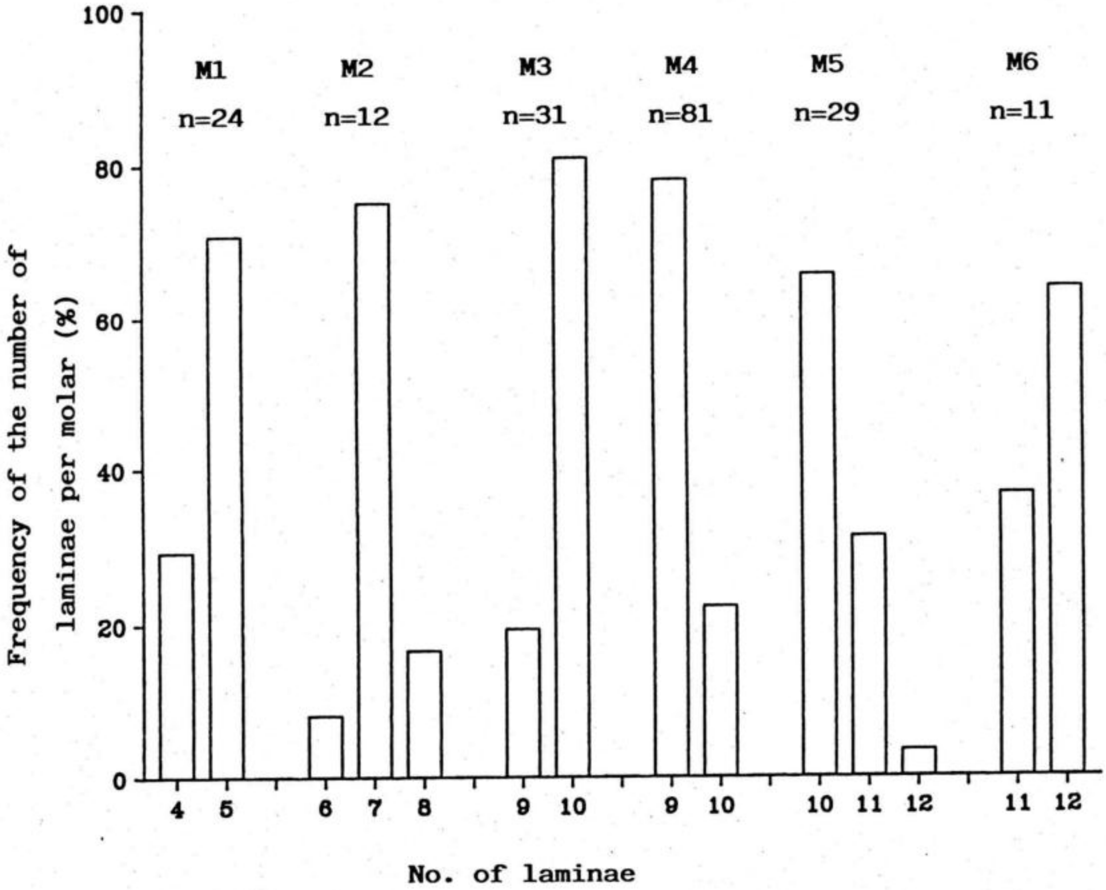


Figure 3.7 Frequency distribution of the number of laminae in intact elephant M1-6 in Etosha National Park (n denotes sample size).

(1968), which may or may not be counted, the visible number of laminae is further reduced by another process. The first, or anterior, lamina of all molars is usually smaller than the rest, and probably does not last as long. The first laminae of M4-6 are in addition sometimes absent or incompletely developed where the developing buttress remains confined below the last lamina of the preceding molar (Fig. 3.2). Not all molars show this reduction to the same degree and the incidence of incomplete first laminae as the only remaining evidence, is shown in Table 3.3. The last functional laminae in M1-5 might similarly be suppressed due to the development of the succeeding first lamina of the next molar (Fig. 3.2). More last laminae are in fact incomplete or absent than first laminae (Table 3.3). The samples from 1983 and 1985 differ in this regard, indicating that variation in molar progression occurs within a population.

Variation occurred in the position and number of foramina mentale (Table 3.4), and the position of foramina on left and right mandibles differed in 7.3% of the total sample. Counts of laminae differed in up to three laminae in M1-M3 and up to two laminae in M4-6 when counted from the posterior and anterior foramina mentale.

Seventeen percent of mandibles had no molar situated directly above the foramen mentale reference point, thus occupying intermediate positions relative to Sikes' age groups. The variable degree of filling of the alveolus above the foramen, and variable degree of abrasion of the anterior edge of the next molar, indicate that some molars are lost at irregular intervals. Although not mentioned as such by Sikes (1966, 1968), the absence of a molar lamina above the foramen is not totally abnormal, as the last few laminae of a particular molar are usually lost in unison. Complete resorption of molar roots occur above the foramen and the part of a molar anterior to the foramen projects as an unrooted shelf. The entire molar progressively loses its roots <u>en passage</u> over the foramen, and the occlusal surface is therefore lost bit by bit. The anterior part of the alveolus itself retrogresses as soon as one or more roots are resorbed, and the alveolus is therefore only visible in the molar row when the last section of the anterior molar of the two or three present is lost. Two different molars are present in a mandible, except in age class III where three molars (M1-3) are present, and age classes XXIII-XXX where only one molar (M6) is present (Fig. 3.1). In the normal sequence of events all mandibles will on occasion have recently evacuated alveoli over the foramen, while partially or completely filled alveoli above and posterior to the foramen indicate the premature loss of a molar. It is not possible to judge from the size of the alveolus which lamina would have been situated above the foramen, thus further limiting the use of

Table 3.3 Number of incomplete first and last laminae in fully erupted molars of elephants culled in 1983 and 1985 in Etosha National Park. Percentage incidence given in parentheses.

Molar	Total no. of elephants examined in 1983	no. with incomplete first laminae		Total no. of elephants examined in 1985	no. with incomplete first laminae	
M1	16	0		13	0	
M2	23	0		30	0	
M3	73	0		108	0	
M4	68	15	(22.1)	86	1	(1.2)
M5	20	2	(10.0)	30	0	
M6	13	2	(15.4)	21	1	(4.8)
	213	19	(8.9)	288	2	(0.7)

		no. with incomplete last laminae			no. with incomplete last laminae	
M1	16	1	(6.3)	13	1	(7.7)
M2	23	9	(39.1)	30	19	(63.3)
M3	73	27	(37.0)	108	49	(45.4)
M4	68	22	(32.4)	86	30	(34.9)
M5	20	6	(30.0)	30	17	(56.7)
M6	13	0		21	0	
	213	65	(30.5)	288	116	(40.3)

Table 3.4 Variation in the number and position of the foramina mentale in mandibles of elephants culled in Etosha National Park. Percentage incidence given in parenthesis.

Anterior molar present in mandible	no. of mandibles	no. of foramina mentale expected	no. of foramina mentale present	no. of mandibles with >2 foramina mentale	no. of displaced foramina mentale in L & R mandibles
M1	32	64	82	12 (37.5)	0 (-)
M2	42	84	110	20 (23.8)	4 (9.5)
M3	69	138	181	32 (46.4)	8 (11.6)
M4	63	126	155	22 (34.9)	4 (6.3)
M5	44	88	106	16 (36.4)	1 (2.3)
M6	32	64	90	16 (50.0)	0 (-)

Sikes' method based on counting laminae. The incidence of lost molars and therefore alveoli situated above the foramen mentale is presented in Table 3.5, as well as the degree of filling of the alveolar socket (Table 3.6). It is not known how rapidly the entire cavity is filled by secondary bone growth, but at least the closed-absent class represents premature losses of M1-4.

Comparisons between ages assigned following Sikes (1968) and Laws (1966)

Figure 3.8 illustrates the correllation between ages of the elephants from Etosha N.P. as derived from the methods of Laws (1966) and Sikes (1968), with ages derived from Laws in general greater than those according to Sikes. Table 3.7 presents the range of laminary indices (Sikes 1968) allocated to mandibles in each of Laws' age classes, in the samples from Etosha N.P., as well as similar ranges described by Sikes (1968). The wide range of FM indices in each of the Lawsian age classes in the samples from Etosha N.P. indicates that the two methods correspond less well than they should, as both describe the same process of anterior progression of molars. Ages derived from one method are therefore not directly convertible to the other system.

Age structure

Frequencies of elephants allotted to the nominate chronological age groups of Laws (1966) are illustrated in Figs. 3.9A and 3.10A for the 1983 and 1985 samples respectively. Proportional frequencies calculated from the ranges given in Laws (1966) and Laws (1967a) are shown respectively in Figs. 3.9B and 3.10B, and Figs. 3.9C and 3.10C. The distinctive peaks in numbers corresponding with the loss of M2-4 at ages 2-4, 12-16 and 20-28 described in all other populations studied (Fatti et al. 1980), are present but far less distinct. Age distributions for other samples have all been constructed using the tentative age ranges per age class given in Laws (1966) and not the revised ranges in Laws (1967a) based in part on eye lens growth and annuli in the roots of molars. The latter method clearly results in a more even distribution than the former (Figs. 3.9C, 3.10C versus 3.9B, 3.10B). Figures 3.9D and 3.10D illustrate frequency distributions of elephants in the 1983 and 1985 samples respectively, using the revision of the method of Laws (1966) by Jachmann (1988).

Table 3.5 Number of mandibles with no molar over the foramen mentale in elephants culled in 1983 and 1985 in Etosha National Park. Percentage incidence given in parenthesis.

Anterior molar present	Total no. of mandibles examined in 1983	no. of mandibles with no molar over foramina mentale		Total no. of mandibles examined in 1985	no. of mandibles with no molar over foramina mentale	
M1	26	10	(38.5)	20	6	(30.0)
M2	26	13	(50.0)	50	25	(50.0)
M3	71	11	(15.5)	99	16	(16.2)
M4	57	4	(7.0)	71	1	(1.4)
M5	15	1	(6.7)	29	0	(0.0)
M6	12	-	-	20	-	-
	207	39	(18.8)	289	48	(16.6)

Table 3.6 Condition of the alveolus of lost molars in mandibles with no molar over the foramen mentale, from elephants culled in Etosha National Park.

Year	Alveolus of	no. of alveoli examined	Fresh fully open (%)	1/2 filled (%)	3/4 filled (%)	Closed - absent (%)
1983	M1	10	6 (60.0)	1 (10.0)	-	3 (30.0)
	M2	13	1 (7.7)	1 (7.7)	5 (38.5)	6 (46.2)
	M3	11	3 (27.3)	1 (9.1)	1 (9.1)	6 (54.6)
	M4	4	1 (25.0)	2 (50.0)	-	1 (25.0)
	M5	1	1(100.0)	-	-	-
1985	M1	6	2 (33.3)	-	1 (16.7)	3 (50.0)
	M2	25	2 (8.0)	1 (4.0)	5 (20.0)	17 (68.0)
	M3	16	1 (6.3)	3 (18.8)	3 (18.8)	8 (44.4)
	M4	1	-	-	1(100.0)	-
	M5	0	-	-	-	-

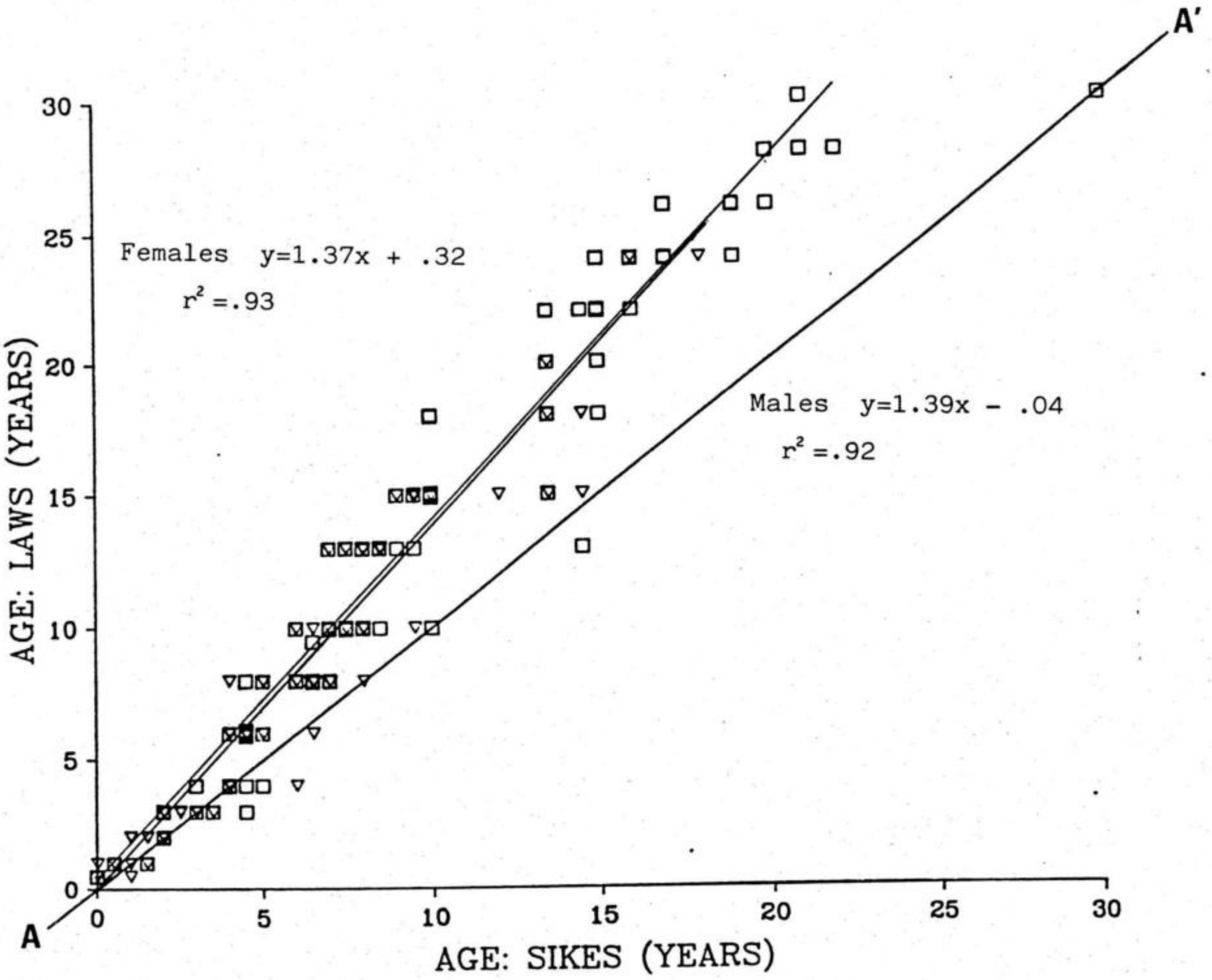


Figure 3.8 Comparison between the ages allocated to female (□) and male (▽) elephants in Etosha National Park according to the methods of Laws (1966) and Sikes (1968) (the diagonal line A-A' represents exact correspondence between the two methods).

Table 3.7 Range of laminary indices per Lawsian age class in elephants in Etosha National Park.

Age class (Laws 1966)	Corresponding laminary index in Sikes (1968)	Range of laminary indices in Etosha elephants	Modal laminary index in Etosha elephants
I		I/0 *	I/0
II	I/1-3	I/0	I/0
III		I/0 - II/0	I/1
IV	I/4-5	I/3 - II/2	II/0
V	II/1-7	II/0 - II/7	II/1
VI	III/1-2	II/0 - III/3	III/0
VII	III/3	III/0-4	III/0
VIII	III/4	III/0-7	III/3
IX	III/5-6	III/1 - IV/1	III/7
X	III/7 - IV/1	III/5 - IV/4	III/8
XI	IV/2	III/9 - IV/4	IV/0
XII	IV/3	IV/0-5	IV/0
XIII	IV/4	IV/3-5	IV/4
XIV	IV/5	IV/3-6	IV/5
XV	IV/6-9	IV/5-9	IV/6
XVI	IV/10 - V/1	IV/7 - V/4	IV/9
XVII	V/2	V/0 - V/5	V/0
XVIII	V/3	V/0 - V/6	V/5
XIX	V/4	V/5 - V/7	-
XX	V/5	V/5 - V/8	-
XXI	V/6-9	V/6-9	V/8
XXII	V/10-12	V/8-10	V/9
XXIII	VI/1-2	V/11 - VI/4	-
XXIV	VI/3	V/9 - VI/4	-
XXV	VI/4-8	V/12 - VI/5	-
XXVI		VI/4 - VI/5	VI/4
XXVII		VI/4 - VI/6	VI/8
XXVIII	VI/9-10	-	-
XXIX		-	-
XXX	VI/11	VI/8-9	-

* entire molar situated posterior to a vertical line through the foramen mentale.

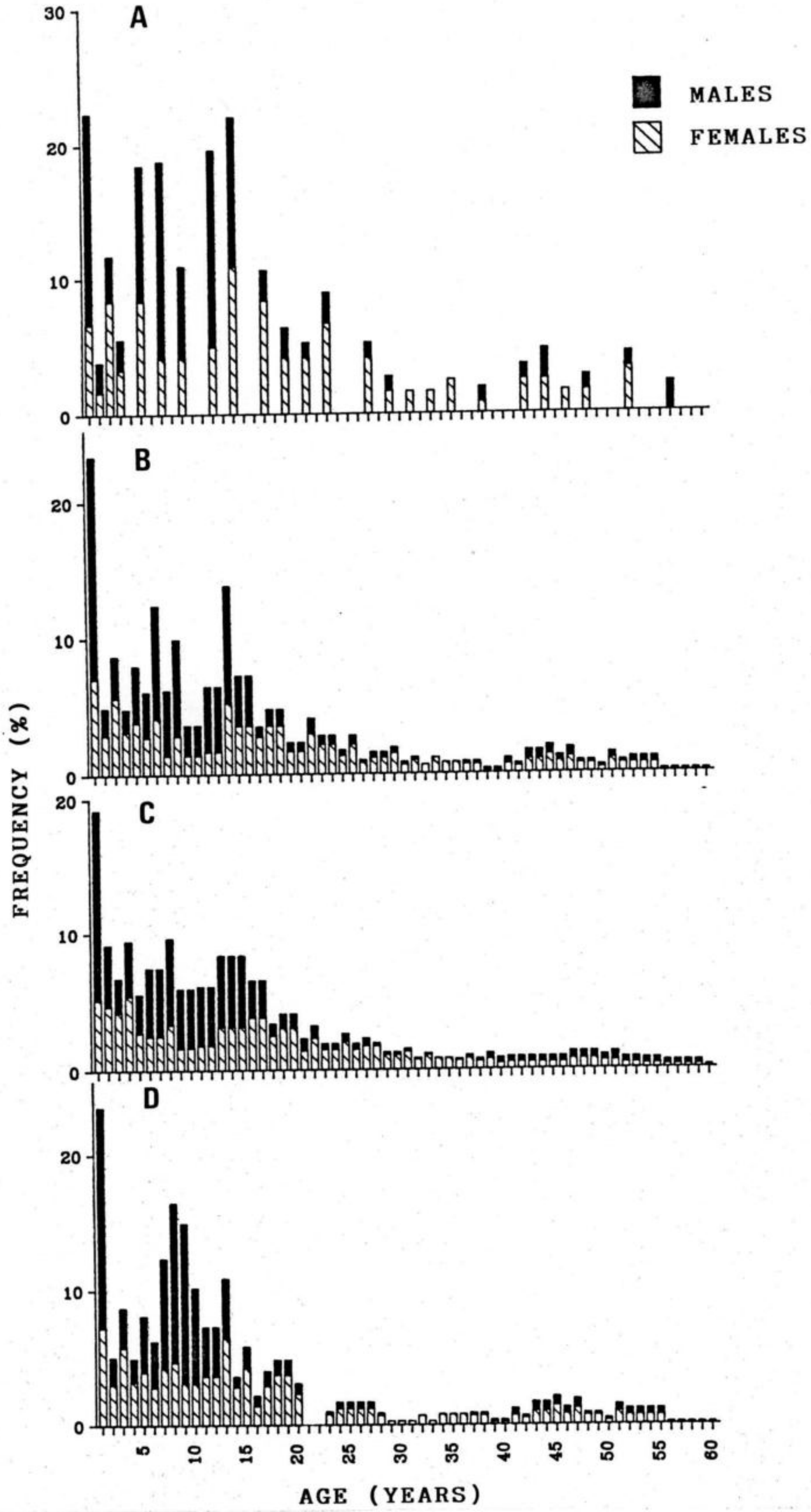


Figure 3.9 Frequency distribution of elephants in each Lawsian age class (A) and in year groups adjusted according to the ranges given in Laws (1966) (B), Laws (1967a) (C) and the age schedule of Jachmann (1988) (D) in the 1983 sample from Etosha National Park.

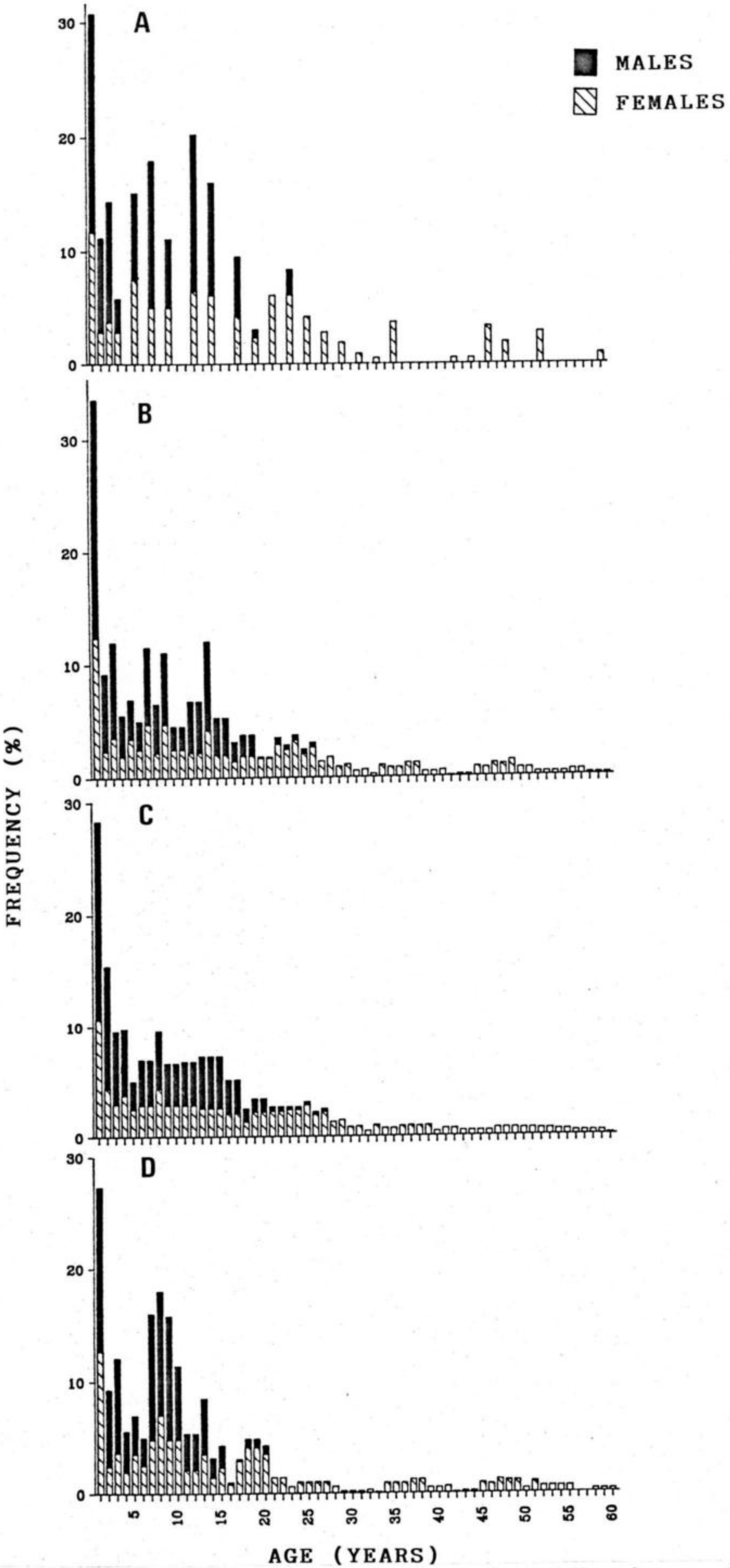


Figure 3.10 Frequency distribution of elephants in each Lawsian age class (A) and in year groups adjusted according to the ranges given in Laws (1966) (B) and Laws (1967a) (C) and the age schedule of Jachmann (1988) (D) in the 1985 sample from Etosha National Park.

As a fair degree of subjectivity is involved when allocating mandibles to one of Laws' (1966) age classes, it was suspected that a biased use of the method could be responsible for some of the problems mentioned above. As a test, all mandibles were re-allocated to age classes using the appearance of the anterior and posterior molars independently. Entirely different numerical distributions are produced in this way (Figs. 3.11 & 3.12). Smoothing by using the estimated age ranges in Laws (1966) and (1967a) increased the similarity between anterior-molar biased and posterior-molar biased distributions (Figs. 3.11 B & D, 3.12 B & D). Anterior-molar bias results in slightly more uneven distributions than posterior-molar bias, the more so in the distributions that emerge using age ranges in Laws (1966) rather than the age ranges in Laws (1967a). This may indicate that eruption of molars is more regular than the eventual loss of their fragments.

Age distributions of the elephant from Etosha N.P. samples, as derived from the method of Sikes (1968) are illustrated in Fig. 3.13. Peaks do not generally correspond with the loss of molars M2-4, and these distributions are potentially useful. Variations in the number of laminae per molar or the position of the mental foramen are not taken into account in Sikes' method. The only modification that could be made to her method was the allocation of prematurely lost molars to the last laminary age group (Fig. 3.13 A,C) or the last two laminary stages of the missing molar (Fig. 3.13 B,D). Age groups 20-30, following Sikes (1968) are underrepresented in both the 1983 and 1985 samples, as compared to the Lawsian age distributions (Figs. 3.9 & 3.10).

Figure 3.14 A-J illustrates female age structures derived from culled samples of elephants from Etosha N.P. and seven other populations (data from graphs in Laws 1969b, Hanks 1972a, Sherry 1975, Williamson 1976, Kerr 1978 and Fatti et al. 1980). All age structures in Fig. 3.14 are three-year running averages based on age estimations following Laws (1966) except those in Fig. 3.14 A & C which were based on the revised method of Jachmann (1988). The age structures derived from the original and revised methods of Laws of female elephants in Etosha N.P. are not significantly different in both the 1983 and 1985 samples ($_{1983}\chi^2_{59} = 13.435$; NS and $_{1985}\chi^2_{59} = 12.839$; NS).

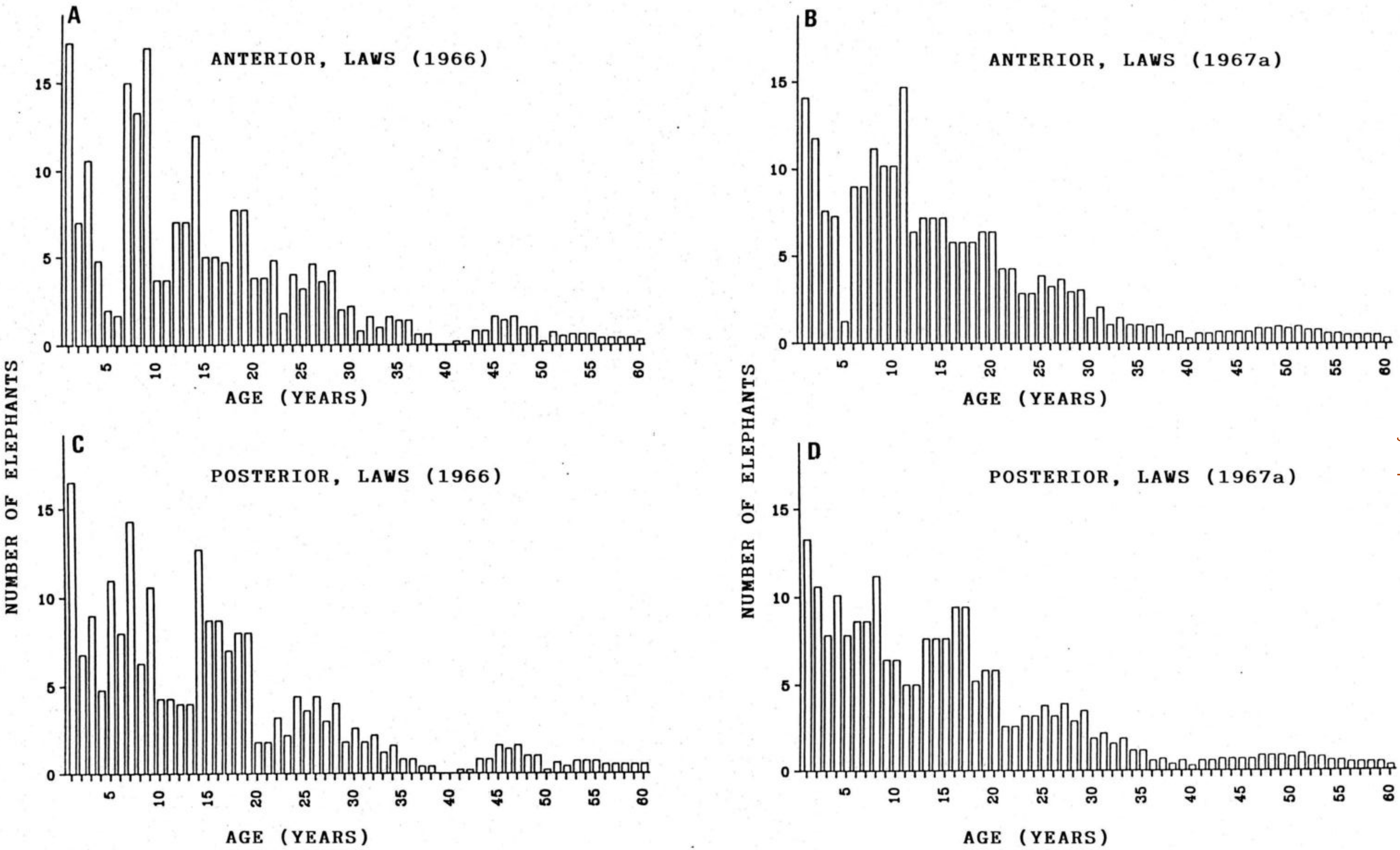


Figure 3.11 Age distributions of female elephants in the 1983 sample from Etosha National Park based on the appearance of the anterior (A & B) and posterior (C & D) molars independently, and smoothed using the age ranges of Laws (1966) and Laws (1967a).

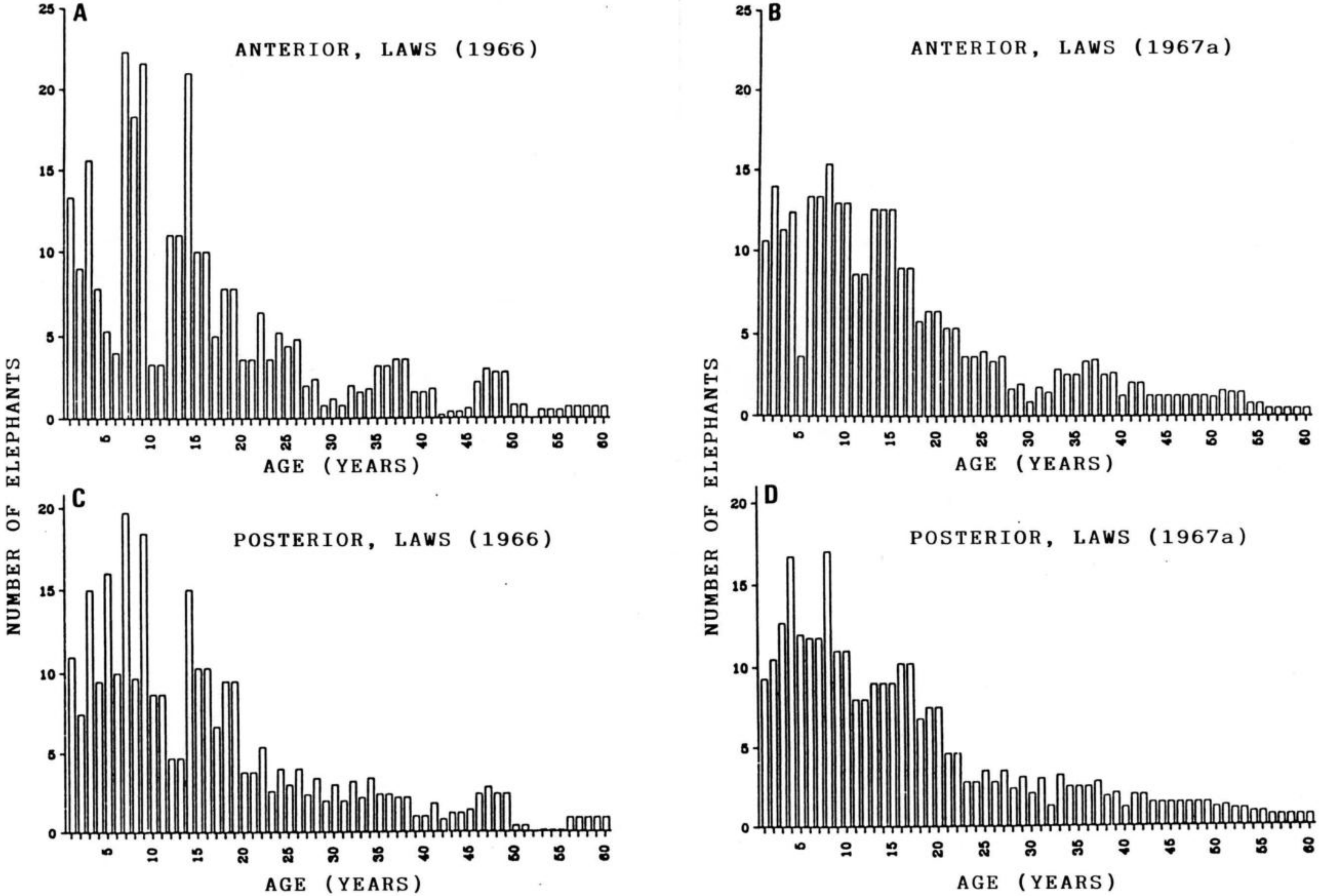


Figure 3.12 Age distributions of female elephants in the 1985 sample from Etosha National Park based on the appearance of the anterior (A & B) and posterior (C & D) molars independently, and smoothed using the age ranges of Laws (1966) and Laws (1967a).

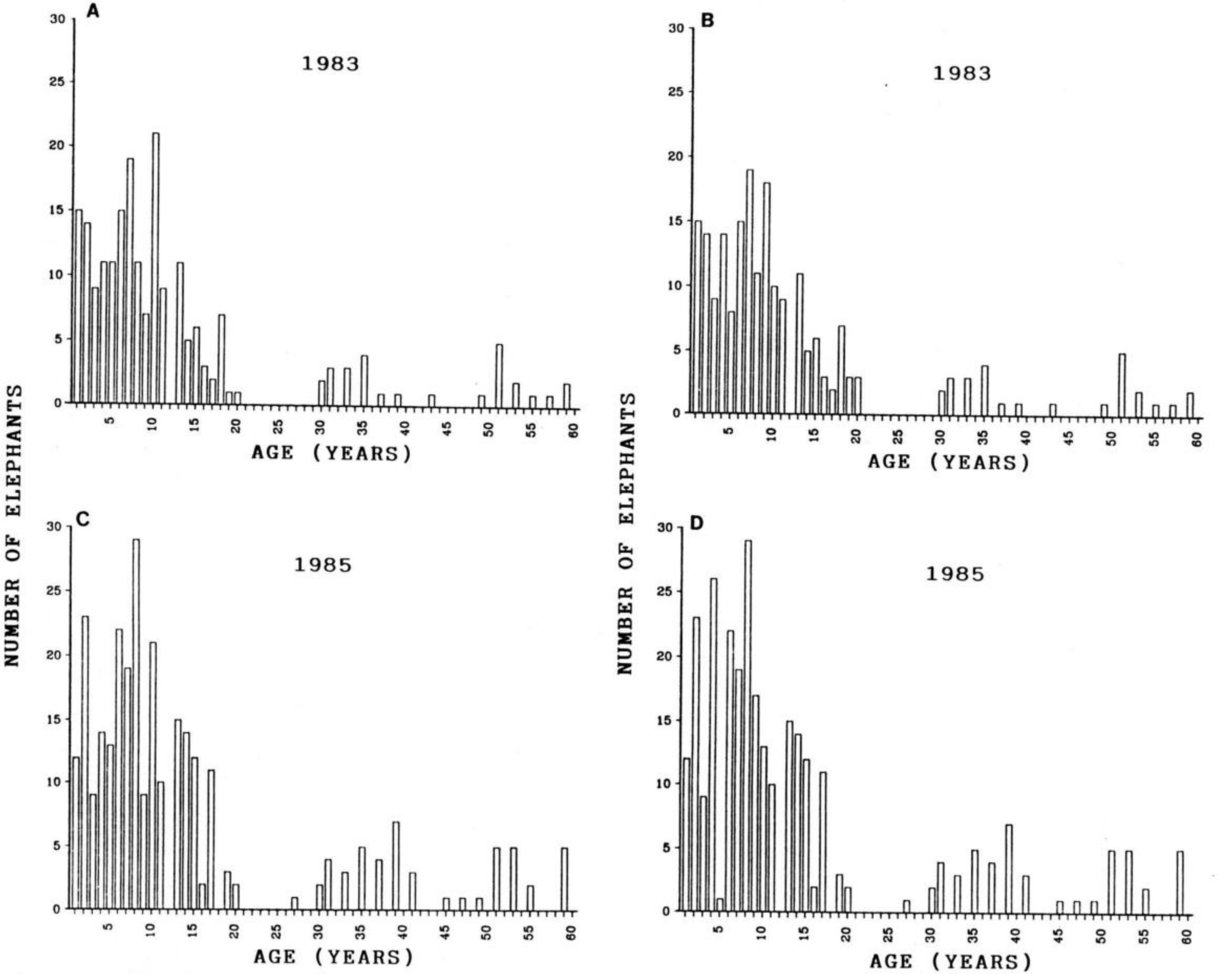


Figure 3.13 Age distributions of female elephants in the 1983 (A & B) and 1985 (C & D) samples from Etosha National Park using the method of Sikes (1968) (see text).

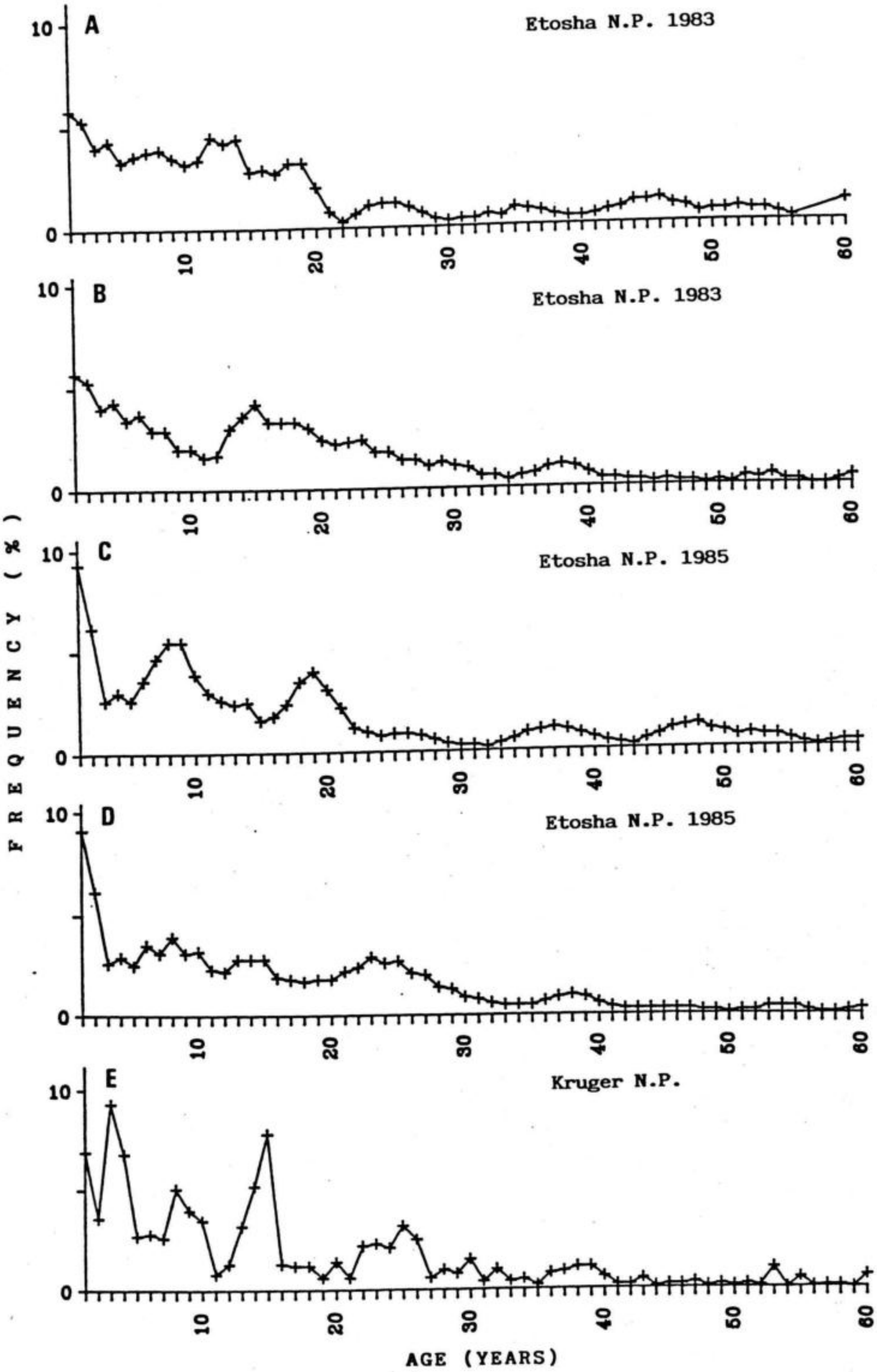


Figure 3.14 Age structures of female elephants derived from the revised age estimation method (Jachmann 1988) : A & C, and the method of Laws 1966 (B,D-J), for culled samples from Etosha National Park (A-D), Kruger N.P. (E), Kabalega Falls N.P. (F), Luangwa Valley N.P. (G), Hwange (H), Mana Pools N.P. (I) and Gonarezhou N.P. (J). Data are three-year running averages from references in text.

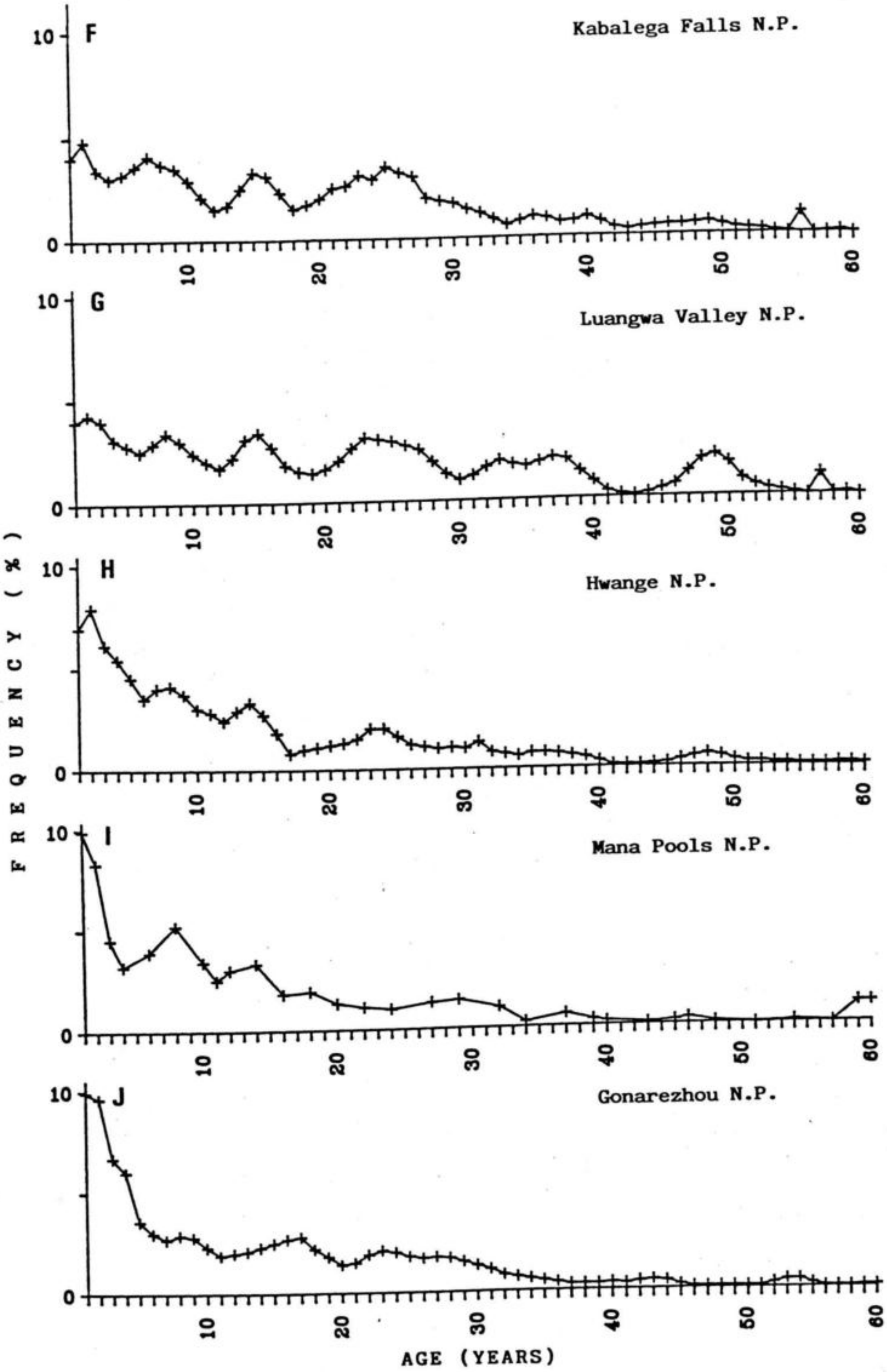


Figure 3.14 continued.

Table 3.8 presents the sampling intensity of elephants measured from photographs after discarding inadequate photographs, relative to populations size. Sample sizes used elsewhere ranged from 6% (Ottichilo 1986b), 8-12% (Leuthold 1976) to 31% (Croze 1972). Smaller samples are also available from four other regions in SWA/Namibia for comparison. Figure 3.15 A & B illustrates the resulting age distributions up to 30 years of age as first-order-averages for five surveys in Etosha N.P. and three elsewhere in SWA/Namibia. The five photogrammetrical age distributions from Etosha N.P. are significantly different from each other (χ^2=181.29; $p<.05$). The age distribution of the elephant population in Etosha N.P. was therefore unstable from 1984 to 1987.

Figure 3.16 illustrates summarized age structures of elephants based on aerial photogrammetry in Etosha N.P. Figure 3.17 illustrates summarized age structures of elephants from 12 samples of eight populations, including three from other localities in SWA/Namibia. Data for populations from East Africa were read off graphs in Laws (1969a), Croze (1972), Leuthold (1976) and Ottichilo (1986b).

The results of classifications of elephants into age groups during ground sightings in Etosha N.P. from 1977-1988 are illustrated in Fig. 3.18. Data for 1977-1978 are from De Villiers (1981) and from 1979-1982 are from unpublished departmental records.

DISCUSSION

Molar width and length are generally sufficient to identify a particular molar. When a molar is partially eroded, fragmented or not fully erupted and therefore not identifiable by measuring its width and length as in Fig. 3.4, the relative sizes of other molars present in the mandible reveal its identity. Confusion between M4, M5 and M6 is resolved in this way, and there was no need to resort to laminae counts or exposing roots for identification, as was found by Laws (1966), Hanks (1972b) and Jachmann (1988). Laws (1966) ascribes the overlap in size between molars as possibly due to the inclusion of both sexes in his sample, but Hanks (1972b) and the present study show that even by

Table 3.8 Aerial surveys and photogrammetrical samples used in constructing age distributions of elephants in Etosha National Park and other localities in SWA/Namibia.

DATE OF SURVEY	LOCALITY	POPULATION SIZE	NO. OF ELEPHANTS MEASURED (% OF POPULATION SIZE)	
May 1984	Etosha N.P.	1158	418	(36.1)
Dec. 1984	Etosha N.P.	2081	503	(24.2)
May 1985	Etosha N.P.	1244	535	(43.0)
Aug. 1985	Etosha N.P.	1186	374	(31.5)
Sept. 1987	Etosha N.P.	2021	666	(33.0)
Aug. 1987	Kaudom G.R. *	593	393	(66.3)
Aug. 1987	W. Caprivi **	c.200	76	(38.0)
Oct.-Nov. 1987	W. Kaokoland ***	c. 45	38	(84.4)
Oct.-Dec. 1987	Damaraland ****	c.250	94	(37.6)

*	in Kavango on the border between Botswana and SWA/Namibia, including Kaudom Game Reserve.
**	including Mahango Game Reserve.
***	northern part of the Kaokoveld, including Kunene River Mouth (10) Hoanib-Hoarusib River group (±35).
****	southern part of the Kaokoveld.

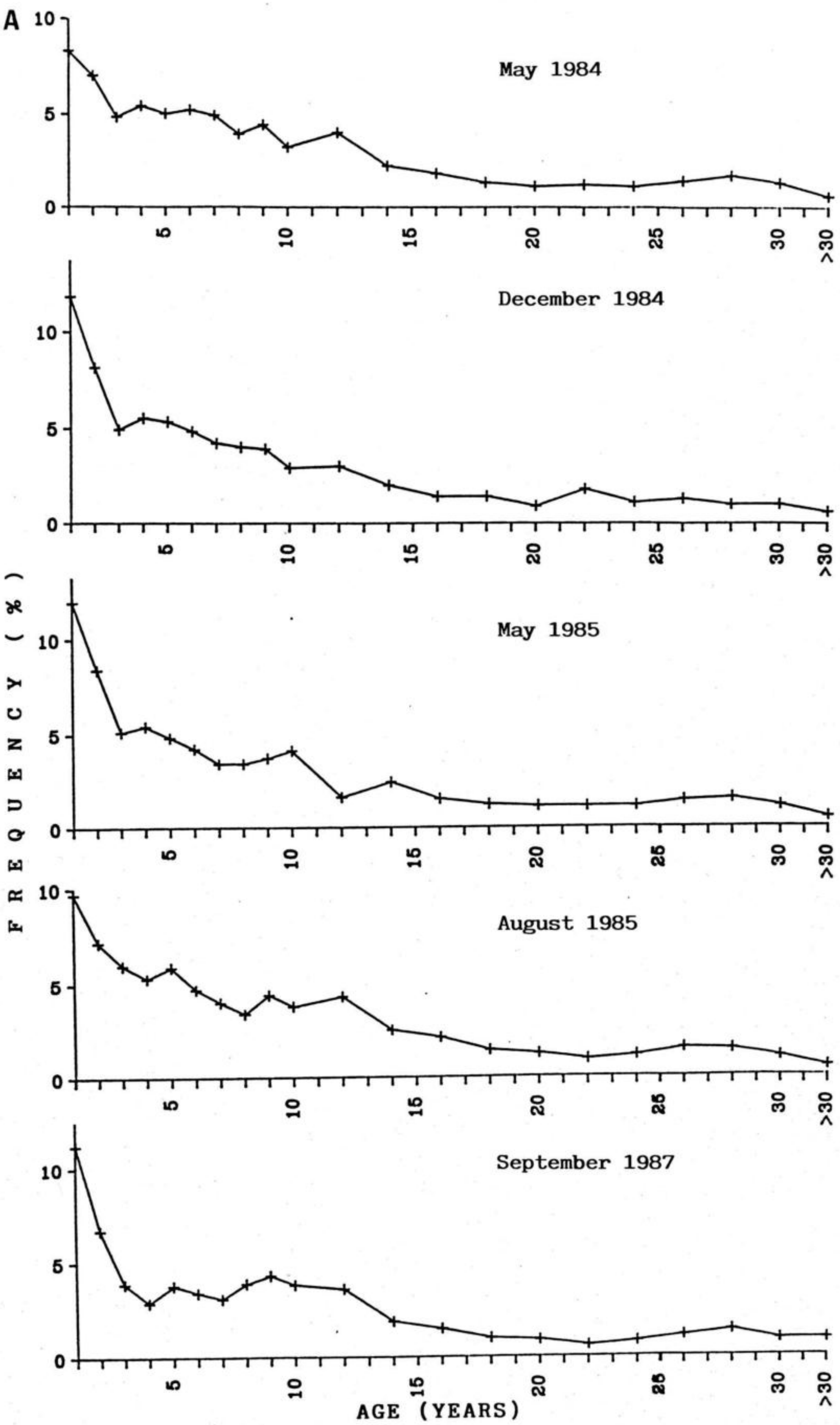


Figure 3.15 Frequency distributions in different age groups of elephants from aerial photogrammetry in Etosha National Park from 1984-1987 (A) and elsewhere in SWA/Namibia (B).

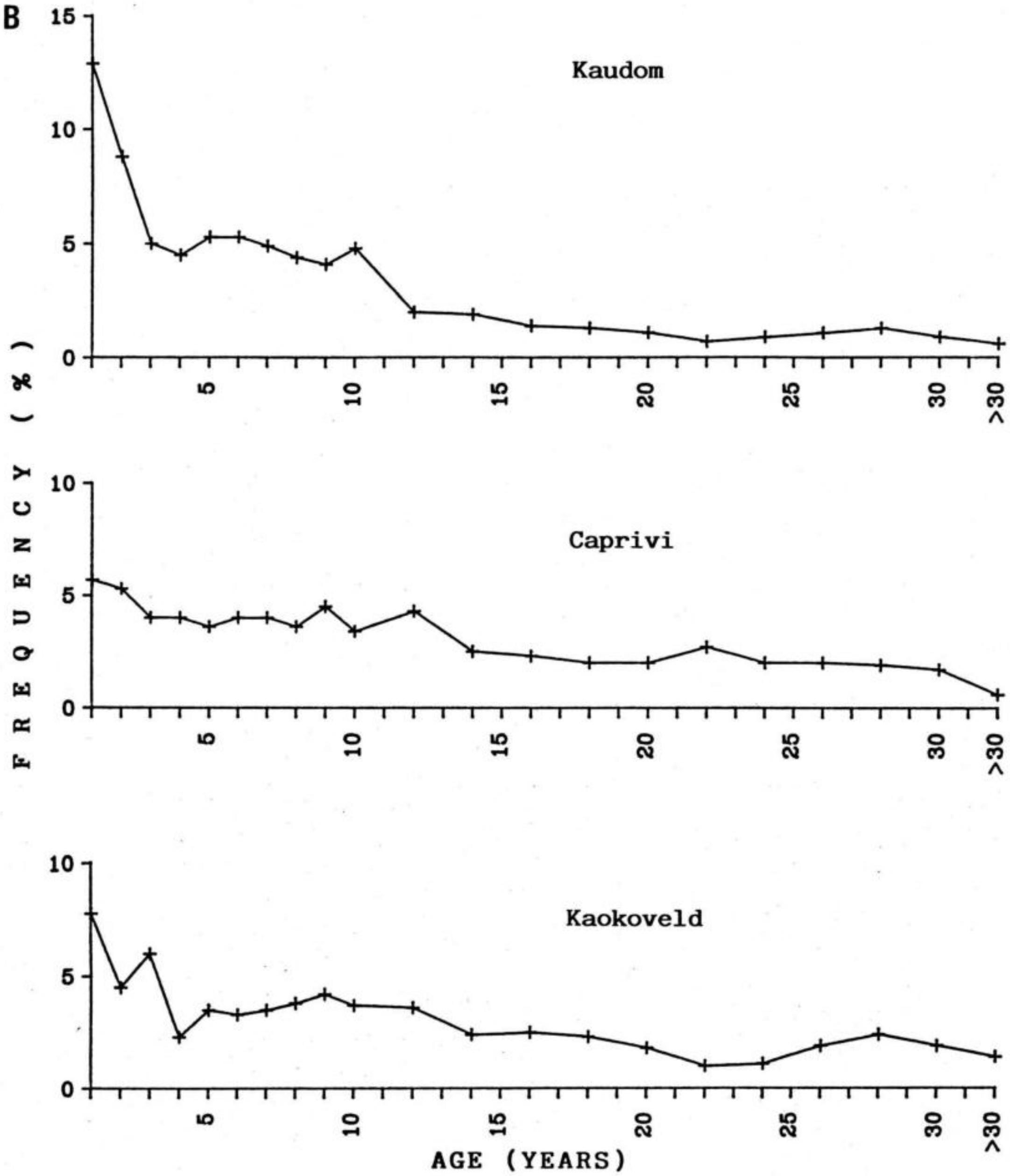


Figure 3.15 continued.

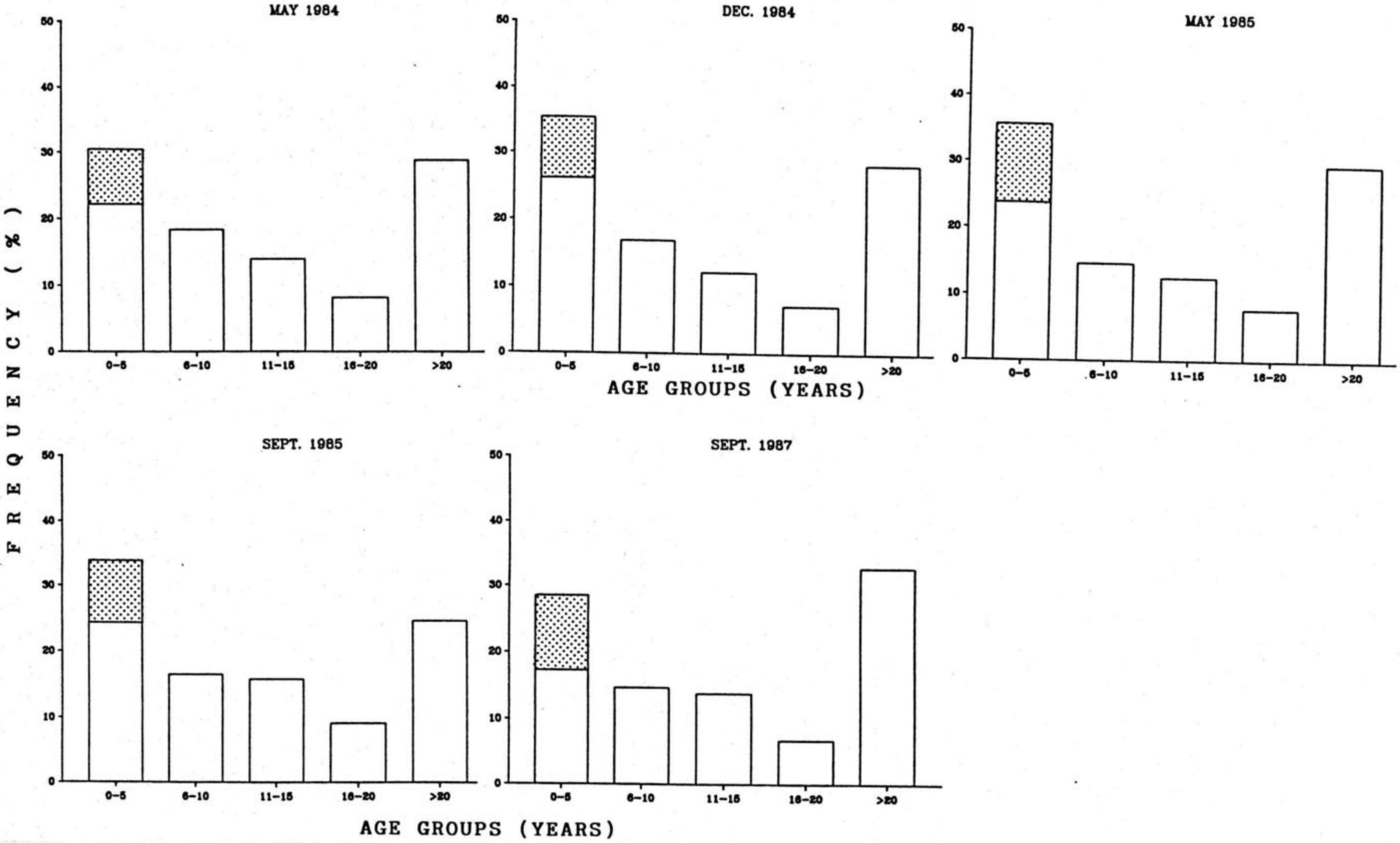


Figure 3.16 Summarized age structures from aerial photogrammetrical surveys of elephants in Etosha National Park. Shaded areas denote elephants < 1-year old.

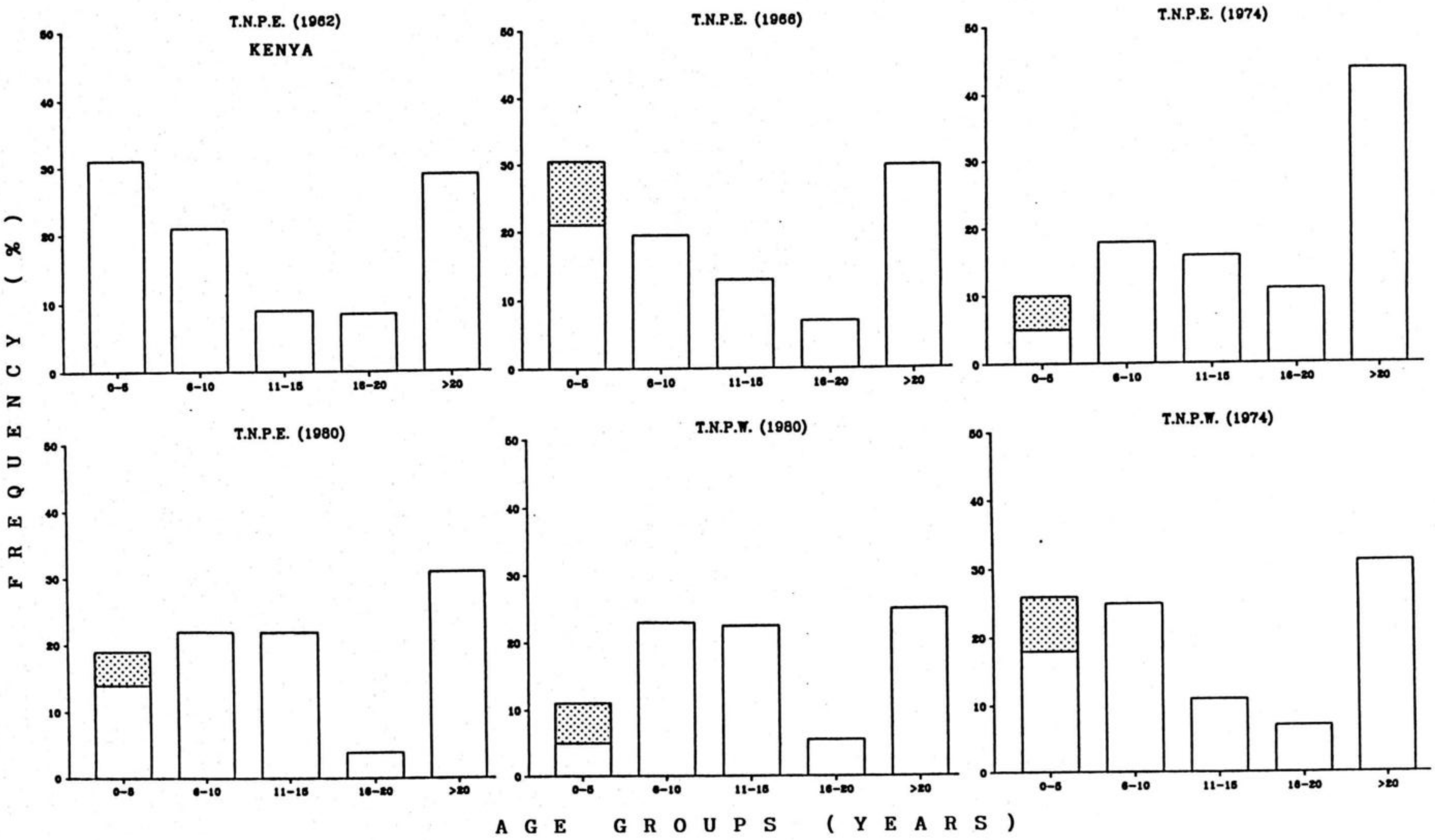


Figure 3.17 Summarized photogrammetrical age structures of 12 samples from eight populations of elephants in East Africa and SWA/Namibia. Data from references in text, all derived from aerial-photogrammetry, except Douglas-Hamilton (1972 in Leuthold 1976) who used ground-based photogrammetry in Lake Manyara N.P. (L.M.N.P.). Shaded areas denote elephants <1 year old, T.N.P.E. & W. = Tsavo N.P. East and West, K.F.N.P.S. = Kabalega Falls National Park South, K.N.P. = Kidepo National Park.

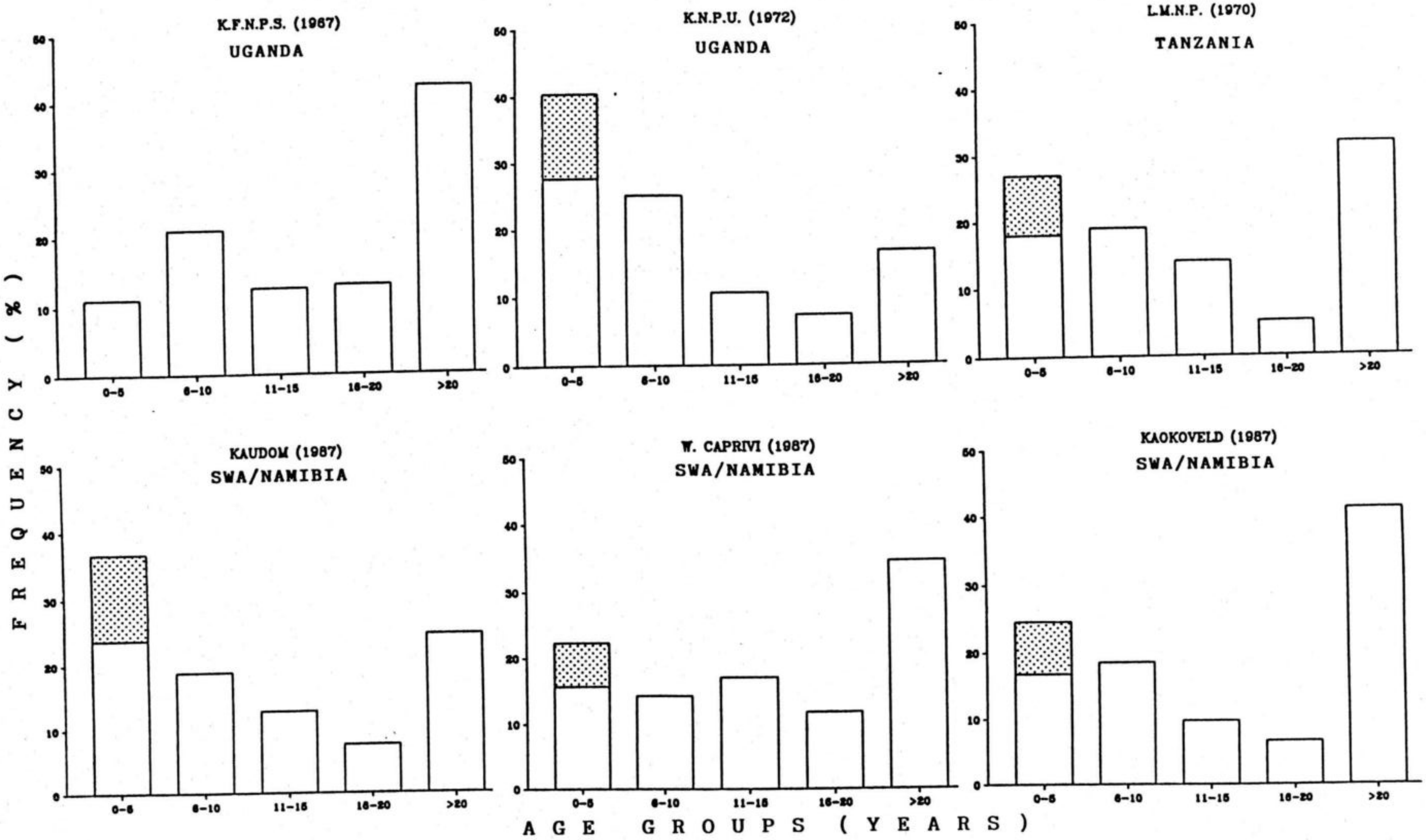


Figure 3.17 continued.

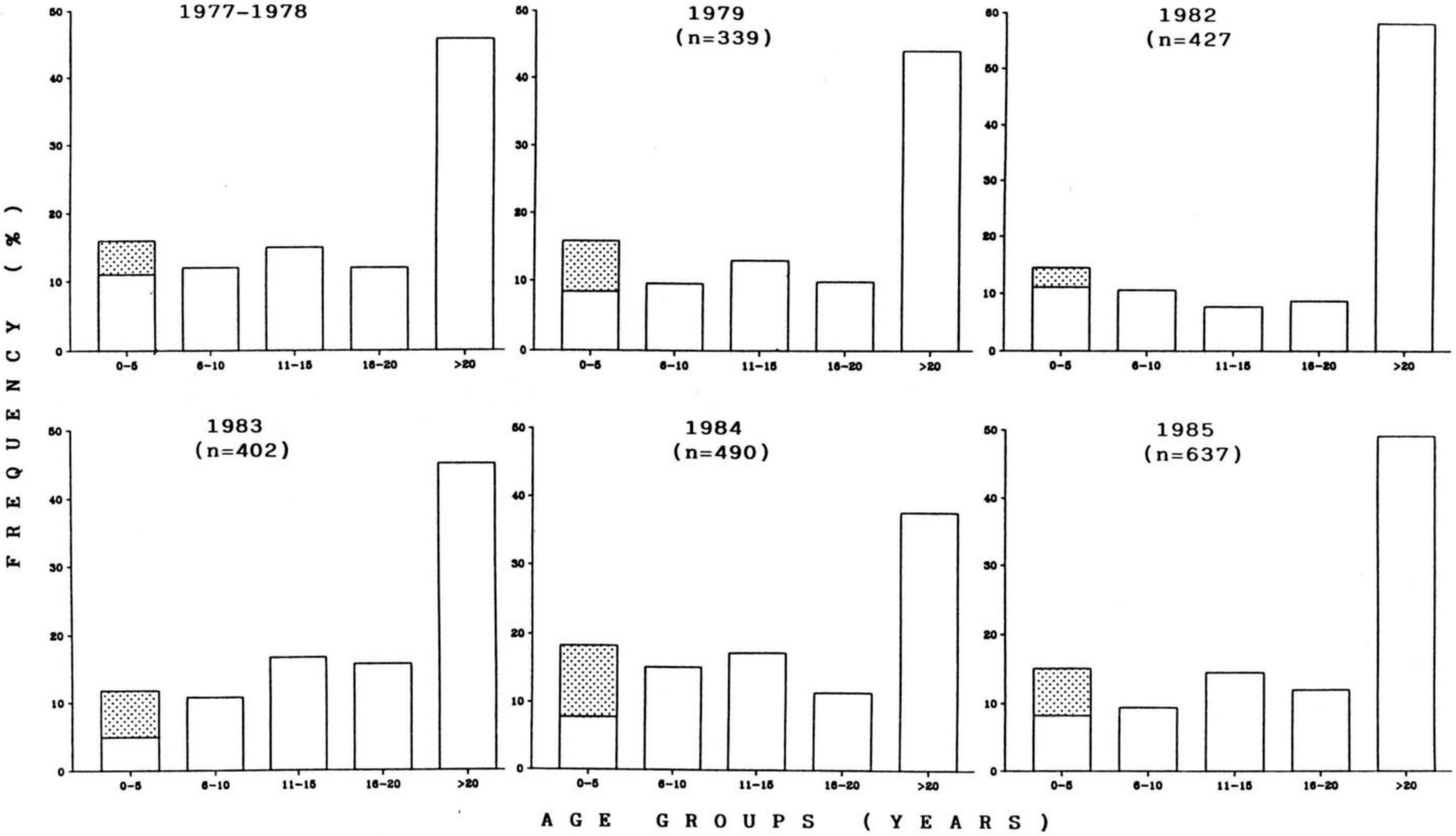


Figure 3.18 Age structures of breeding herds of elephants in Etosha National Park from 1977 to 1988, based on ground observations. The number of elephants classified per year is given in parenthesis. Shaded areas denote elephants <1 year old.

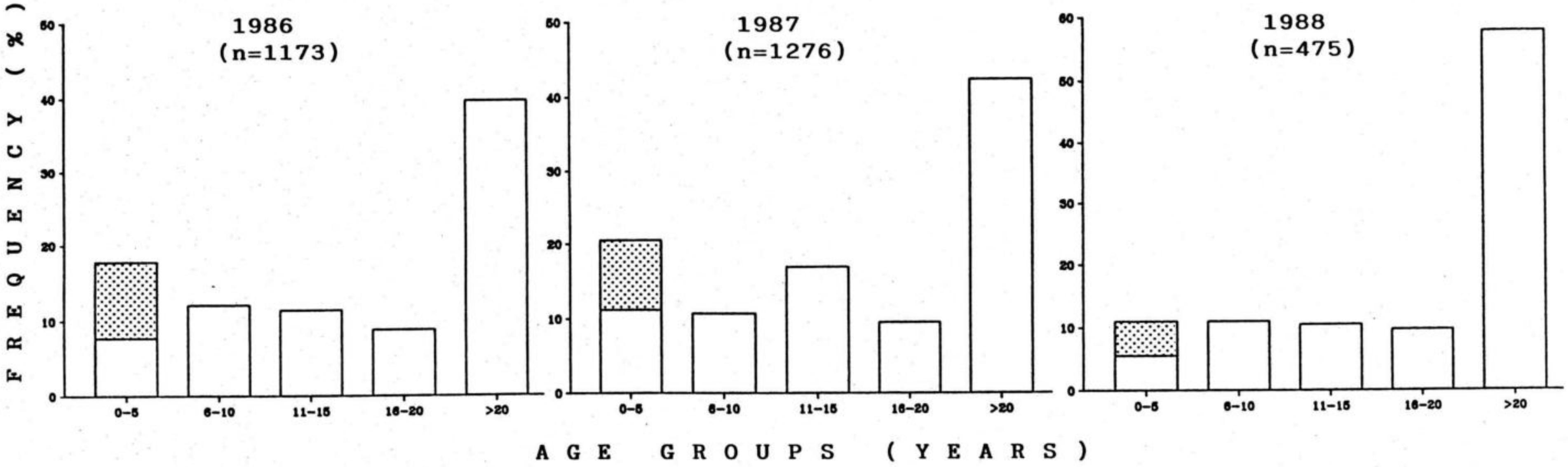


Figure 3.18 continued.

separating the sexes, the overlap remains, albeit reduced. The respective widths and lengths of molars from the sample from Etosha N.P. are similar to those from Zambia (Hanks 1972b) and smaller samples from Uganda (Laws 1966) and Kenya (Sikes 1968). Molars 3-6 from elephants in Malawi are considerably smaller than M3-6 from Etosha N.P., Uganda and Kenya (Jachmann 1985). Few abnormalities occurred in molars in the Etosha N.P. samples, similar to the sample of Hanks (1972b). Molar abscesses are regarded as indicative of loss in condition and population stress (Laws & Parker 1968), with a high incidence in Uganda (approximately 10%) but were rare in Etosha N.P. (0.4% of all jaws) and absent in Zambia (Hanks 1972b). Supernumerary molars in Etosha N.P. (0.2%) and Zambia (0.1%) were likewise less abundant than in Uganda (1.0%).

As both the methods of Sikes and Laws are based on the forward progress of the molar series in the jaw, the degree of correlation between age distributions derived from both methods is to be expected. This was also found by Malpas (1978, in Eltringham 1982) and Lark (1984). Individual ages assigned using the two methods may, however, differ greatly. The use of both methods require a degree of subjectivity, and no two workers will assign all mandibles to the same categories using either method. Ages derived by the method of Laws (1966) cannot be converted directly into Sikesian ages, as shown by the range of laminary indices occurring in each age class of Laws (1966). Such ranges were greater in Etosha N.P. elephants than suggested by Sikes (1968) and may reflect interpopulation differences.

Apart from Hanks (1972b) and Jachmann (1985, 1988) who counted laminae but used the Laws (1966) method to allocate ages, only Corfield (1973), Malpas (1978) and Lark (1984) seem to have used Sikes' method. Variation occurred in the number of laminae in the intact and fully developed M1-6 in all populations studied. There appears to be no standard number of laminae for each molar and variable numbers are more common than suggested by Sikes (1968). The same degree of variation was found in Etosha N.P. as by Laws (1966), Hanks (1972b) and Jachmann (1988), in Uganda, Zambia and Malawi. Identification of molars can therefore not rely on lamina counts only. Variation in the degree of reduction of the rudimental laminae, and complete development of first and last functional laminae due to the state of development of adjacent molars, is a further drawback in the use of referenced laminary counts as an index of age, as also found by Corfield (1973) and Jachmann (1988). Additional uncertainty is caused by the variation in the number and position of the foramina mentale which are supposed to be a fixed reference point for counting laminae. Variation in the number of laminae, reduction of rudimental laminae, and the position of the foramen mentale disqualify Sikes' method, and have consequently restricted its use.

Sikes (1968) furthermore provides only six ages for her 57 classes, but maintains that intermediary ages can be read off her age reference chart. This is problematical, as there is no evidence that intermediate groups follow in regular increments when in fact the six known ages do not. In Etosha N.P. at least, it seems wrong to regard the presence of the last lamina of M6 as placing an elephant in the terminal age group. This lamina is only a small portion of the normal occlusal surface of M6 in adult elephants, and death through starvation will ensue long before only the last lamina remains.

The most severe shortcoming of the use of Sikes' method for age determination of the mandibles of elephants from Etosha N.P., is that up to 18% of mandibles have no molar situated over the mental foramen, due to the premature loss of the last portion of the anterior molar present. It would not be correct to regard alveoli above the foramen mentale as equivalent to the last laminary group of the now lost molar, as a variable degree of erosion of the next molar and variation in the appearance of the empty socket from fresh to undetectable indicate that the preceeding molar is lost at different stages in molar progression in different elephants.

Premature loss of molars is regarded as premature only in terms of the age estimation methods, as no detrimental effects should necessarily be experienced by the individual elephant. Not only may individual elephants have different rates of molar progression, but other factors may also contribute to premature or delayed loss of some molars. At least two molars are lost coincidentally with major life history events, both of which may occur at variable ages, namely weaning and first lactation in females (Laws 1966, Laws 1969a). Calves are weaned at age 2-4 years, which coincides with the loss of M2. Increased demands on the occlusal surface during and after weaning may well unseat the partially resorbed roots of M2 earlier than otherwise. Cows may start lactating from 10-18 years, and greater nutritional demands during this phase may similarly effect the time of loss of M3. This of course would only affect females, and any such effect would have been easy to describe, were it not that males from about 10-20 years old are underrepresented in breeding herds and by consequence also in typical culled samples.

The most vexing issue regarding the elephants in the Etosha N.P. samples is the evenness of their Lawsian age distributions. Is this a mere chance effect of individual variation in molar progression combining with local environmental effects on occlusion and possibly interpopulation differences in the rate of molar progression, to make an age estimation method said to be biased in other situations, appear adequate? In this study, greater caution was applied in the identification of molars and allocation of mandibles to age classes in view of the findings of Fatti et al. (1980). Less emphasis was possibly placed on the status of a single feature in the mandible in favour of the overall appearance. The absence of peaks in the age distribution could well be of biological significance and suggests the operation of another mechanism on molar progression or population age structure, such as the premature loss of molars, synchronized breeding or even periodic changes in the mortality rate.

For unknown reasons, the refined age ranges in Laws (1967a) were ignored by Hanks (1972a), Sherry (1975), Smuts (1975), Williamson (1976) and Fatti et al. (1980). Age ranges in Laws (1966) are arbitrary, while those in Laws (1967a) were based on variation in the only independent criterion of age used in elephants other than molar progression, namely growth of the eye lens. Age distributions constructed from age class frequencies with the age ranges of Laws (1967a) are far more even than those using ranges in Laws (1966). It would be informative to have a sample from one of the populations with markedly uneven age distributions reassessed by more than one person, with regard to emphasis on eruption or loss of molars, and the ignored age ranges in Laws (1967a).

The validity of using a single series of captive elephants in Basel Zoo (Lang 1965, 1980) to discredit Laws' (1966, 1967a) method is questionable. Artificial diets and individual variation in the loss of molars as found in this study complicate this issue. Observations that individual growth rates are faster than previously believed and individual ages are overestimated by Laws' method will have to be substantiated in Africa. The revision of Laws' (1966) method proposed by Jachmann (1988) is a step in the right direction, but caution has to be exercised in the use of this revision. The fact that elephants in Malawi, on which the revision was based in part, are apparently smaller than savanna elephants (Loxodonta africana africana) elsewhere, and show some differences in their molars (Jachmann 1985, 1988) might not support the use of the revised method in other populations.

The use of frequency distributions of the number of individuals in each year group, or age distributions, as derived from molar progression or photogrammetry, to indicate change in the age structure of a population might be misleading. Age estimation methods for elephants are presently not sufficiently accurate or precise to show changes other than gross perturbations such as in the series of age structures before and after the population crash in Tsavo N.P. (Fig. 3.17). The age structure of a population furthermore does not always provide conclusive evidence of a population increase or decrease, as explained by Caughley (1977a, p 120-123). The summarized age structures for the Tsavo N.P. (East) elephant population in Fig. 3.17 also illustrate this point. This population would have been decreasing in 1966, were it not for large-scale immigrations due to compression (Laws 1967a, 1969a, b, Laws & Parker 1968), as the mean calving intervals increased and the age at first conception was delayed. After the drought in Tsavo N.P. and the population crash, the population apparently increased (Leuthold 1976) until poaching caused a further decline (Ottichilo 1986a, b). The age structure in 1974 (Fig. 3.17) at a time when the population was increasing, still reflected the effects of the drought and mass mortality of young elephants in particular.

The age structure of the Etosha N.P. elephants from 1983 to 1987 appears similar to those from age structures from Tsavo N.P. in 1966 and Lake Manyara N.P. in 1970. No homeostatic delays in reproduction occurred in the latter population (Douglas-Hamilton 1972, Croze et al. 1981). In view of the limitations on the age estimation methods, the only conclusion that can be reached is that the age structure of elephants in Etosha N.P. has not changed dramatically from 1983 to 1987 based on aerial photogrammetry, or from 1977 to 1988 using ground observations. Classification of elephants into age groups in ground counts is clearly biased, but the error is probably systematic. Calves are undercounted from the ground while the number of adults appears to be overestimated.

In the last decade, however, the number of elephants changed dramatically in Etosha N.P. From 1977 to 1983 the population more than doubled, and declined from 1983 to 1986 by approximately 60 percent. It is unlikely that the age structures over this period would have remained so similar if the population increase and decrease were due to changes in the age-specific rates of births and deaths only. The apparent stability of the age structure of elephants in Etosha N.P. therefore supports the suggestion that the observed changes in elephant abundance in Etosha N.P. from at least 1973 to 1987 were due to movements by elephants in and out of the park.

CHAPTER 4 REPRODUCTION

INTRODUCTION

Perry (1953, 1964, Amoroso & Perry 1964) pioneered the study of reproduction in the African elephant. Numerous studies followed and reproduction has received more attention than any aspect of elephant biology, other than the effect of elephants on vegetation. Most studies on reproduction can be divided in two groups, namely physiological and in terms of the reproductive output of a population. The physiological studies may be characterized by the work of Short & Buss (1965), Buss & Smith (1966), Short (1966, 1969), Laws (1969 a,b), Smith, Hanks & Short (1969), Hanks & Short (1972), Hanks (1973a), Smith & Buss (1973) and Plotka, Seal, Schobert & Schmoller (1975), who described the reproductive and ovarian cycles and the function of the corpus luteum. Elephants are generally accepted to have a gestation period of 22 months, with rare exceptions; a single foetus, a polyovular oestrus and a number of oestrous cycles before conception. The great variation in luteal tissue mass during gestation as well as the relatively low levels of progesterone during pregnancy still have to be explained convincingly. Recent evidence from long-term behavioural work in Amboseli N.P. indicates that behavioural oestrus might not be recurrent (Moss 1983), and serves as a general indication that reproduction in female elephants is imperfectly understood.

Reproduction in the male is also unusual, as the elephant is a testicond and lacks the typical mammalian epididymus. Buss & Johnson (1967), Johnson & Buss (1967a, b), Short, Mann & Hey (1967) and Hanks (1973b) described the development of the male reproductive tract and the temporal gland. Jones (1973, 1980), Jones, Rowlands & Skinner (1974) and Jones, Bailey & Skinner (1975) described sperm maturation in the Wolffian duct in view of the absence of an epididymus, as well as sperm collection and storage for captive breeding purposes. Semen characteristics were also described by Howard, Bush, De Vos & Wildt (1984). Puberty is reached from about 11 years of age and there appears to be no annual cycle. The most vexing issue was the presence of musth in the African elephant and its function in male reproduction. Musth was first described in this species by Poole & Moss (1981), Poole (1982), Poole, Kasman, Ramsay & Lasley (1984) but several aspects, notably the endocrine pathways involved in the onset and periodicity of musth, are still unclear. Several studies have also reported on androgen concentrations in musth and non-musth males (Howard et al. 1984, Hall-Martin & Van der Walt 1984, Hall-Martin 1987).

Young males are evicted from the breeding herd or family unit at the onset of puberty, and form temporary associations with other and often older males. Single old bulls are not necessarily senile as suggested by Sikes (1971) and represent at least some individuals seeking out breeding herds. Bulls in musth leave male groups, actively search for breeding herds and dominate mating activities. Other non-musth bulls may nevertheless also be found in loose association with a breeding herd, and are also fertile and mate whenever an opportunity arises (Poole 1982). Conceptions occur throughout the year, although there may be a peak in the wet season, which is also the time when herds aggregate (Hanks 1972a, Smuts 1975).

The role of musth in African elephants is explained as a secondary reproductive strategy allowing lower ranking bulls to escape hierarchial constraints on access to cows and opportunities to mate. The fact that bulls in musth mate far from their normal ranges is seen as a strategy ensuring outbreeding (Hall-Martin 1987). Elephants have nevertheless been found to be the most inbred of all wild or domestic mammals studied (Osterhoff, Young & Ward-Cox 1972; Osterhoff, Schoeman, Op't Hof & Young 1974) and musth as an outbreeding mechanism seems conjectural. Furthermore, if musth is a device to allow an escape from hierarchical positions, why should there be a male social hierarchy at all? Other aspects of musth and home range fidelity described elsewhere are perhaps also incompletely explained, and are certainly less than evident in the low density situation in Etosha N.P.

The second field of interest, and more relevant to this study, is the reproductive pattern of individual populations. Laws (1967b, 1969a, b, 1971, 1981), Laws & Parker (1968) and Laws, Parker & Johnstone (1975) described the role of reproductive homeostasis in population regulation. The age at first reproduction in the female, the mean length of the calving interval and the mean age of reproductive senescence were suggested to be the three variables dependent on density, stress, nutrition and rainfall. The initial work was done on five populations in Uganda and Kenya, but several other populations - in Zambia (Hanks 1972a), Zimbabwe (Sherry 1975, Williamson 1976, Kerr 1978, Dunham 1988), South Africa (Smuts 1975) and Malawi (Jachmann 1980, 1986) - have now been studied on this level. Most samples were derived from culling operations and a good framework exists to compare similar samples from Etosha N.P.

METHODS

A total of 316 female elephants were culled during the present study: 102 in 1983 and 214 in 1985. Uteri and ovaries were collected intact, except in the case of large foetuses. The latter were removed and processed on site. All foetuses were weighed and sexed, and standard foetal body measurements were recorded as described by Ansell (1965) and Van Zyl & Skinner (1970). Foetal age and theoretical conception and parturition dates were determined using the Huggett & Widdas (1951) formula, as first used by Perry (1953) and subsequently in all later studies. The same parameters were calculated from the revised foetal growth formula of Craig (1984), as based on observed differences in growth increments in foetuses from the same conception season sampled a year apart.

Reproductive status of all culled females was determined from the condition of the reproductive tract following Laws (1969a). Ovaries were examined macroscopically for the presence of corpora lutea, follicles and ovulation scars. Ovaries in the prepubertal class contained no large follicles or luteal bodies. Pubertal females had ovaries with at least one follicle over 5 mm in diameter but no luteal bodies. Parous females had at least one corpus luteum or corpus albicans in their ovaries. Both uterine cornu were slit longitudinally from the cervix to the uterotubal junction. Placental scars were counted and measured as described by Laws (1967b). Obvious pathologies of the reproductive tract were described from macroscopical appearance, and in 1985 confirmed by a veterinary surgeon.

Calving intervals were estimated from placental scar counts as described by Laws (1967b), and also from the ratio of pregnant to non-pregnant parous cows in the sample, as described by Perry (1953).

Foetal growth

The generalized formula of Huggett & Widdas (1951) for determining foetal growth is :

$$w^{1/3} = a\ (t-t_0) \qquad (1)$$

where w = foetal mass(kg), a = specific foetal growth velocity, t = age of the foetus (days) and t_0 is a constant. Hereafter t refers to foetal age in days unless otherwise stated. Initial growth of a mammalian foetus is less than the rate of growth throughout gestation. The initial growth was estimated by Huggett & Widdas (1951) to be equal to 10% of the gestation period for mammals with a gestation time exceeding 400 days. The initial growth phase is not described by the typical geometric Huggett & Widdas (1951) relationship between foetal mass and time, and t_0 denotes the point on the time axis where linear growth presumably starts. The suggestion that $t_0 = 0.1$ for elephants is somewhat arbitrary. With a birthmass of 120 kg and gestation perid of 660 days (and t_0 therefore equals 66) the formula commonly used for determining foetal age, as in Buss & Smith (1966), Laws & Parker (1968), Laws (1969), Sherry (1975), Smuts (1975), Williamson (1976) and Kerr (1978) is :

$$t = 120.5\ \ w^{1/3} + 66 \qquad (2)$$

Craig (1984) has shown that when foetuses from a single conception season are sampled twice, a discrepancy of 57-90 days occurs, and his revised formula for determining foetal age is :

$$t = 106\ w^{1/3} + 138 \qquad (3)$$

using the lower limit of the observed discrepancy of 57 days.

RESULTS

Foetal growth and seasonal breeding

The presence of two distinct size classes of foetuses in a sample taken in any one year in Etosha N.P. and elsewhere in southern Africa indicated an annual breeding season for elephants in this region as suggested by Craig (1984). The two size modes corresponding to ≤ 5 kg and 50-70 kg foetal mass from Etosha N.P. were similar to samples from elsewhere, but intermediary sizes occurred (Fig. 4.1). The degree of variation between the two samples from 1983 and 1985 is better illustrated in Table 4.1, where more intermediary sizes occurred in the 1985 sample than in 1983.

No single cohort of conceptions were represented in both the 1983 and 1985 samples, as the interval between the two samples exceeded the gestation length by 2-3 months. Discrepancies in the mean conception ages of such a cohort sampled at different times could not be used to verify Craig's (1984) revised formula describing foetal growth. The frequency of conceptions and births from both samples as determined from the standard formula (Perry 1953) and the revised one (Craig 1984) are presented in Fig. 4.2 A & B respectively. The effect of the revised formula is to contract the breeding season to a shorter period. Both schedules indicate that 75-84% of conceptions and 55-66% of parturitions were synchronized with the rainy season.

Figure 4.3 A & B illustrates the frequency of conceptions and births in different months from the 1983 and 1985 samples separately. Approximately 80% of the conceptions occurred in the period November-March, while less than 60% of parturitions occurred in the same period, following Craig (1984). The distribution of births and conceptions correspond well in the 1983 and 1985 samples, and the absence of foetuses other than in the modal sizes in 1983 is likely to be the result of inadequate sampling. There are nevertheless conceptions from two different conception seasons in both samples, and variation due to rainfall is not evident from Fig. 4.4. In Fig. 4.4, actual rainfall per month and the frequency of conceptions and births are illustrated for the 1983-1984 and 1985-1986 seasons respectively. This is the only cohort that was adequately represented in the sample, and 70.8% of conceptions occurred during the rains from November to April. Only 41% of parturitions coincided with the rains from November to April.

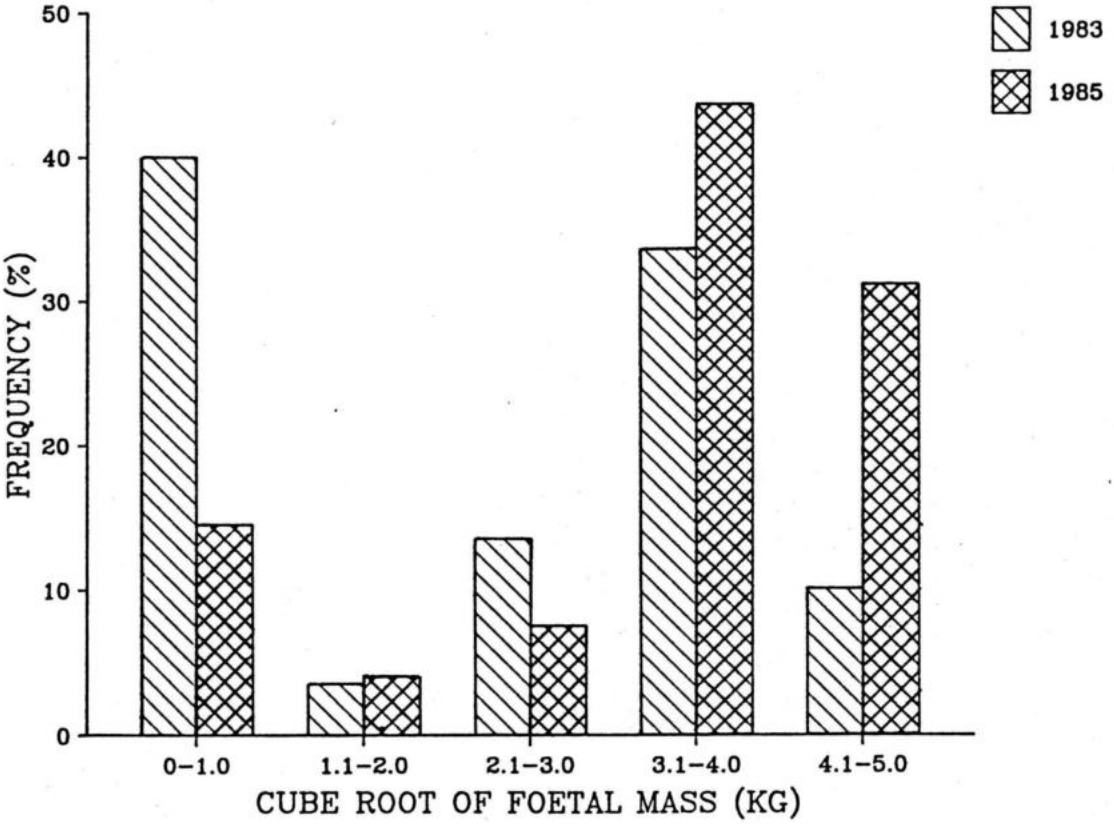


Figure 4.1. Frequency distribution of elephant foetal mass in Etosha National Park in 1983 and 1985.

Table 4.1 Frequency distribution of elephant foetal mass in two samples from Etosha National Park.

FOETAL MASS (kg)	1983 No. of foetuses	%	1985 No. of foetuses	%
0 - 5.0	13	43.3	9	16.4
5.1 - 10.0	-	-	2	3.6
10.1 - 15.0	1	3.3	-	-
15.1 - 20.0	2	6.7	1	1.8
20.1 - 25.0	1	3.3	1	1.8
25.1 - 30.0	-	-	3	5.5
30.1 - 35.0	-	-	1	1.8
35.1 - 40.0	-	-	7	12.7
40.1 - 45.0	-	-	4	7.3
45.1 - 50.0	-	-	1	1.8
50.1 - 55.0	7	23.3	2	3.6
55.1 - 60.0	2	6.7	6	10.9
60.1 - 65.0	2	6.7	1	1.8
65.1 - 70.0	2	6.7	2	3.6
70.1 - 75.0	-	-	4	7.3
75.1 - 80.0	-	-	4	7.3
80.1 - 85.0	-	-	3	5.5
85.1 - 90.0	-	-	2	3.6
90.1 - 95.0	-	-	-	-
95.1 - 100.0	-	-	2	3.6
TOTAL	30		55	

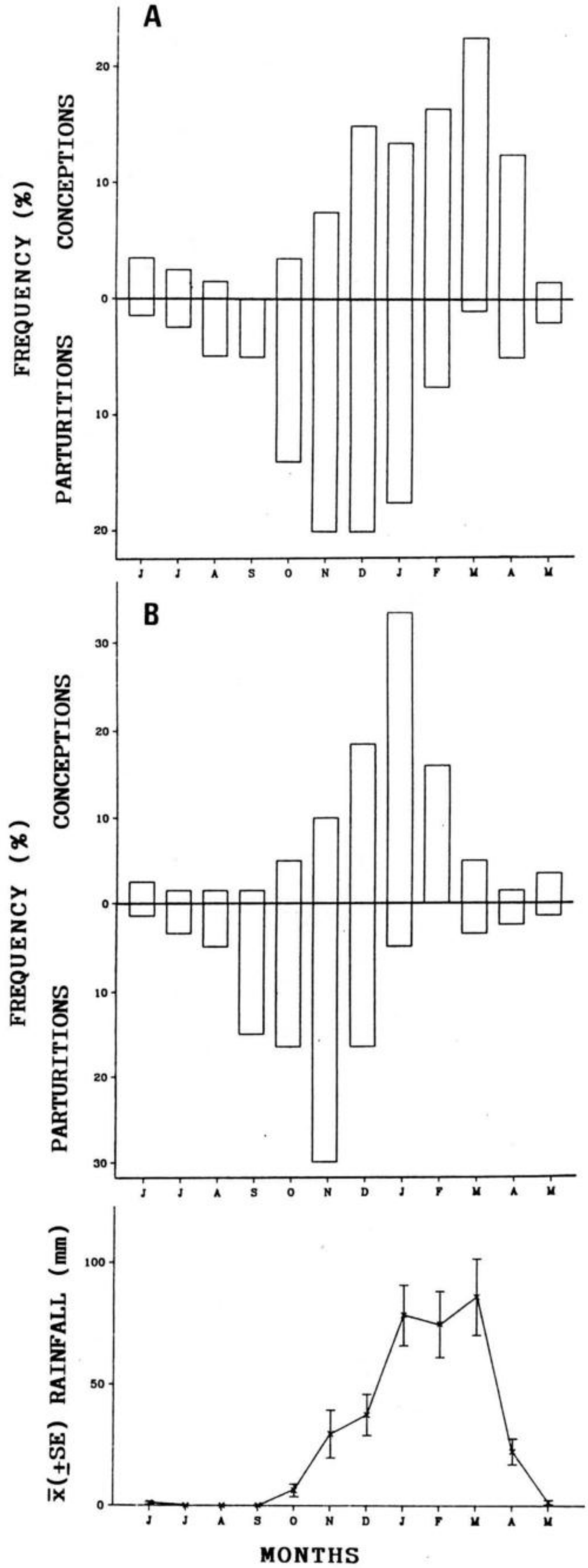


Figure 4.2 Distributions of conceptions and parturitions of elephants in Etosha National Park and rainfall, based on conception dates derived from A : Perry (1953) and B : Craig (1984).

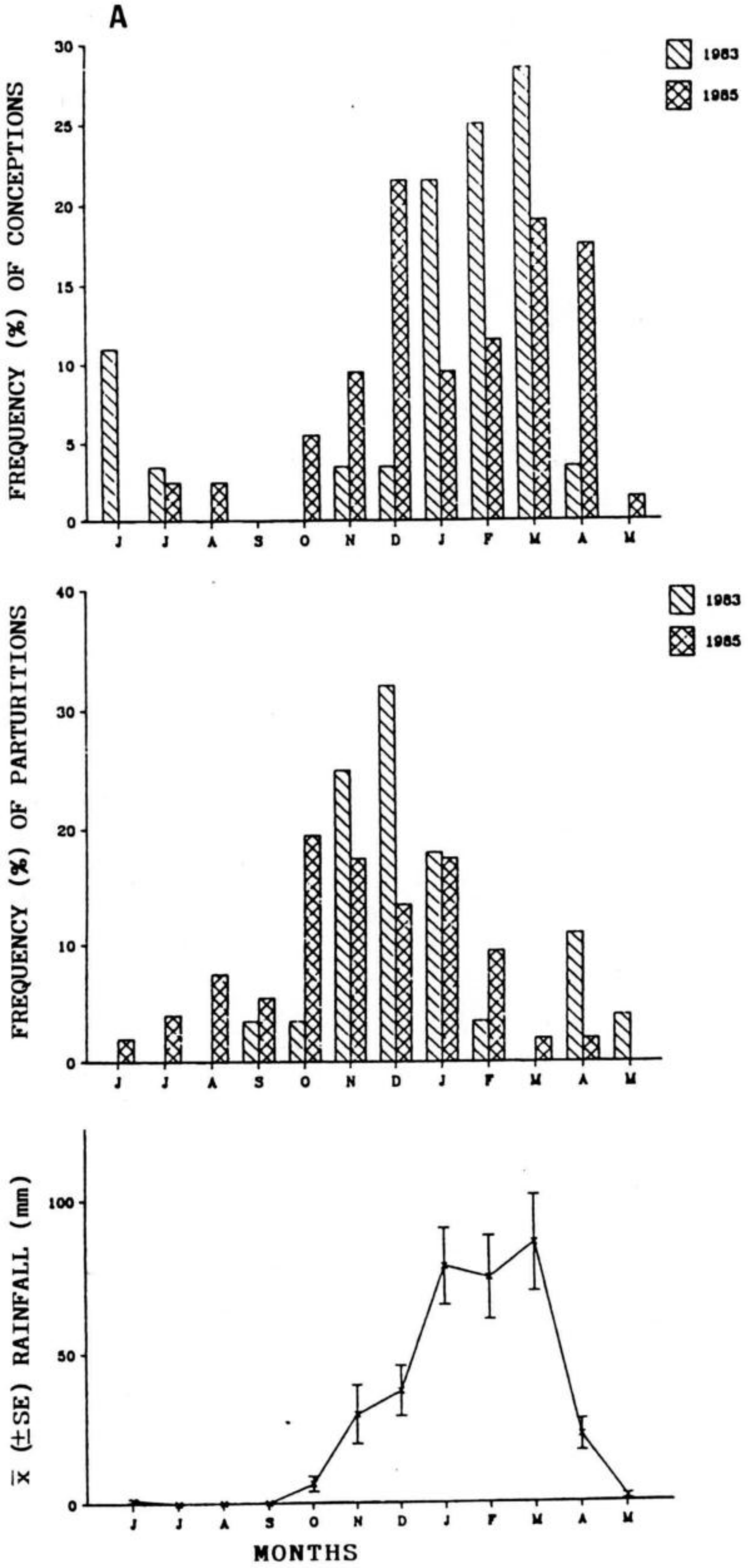


Figure 4.3 Frequencies of conceptions and births of elephant in Etosha National Park for the 1983 and 1985 samples separately according to A : Perry (1953) and B : Craig (1984).

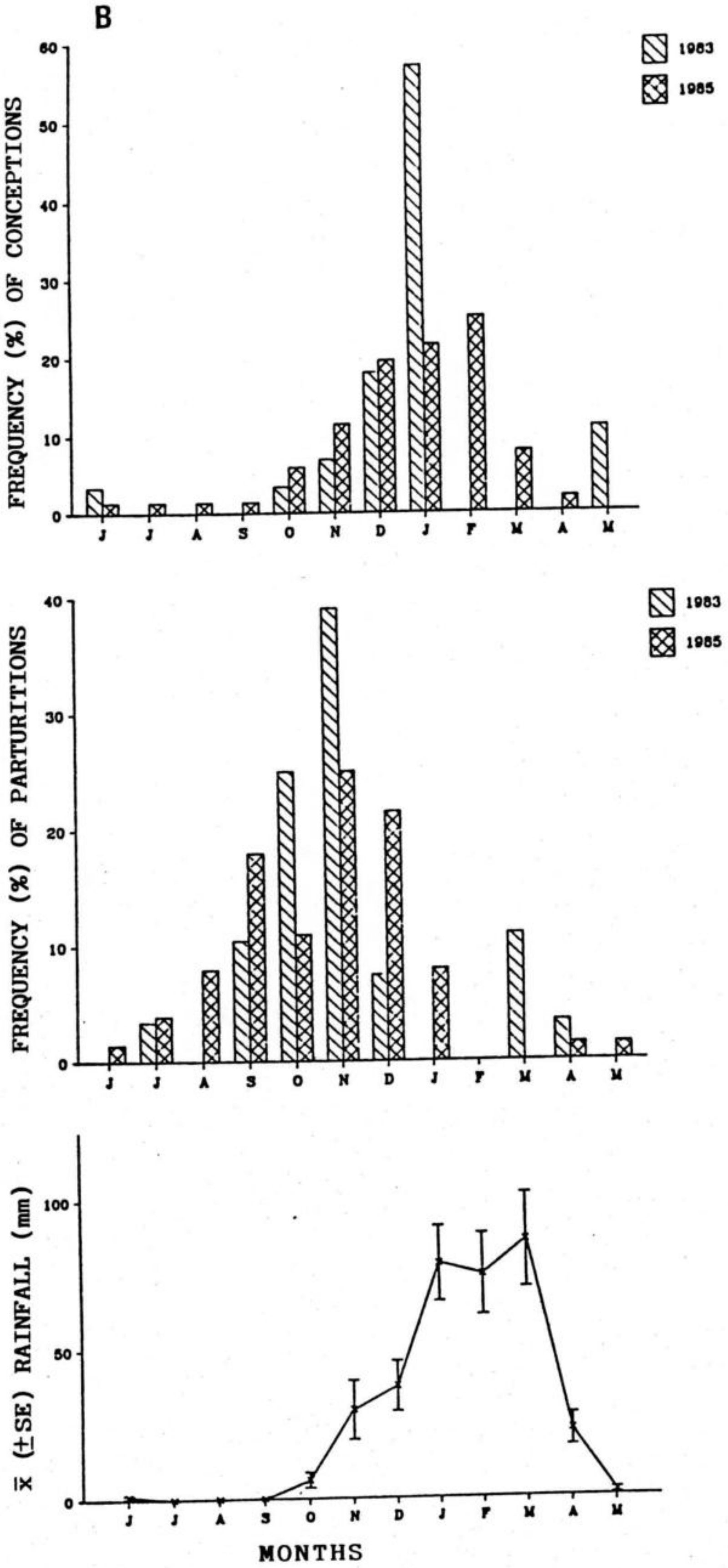


Figure 4.3 B. Continued.

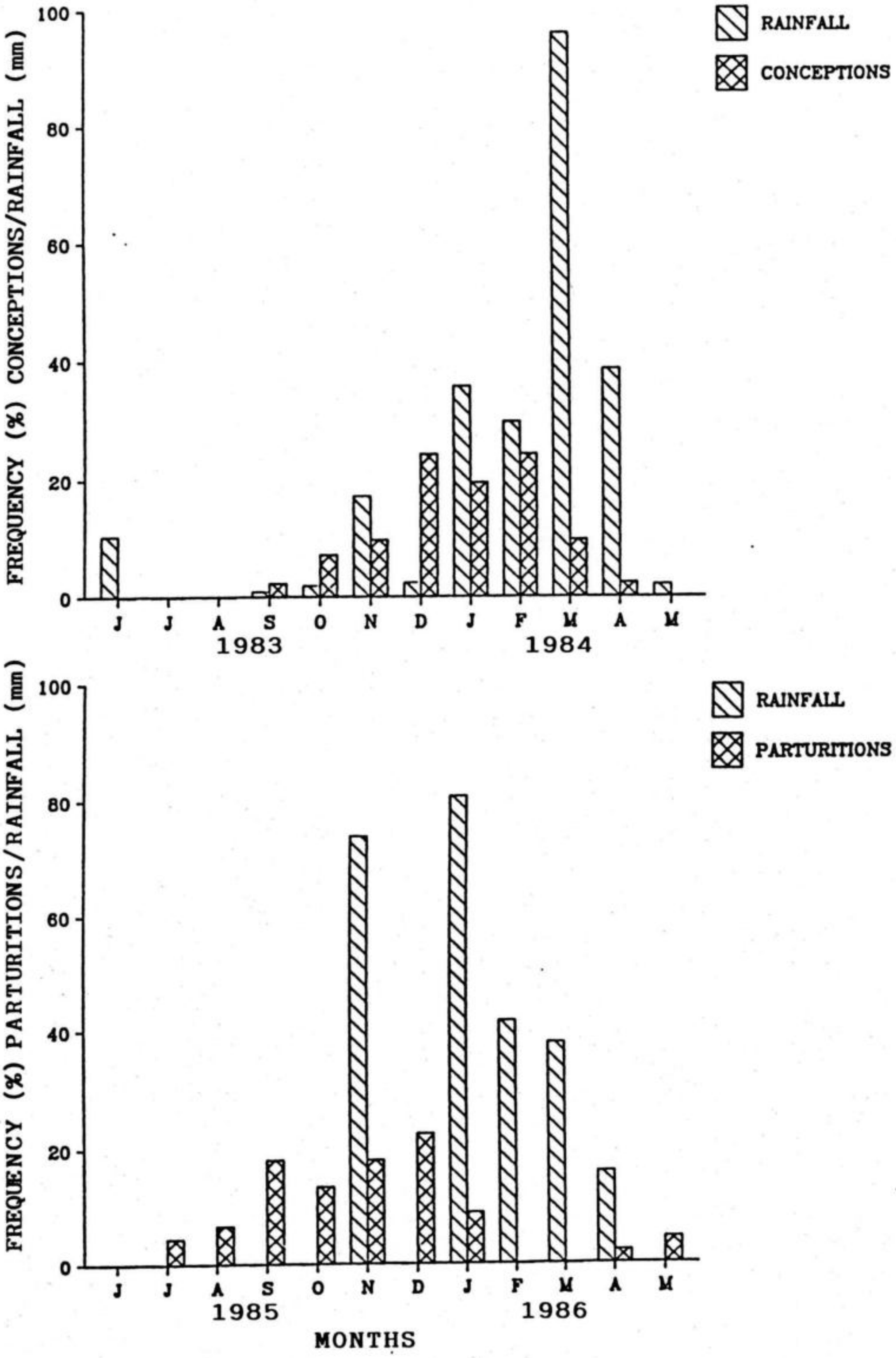


Figure 4.4 Monthly rainfall and the frequency of elephant conceptions and births for foetuses from one conception season, in Etosha National Park.

Table 4.2 presents the distribution of primiparous and multiparous females which conceived in and out of the peak of conceptions from November to March. The mean ages of females conceiving during the peak and outside it, are not significantly different in 1983 or 1985. Females with perhaps a recent attempt disrupted by mortality, could account for most conceptions at odd times of the year. Only four of the 13 pregnant females which conceived outside the breeding peak were lactating which may indicate calf mortality in the remainder.

Variation in the size of elephant neonates or the length of the gestation period may possibly be related to the age, condition and size of the mother or the sex of the foetus. The difficulty in proving any factor is that foetuses of the same age have to be compared, and foetal age is determined as a function of foetal mass. Figures 4.5 and 4.6 illustrate the correllation between crown-rump length, vertebral column length and foetal age in the two samples in 1983 and 1985. If nutritional stress influences foetal size at a given age, the slopes of regressions in Figs. 4.5 and 4.6 should differ, as nutritional stress was evident during the 1980-1983 drought. In 1983, last trimester foetuses appeared lean with loose skin, quite different from the well-rounded foetuses collected in 1985.

A testing procedure for determining whether two regressions have different slopes is given by Steel & Torrie (1980). There is no significant difference in slopes of regressions of foetal crown-rump length over age in 1983 and 1985. The slope of the regression of vertebral column length over foetal age was, however, significantly greater in 1985 than in 1983 ($t_{73}= 2.2358$ $p < 0.05$; $F_{1,73}= 4.9987$ $p < 0.05$). Measuring the length of the vertebral column is relatively free of error compared to measuring crown-rump length, which depends on posture as well as size. It seems that foetuses were growing slower in 1983 than in 1985, probably the result of maternal nutritional stress during the 1980-1983 drought, as length increments occurred at a slower rate when scaled on foetal mass. An effect like this might explain the variation in birth mass and gestation period recorded. When foetal age is calculated following Perry (1953), the slope of the regression of vertebral column length/foetal age is similarly greater in 1985 than in 1983 ($t_{73}= 2.3053$ $p < 0.05$; $F_{1,73}= 5.3145$ $p < 0.05$). The slopes of crown-rump length/foetal age are not different between 1985 and 1983, as in the other calculation of foetal age following Craig (1984) ($t_{73}= 1.3817$ NS; $F_{1,73}= 1.9092$ NS).

Table 4.2 Number of primiparous and multiparous females and age of females which conceived during and outside the peak conception season (November - March) in Etosha National Park.

	NO. OF FEMALES CONCEIVING IN NOV. - MARCH	NO. OF FEMALES CONCEIVING IN APRIL - OCT.	p
1983			
NO. PRIMIPAROUS	3	2	
NO. MULTIPAROUS	20	3	
$\bar{x}$ AGE ± SE	28.0 ± 2.5	24.6 ± 5.2	NS,P<0.05*
1985			
NO. PRIMIPAROUS	7	2	
NO. MULTIPAROUS	42	6	
$\bar{x}$ AGE ± SE	25.4 ± 1.7	20.8 ± 3.3	NS,p<0.05*

* t-test

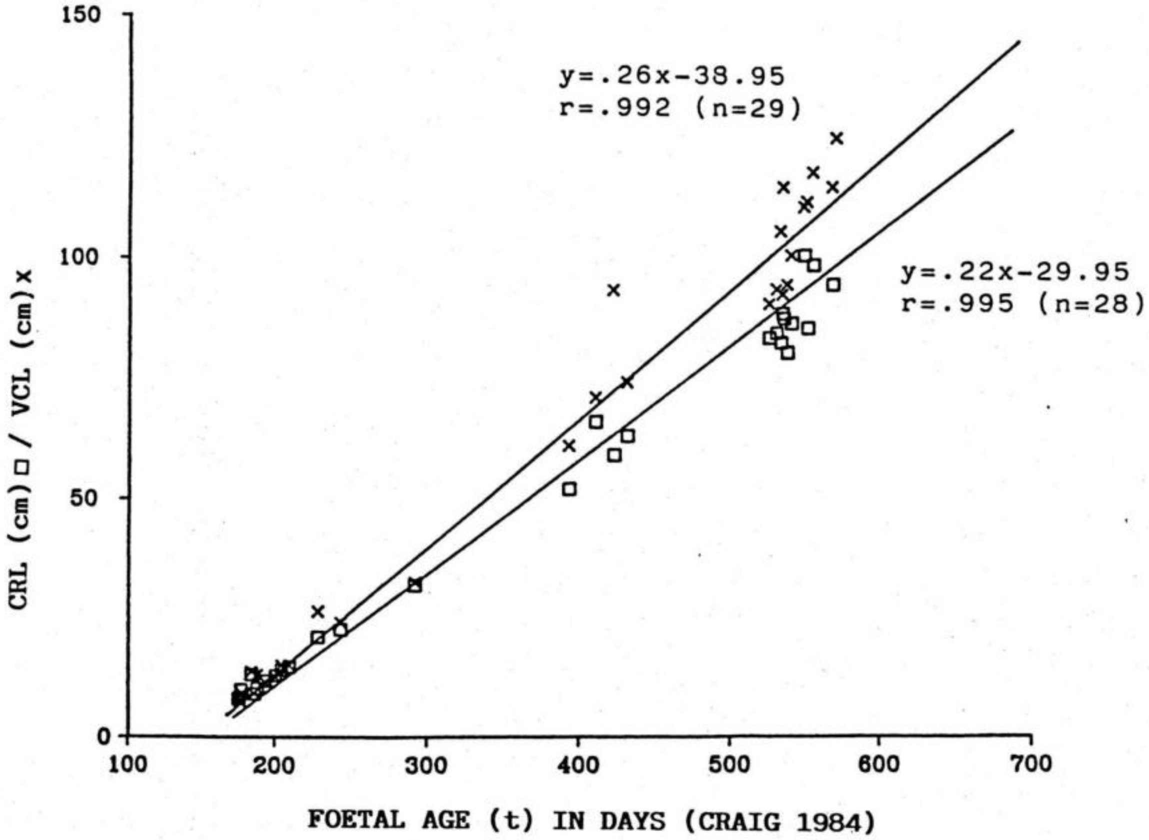


Figure 4.5 Correlation between crown-rump length (CRL), vertebral column length (VCL) and foetal age in 1983, of elephant foetuses collected in Etosha National Park.

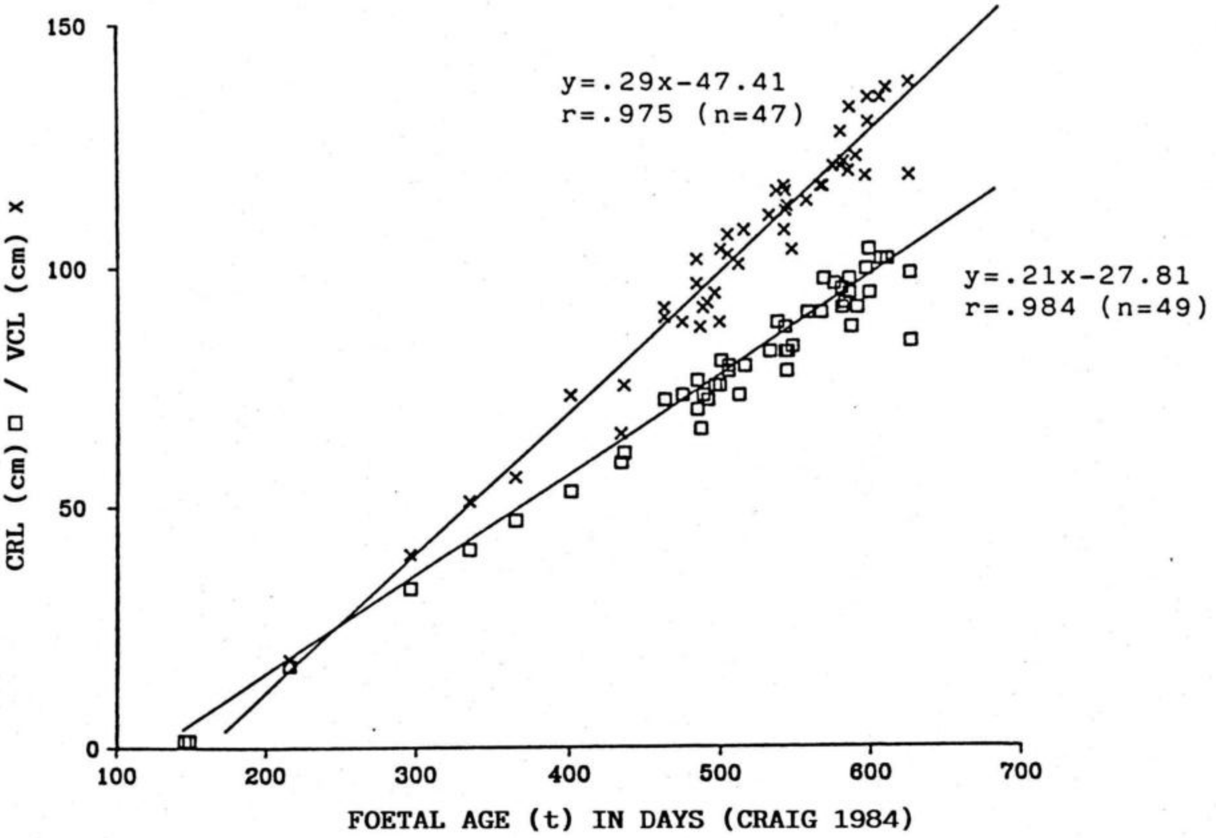


Figure 4.6 Correlation between crown-rump length (CRL), vertebral column length (VCL) and foetal age in 1985, of elephant foetuses collected in Etosha National Park.

As a test of the effect of maternal size on foetal size, the hypothesis that larger or older cows should have relatively larger or older foetuses can be examined for specific age groups of foetuses. No relationship was found between mean ages of foetuses from cows of different size and age classes using all pregnancies available ($p > 0.01$; $n = 81$) and also within smaller groups of foetuses at similar ages ($p > 0.01$; $n = 11, 11, 8$). Sample sizes are limiting, but there appears to be no correlation between maternal size or age and foetal size at age. A comparison between mass at birth of calves produced by cows of different ages and sizes seems to be the only chance of proving such a relationship. This data will not, however, be easy to assemble.

Possible differences in size at age between male and female foetuses are examined in Table 4.3. If male foetuses are generally larger than female foetuses at the same age, the Huggett & Widdas equation for estimating foetal age will render male foetuses older than female foetuses at the same real foetal age. The mean age in days of all male foetuses ($x = 474$, $n = 38$) in the sample was not significantly different ($p<0.01$) from the mean age of female foetuses ($x = 457$, $n=39$). The slopes of regressions of vertebral column length and crown-rump length over foetal age (Figs. 4.5 & 4.6) were not different for males or females separately within and between the two samples. The available data therefore show no difference between the size of male and female foetuses at a comparable age.

Four sets of twins occurred in the series of 85 pregnancies, with an incidence of 4.7%, the highest recorded so far. Substantial differences in size occur between twins of the same sex (Table 4.4) and the male of the rare heterozygotic twinned pair was slightly larger than the female.

In order to classify the elephant population in Etosha N.P. as a birth-pulse or birth-flow population, which affects further demographical analysis, mean and median days of birth were calculated following Caughley (1967) and Caughley & Caughley (1974) and are given in Table 4.5 A & B. Foetal ages derived from Perry (1953) and Craig (1984) yield median days of birth of 29 November and 5 November respectively. A birth-pulse interpretation of the breeding cycle seems to be the best approach in further analysis, at least for elephants in Etosha N.P. and the rest of southern Africa.

Table 4.3 The relationship between foetal sex and size at age for three 30-day-intervals in the gestation period, of elephant foetuses in Etosha National Park.

	$\bar{x}$ ± SE Mass (kg)	$\bar{x}$ ± SE Crown-rump length (cm)	$\bar{x}$ ± SE Vertebral column length (cm)	$\bar{x}$ ± SE Foetal age (days)
Foetal age (days) 480-510				
Females (n = 8)	38.1 ± 0.7	73.1 ± 1.3	94.4 ± 2.3	493.6 ± 2.7
Males (n = 3)	38.7 ± 2.9	77.3 ± 3.3	97.7 ± 4.8	487.7 ± 9.7
t *	0.202	1.107	0.475	0.823
Foetal age (days) 530-560				
Females (n = 4)	54.3 ± 0.3	84.3 ± 1.9	101.3 ± 5.1	538.8 ± 0.9
Males (n = 4)	55.3 ± 2.6	84.5 ± 0.6	98.5 ± 4.7	541.8 ± 6.1
t *	0.238	0.070	0.286	0.343
Foetal age (days) 570-600				
Females (n = 5)	73.2 ± 1.5	94.0 ± 1.1	120.6 ± 1.8	581.0 ± 3.0
Males (n = 5)	77.8 ± 1.3	93.8 ± 2.2	122.2 ± 2.5	590.4 ± 2.7
t *	1.440	0.052	0.325	1.484

* All t-tests not significant, $p > 0.05$.

Table 4.4 Size differences (% difference) in four sets of twin foetuses from elephants in Etosha National Park.

SEX	FOETAL MASS (kg)	CROWN-RUMP LENGTH (cm)	VERTEBRAL COLUMN LENGTH (cm)	PLACENTA
M	60	100	110	
	(8.3)	(2.0)	(6.4)	SHARED
M	65	98	117	
F	29	72	89	
	(31.8)	(22.0)	(36.9)	SHARED
F	22	59	65	
F	37	76	96	
	(2.8)	(8.6)	(5.2)	SHARED
F	36	70	101	
F	54	88	92	
	(7.4)	(2.3)	(8.7)	SEPARATE
M	58	86	100	

Table 4.5 Frequency of births of elephants in Etosha National Park in the 1983 and 1985 samples according to foetal ages derived from Perry (1953) : A and Craig (1984) : B.

A

MONTH	PERIOD CODE x	NO. OF BIRTHS f	fx	fx^2
June	0	2	0	0
July	1	2	2	2
Aug	2	4	8	16
Sept	3	4	12	36
Oct	4	11	44	176
Nov	5	16	80	400
Dec	6	16	96	576
Jan	7	14	98	686
Feb	8	6	48	384
Mar	9	1	9	81
Apr	10	4	40	400
May	11	1	11	121
		$\Sigma f = 81$	$\Sigma fx = 448$	$\Sigma fx^2 = 2878$

Mean date of birth = $\Sigma fx / \Sigma f$, variance = $\dfrac{\Sigma fx^2 - (\Sigma fx)^2 / \Sigma f}{\Sigma f - 1}$

= 166 days after 15 June (± 8 days)

= 28 November (26 September - 31 January)

Median date of birth = 29 November

B

MONTH	PERIOD CODE x	NO. OF BIRTHS f	fx	fx^2
June	0	1	0	0
July	1	3	3	3
Aug	2	4	8	16
Sept	3	12	36	108
Oct	4	13	52	208
Nov	5	24	120	600
Dec	6	13	78	468
Jan	7	4	28	196
Feb	8	0	0	0
Mar	9	3	27	243
Apr	10	2	20	200
May	11	2	22	242
		$\Sigma f = 81$	$\Sigma fx = 394$	$\Sigma fx^2 = 2284$

Mean date of birth = $\Sigma fx / \Sigma f$, variance = $\dfrac{\Sigma fx^2 - (\Sigma fx)^2 / \Sigma f}{\Sigma f - 1}$

= 146 days after 15 June (± 7 days)

= 8 November (10 September - 26 January)

Median date of birth = 5 November

Reproductive status and mean calving interval

Table 4.6 presents a summary of the reproductive status of female elephants culled in 1983 and 1985, and Table 4.7 presents the mean age of females in each reproductive class. The two samples are similar, with the 1985 sample of females appearing slightly more productive than the 1983 sample. The percentage of anoestrous females decreased from 1983 to 1985, which may indicate a slight improvement in environmental conditions after the 1980-1983 drought. Different ratios of pregnant : lactating individuals are attributed to a temporal change in the breeding season, with more first-trimester foetuses found in June-August 1985 than in June-July 1983. Mean age of pubertal cows decreased slightly from 12 ± 1 year in 1983 to 11 ± 2 years in 1985, but samples are small. The fecundity of the female segment had apparently increased marginally after the drought, with potentially more units produced by more females at an earlier age.

Parturition-conception intervals (including the duration of lactation anoestrus) and consequently also the mean calving interval can be estimated from the ratio of mature pregnant to mature non-pregnant cows (Perry 1953, Hanks 1972a, Smuts 1975). The duration of anoestrus which in fact represents the parturition-conception interval is estimated as:

$$x = \frac{\text{gestation period (no. of mature non-pregnant cows)}}{\text{no. of pregnant cows}}$$

and mean calving interval as x + 22 months. Mean calving intervals from the 1983 and 1985 samples are thus both estimated at 3.8 years.

Placental scars (Fig. 4.7) were visible in the uteri of all mature cows examined, except where gross change in the endometrium as in pregnancy, oestrus, recent partus and chronic endometritis obscured any scars. A single 22 year-old cow with coxal achondroplasia which rendered a hindleg immobile and permanently disarticulated from the pelvic joint, had no placental scar in spite of corpora lutea in both ovaries. It is doubtful if she

Table 4.6 Reproductive status of all female elephants culled in 1983 and 1985 (including calves captured in 1985) in Etosha National Park.

NO. OF FEMALES	1983 (% OF TOTAL)*		1985 (% OF TOTAL)*	
Total culled	102		214	
immature	44	(43.2)	95	(44.4)
prepubertal	40	(39.2)	91	(42.5)
pubertal	4	(3.9)	4	(1.9)
parous	58	(56.9)	119	(55.6)
anoestrous	9	(15.5)	9	(7.6)
pregnant	28	(48.3)	57	(47.9)
pregnant and lactating	6	(23.1)	29	(50.9)
lactating	21	(36.2)	52	(43.7)

* Percentages not additive.

Table 4.7 Mean ages in years (± SE) of female elephants in 1983 and 1985 per reproductive class in Etosha National Park.

	1983	n	1985	n
Prepubertal	5.3 ± 0.6	40	5.2 ± 0.4	91
Pubertal	12.0 ± 1.2	4	10.8 ± 1.5	4
Pregnant	27.4 ± 2.2	28	25.2 ± 1.6	57
Lactating	27.2 ± 2.6	21	30.2 ± 1.6	53
Anoestrous	24.7 ± 4.2	9	31.8 ± 6.8	9
All parous	26.9 ± 1.5	58	27.9 ± 1.2	119

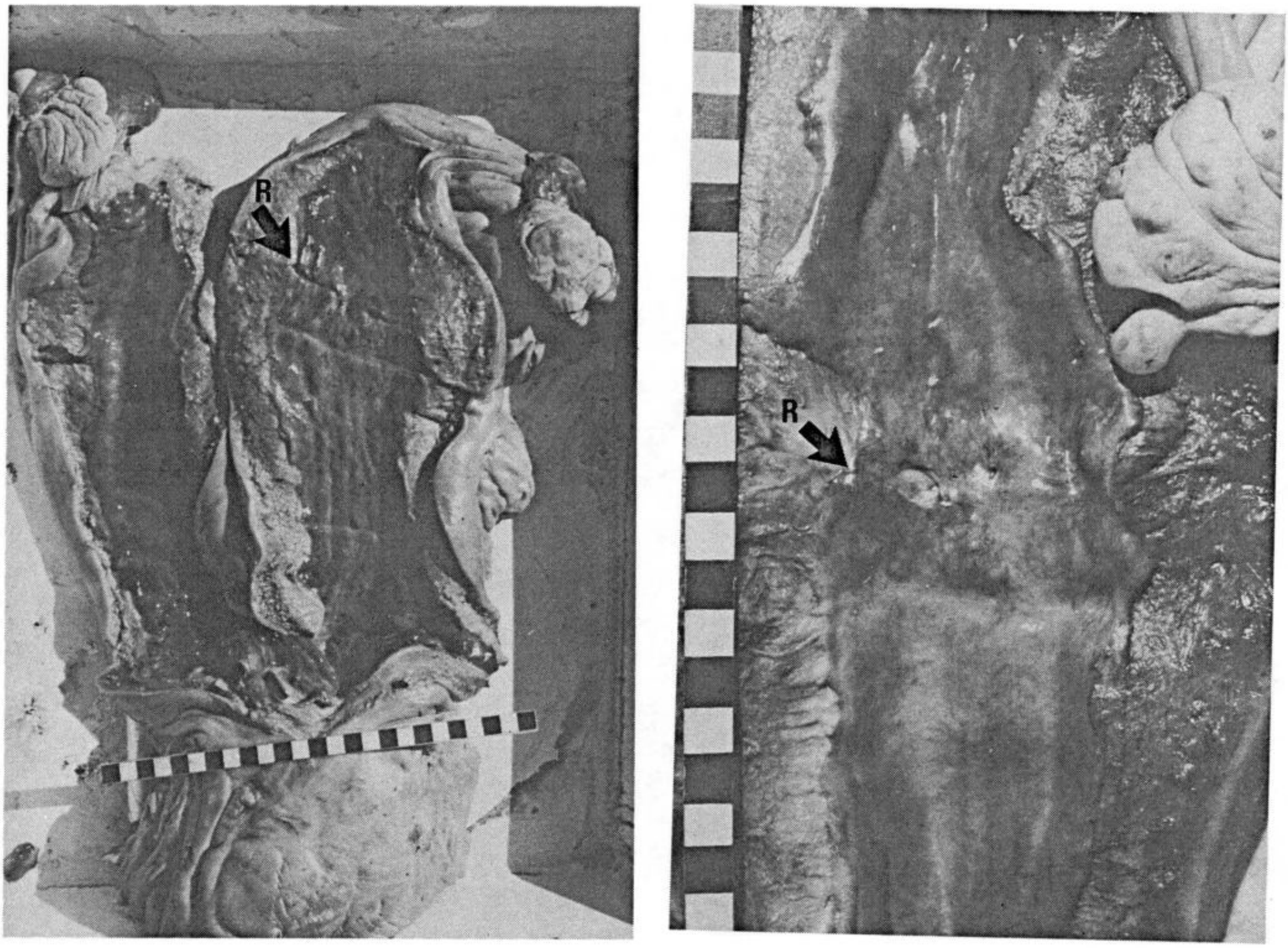


Figure 4.7 Placental scars in elephant uteri from Etosha National Park, in longitudinal section (R = recent scars, scale in cm).

could have supported a mating bull, and this is believed to be the cause of her infertility. In practice, the number of uteri suitable for counting placental scars is limited to those from non- pathological- parous- anoestrous females and cyclical-anoestrous-parous- lactating cows. Scars may be visible during early pregnancy but were excluded from the analysis as the older scars may not necessarily be counted accurately.

Figure 4.8 A & B illustrates the relationship between number of placental scars and age of female elephants in 1983 and 1985. Laws (1967b) recommends the exclusion of individuals older than 36 years, as there is some doubt over the longevity of scars. The slope of the linear regression of number of scars on age is an estimate of the mean calving interval (Laws 1967b), which is 2.1 and 2.5 years respectively in the 1983 and 1985 samples. Both estimates are considerably lower than any recorded previously.

The difference between the mean age of females with one scar and those with two scars also indicates the calving interval (Laws et al. 1975). In 1983 and 1985 the duration of the first calving interval was 3.0 and 2.8 years respectively. The first calving interval is however not necessarily representative of calving intervals throughout the reproductive lifespan. The mean number of placental scars in elephant cows from Etosha N.P. in 1983 (6.6) and 1985 (5.0) is greater than reported so far for other populations (Table 4.8). Compensatory breeding was possibly the reason for the comparatively faster accumulation of scars in elephants from Etosha N.P. Possible differences in the fractions of the regional population represented in the samples in 1983 and 1985 furthermore complicates the use of placental scar:age relationships in estimating calving intervals or the age at first conception.

Attainment of sexual maturity

Age at first conception is also estimated from the regression of number of placental scars over age of female, where s=1, t=12.8 in 1983 and t=14.4 in 1985 (Fig. 4.8). Laws (1967b) argues that t minus the gestation period minus a lactation anoestrous of at least 22 months should indicate the average age when the first pregnancy was initiated. The resulting average age of first conception is thus 9-11 years in 1983 and 11-12 years in 1985. Lactation anoestrus can, however, be much shorter than 22 months. When lactation anoestrus periods estimated from the slope of the scar-age regressions are used, the average ages at first conception are equivalent to t(s=0), namely 10.7 years in 1983 and 11.9 years in 1985.

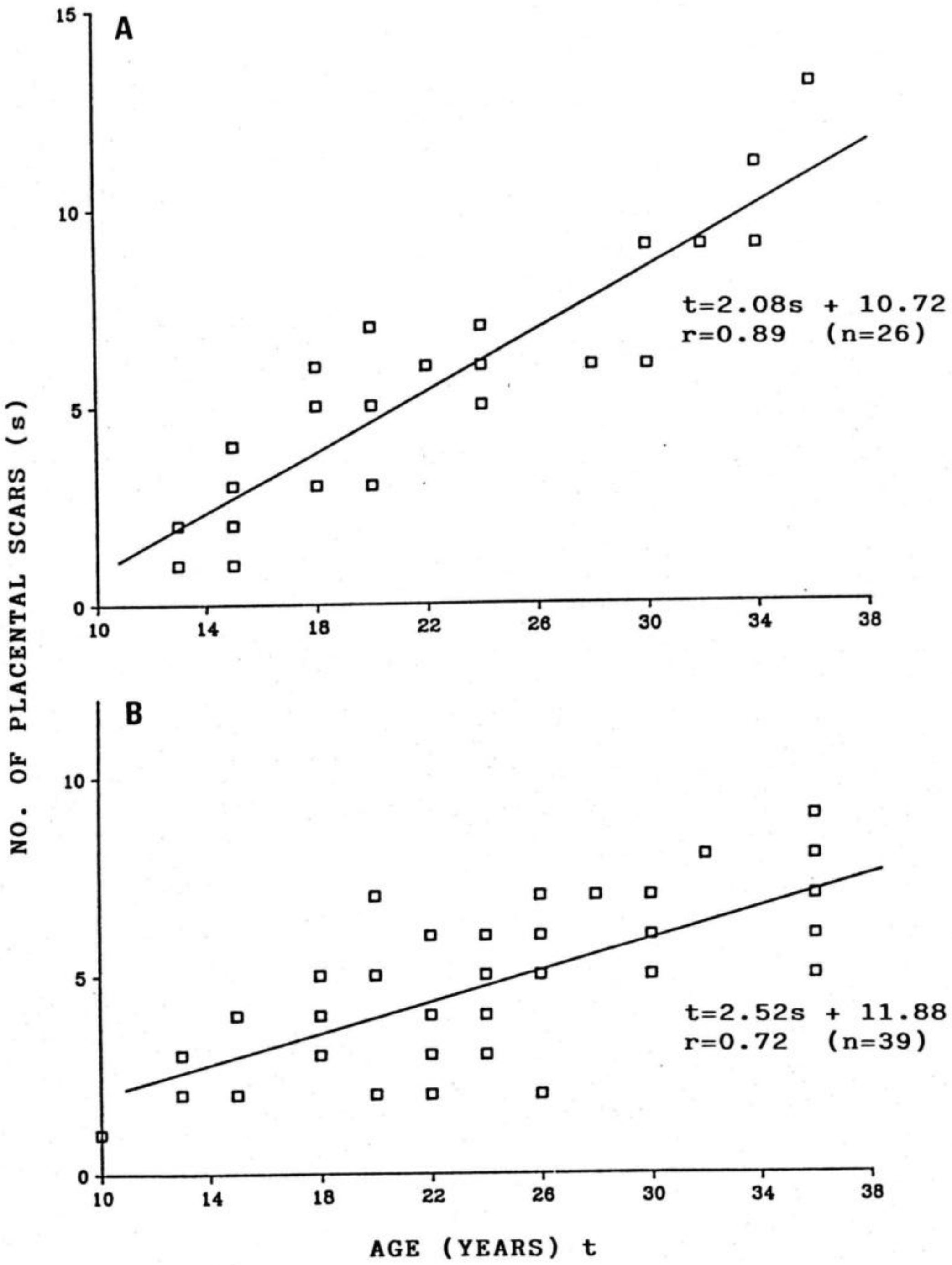


Figure 4.8 The number of placental scars and age of female elephants in the 1983 (A) and 1985 (B) samples from Etosha National Park.

Table 4.8 Mean calving intervals (MCI) in years and number of placental scars per female in eight populations of African elephants.

Locality ***	$\bar{x}$ placental scars/ female (range)	no. of females with placental scars	MCI from age difference between females with 1 and 2 placental scars	MCI from placental scars	MCI from incidence of pregnant females	Reference
K.F.N.P.N.	-	-	5.2	-	4.5	Laws (1969a)
K.F.N.P.S	-	-	4.9	4.9	4.6	Laws (1969a)
T.N.P	3.6 (1-9)	44	6.7	4.1	6.8	Laws (1969a) & Laws & Parker (1968)
K.N.P.	3.7 (1-11) *	85 *	4.3 *	4.3	4.5	Smuts (1975)
L.V.N.P.	3.9 (1-10) *	98 *	3.7 *	3.4 (3.8)**	3.5	Hanks (1972a) & Malpas (1978)
G.N.P.	3.0 (1-10) *	131 *	5.2 *	4.3	3.7	Sherry (1975)
H.N.P.	2.6 (1-8) *	118 *	6.7 *	4.3	4.0	Williamson (1976)
E.N.P.(1983)	6.6 (1-13)	21	3.0	2.1	3.8	This study
E.N.P.(1985)	5.0 (1-12)	41	2.8	2.5	3.8	This study
Average (range)	4.1 (1-13)		4.7 (2.8-6.7)	3.4 (2.1-4.9)	4.4 (3.5-6.8)	
E.N.P.(1983)	A 4.8 (1-11)	4				
	L 7.1 (1-13)	17				
E.N.P.(1985)	A 2.5 (2-3)	4				
	L 5.2 (1-12)	37				

* Calculated from data in references

** Recalculated as 3.8 by Malpas (1978, in Eltringham 1982)

*** Abbreviations explained in Appendix 1

A Calculated from non-lactating anoestrous females

L Calculated from lactating females

This approach to estimating the age at first conception as advanced by Laws (1967b) was abandoned in his later work (Laws 1969a,b, Laws & Parker 1968). The mean age (± SE) of pubertal cows culled in 1983 and 1985 were 12.0 ± 1.2 and 10.8 ± 1.5 years respectively (Table 4.7), the opposite trend from the regression-derived estimates. The minimum age of pregnant cows was 13 years in 1983 and 10 years in 1985. An additional way of estimating the age at first conception is by calculating the mean age from the range of overlap between immature and mature cows, as in Fig. 4.9. For 1983, the value is 13.5 years (12-15) and for 1985 11.5 years (8-15).

Senescence, anoestrus and reproductive disorders

Table 4.9 presents the classification of parous anoestrous (non-lactating) cows in the 1983 and 1985 samples. Only one case out of three with reproductive disorders can be regarded as permanently senescent, namely that of a 60 year-old cow with a neoplastic uterus. Most of the anoestrous cows were judged to be cyclically anoestrous, of which six out of nine with non-oedematous uteri had recent placental scars (5-15 mm wide). These scars may represent intrauterine or neonatal mortalities.

The incidence of reproductive disorders in all females is presented in Table 4.10. No prepubertal or pubertal female had any obvious reproductive disorder. Ovarian cysts were found in one pregnant, two lactating and one anoestrous cow and are therefore not regarded as a serious or permanent impairment of reproduction. Corpora lutea, corpora albicantia and developing follicles accompanied cysts in all ovaries thus affected. It appears that cysts may persist for substantial periods, as all those observed were distinctly separated from the rest of the ovary, being attached by a stout fibrotic peduncle or thin fibrous band of tissue. All cysts were simple unilocular bodies measuring from 2x3 cm to 5x8 cm, containing clear amber fluid. One of these appeared multilocular, due to radial constrictions in the capsule, but without internal septa.

Inflammation of the uterus occurred in different forms in the two lactating and one anoestrous cows where this condition occurred. Early cystic endometriosis characterized by numerous superficial globular cysts (1-5 mm diameter) scattered along the entire endometrium in both cornu, was found in one lactating cow. Chronic endometritis without the formation of cysts was found in the anoestrous cow, and was characterized by the deep

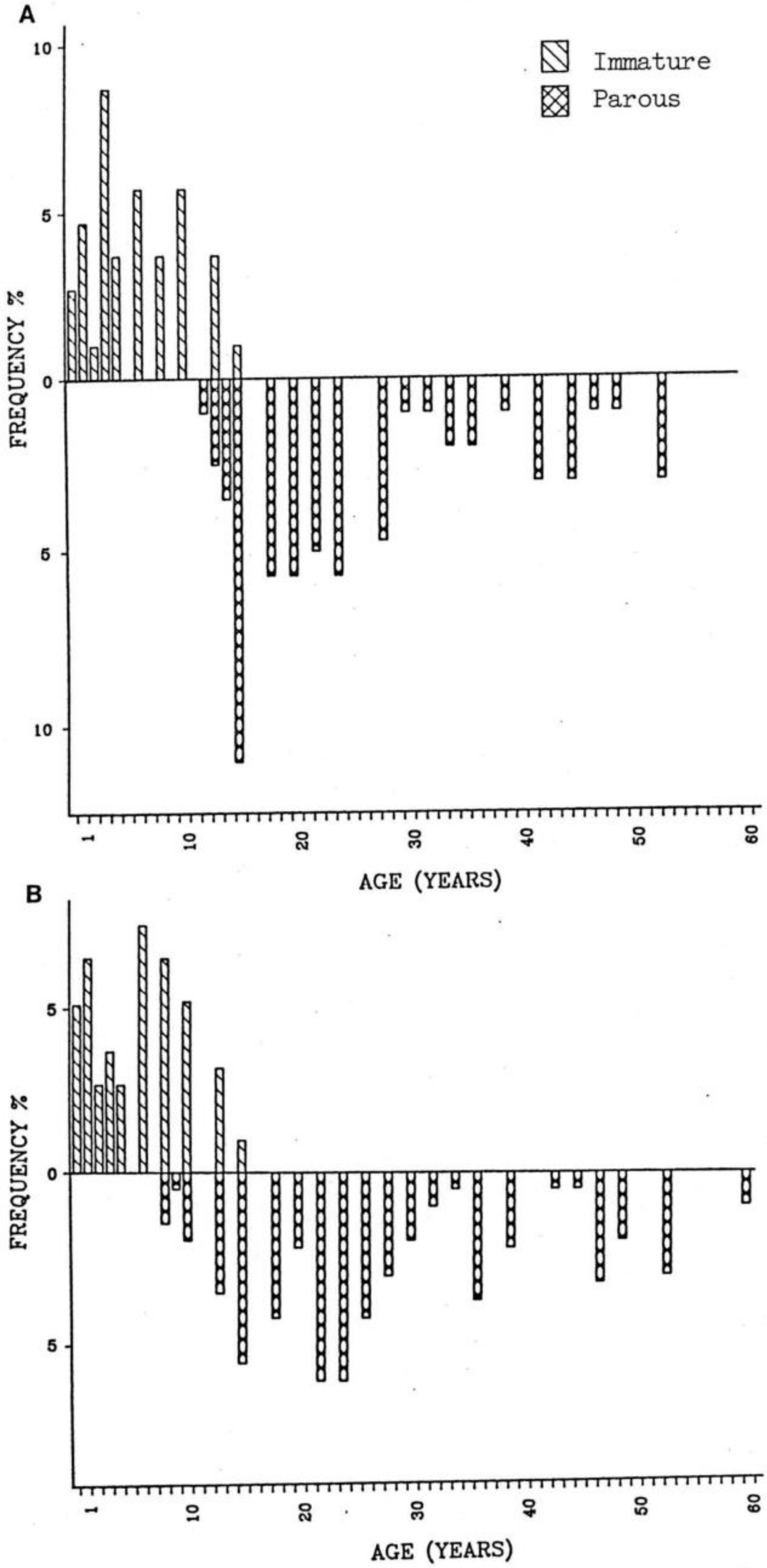


Figure 4.9 The range of overlap in the ages of parous and immature elephant females in 1983 (A) and 1985 (B) in Etosha National Park.

Table 4.9 Uterine and ovarian characteristics of parous anoestrous (non-lactating) female elephants in the 1983 and 1985 samples from Etosha National Park.

	UTERUS		OVARIES			
AGE IN YEARS	TOTAL PLACENTAL SCARS	NO. OF RECENT SCARS	NO. OF FOLLICLES >5mm	NO. OF CORPORA LUTEA	NO. OF CORPORA ALBICANTIA	STATUS
1983						
15	3*	0	0	2	5	Cycling anoestrous
15	4*	2	0	4	4	Cycling anoestrous
15	2*	2	0	7	4	Cycling anoestrous
18	1	1	0	3	5	Cycling anoestrous
20	3	0	3 cystic**	5	4	Disorder
24	not examined		0	7	9	Cycling anoestrous
28	chronic endometritis		2	1	11	Disorder
34	Oedemateous		2 atretic	2 fresh	17	Cycling, post oestrus
53	Oedemateous		4 atretic	3 fresh	24	Cycling, post oestrus
1985						
10	2*	1	0	3	1	Cycling anoestrous
13	2*	1	0	5	5	Cycling anoestrous
15	0	0	0	1	1	Nulliparous cycling
15	2*	1	0	3	7	Cycling anoestrous
22***	0	0	1 atretic	3 fresh	14	Cycling anoestrous
45	Oedemateous		4	3	21	Cycling pro-oestrous
53	Oedemateous		5 atretic	3 fresh	26	Cycling anoestrous
53	Oedemateous		1 atretic	2 fresh	34	Post oestrus, possibly pregnant
60	Neoplastic		0	0	22	Disorder

* Multiple placental scars in young females could be the result of compensatory breeding after calf mortality or twinning.

** Cystical follicles or alternatively para-ovarian cysts.

*** severe skeletal abnormality, coxal achondroplasia of right hind leg, condition fair.

Table 4.10 Incidence of reproductive disorders in elephant cows in 1983 and 1985, in Etosha National Park.

	1983	1985	TOTAL
Total no. of cows examined	102	214	316
Immature females	44	96	140
Mature females	58	118	176
Disorders in immature females	0	0	0
Disorders in mature females	4 (6.9%)	8 (6.8%)	12
Disorders in pregnant females	0	2	2
Disorders in lactating females	2	5	7
Disorders in anoestrous fem.	2	1	3
TOTAL	4	8	12
Females with ovarian cysts	2	4	6
Females with endometritis	1	1	2
Fem. with placental disorders	1	2	3
Females with neoplasms	0	1	1
TOTAL	4	8	12

red colour of the endometrium caused by abnormal vascularization. Figure 4.10 illustrates a case of occlusion of the left uterine cornu in the upper third of the uterus in a lactating cow. Both cornu were hyperaemic, similar to endometritis, and previous placental scars occurred in both cornu and on both sides of the occlusion. This condition was probably caused by placentitis during a previous pregnancy or even endometritis. Complete fusion of a placental scar as a cause of occlusion is not supported by a very recent placental scar situated posterior to the occlusion.

One retained placenta was found in a lactating cow, indicated by putrified amorphous tissue in the right cornu. The entire uterus was hyperaemic but the endometrium was intact and distinct from the unattached tissue in the lumen. The mass of tissue measured approximately 500 ml, and represents either a partial retention or a partial recovery from a complete retention. A rare case of hydroallantois was found in a young pregnant cow. Before evisceration, the abdomen appeared unusually large, indicating a near-term foetus. A much smaller foetus was found, but the allantois was abnormally large and contained approximately 100 l of bright amber liquid. The foetus showed severe conformational defects, similar to the bulldog syndrome in cattle and dogs (Fig. 4.11). Evidence of the abnormally high intra-uterine pressure is shown by the indentations and even open wounds left by the tail and hindlegs on the rump and abdomen (Fig. 4.11). This condition was probably caused by placental malfunction as the result of the extensive diffuse necrotic placentitis observed.

Table 4.11 presents a summary of the reproductive status of all cows over 50 years of age collected in 1983 and 1985. Senior cows are poorly represented in the culled samples, but appear fully capable of lactation and pregnancy. Of 16 senior cows, only one appears to be senescent. The oldest recorded pregnant cow was 53 years old with a parturition date nearly two years later. The oldest lactating cow was 60 years old with developing follicles and slight oedema of the endometrium typical of pro-oestrus.

Breeding synchrony

Apart from the seasonality of conceptions which synchronizes births in the population to the same part of the year, every year, evidence of another form of synchrony within herds

Figure 4.10 Complete uterine occlusion in an adult lactating elephant in Etosha National Park, with placental scars on both sides of the occlusion, in longitudinal section. Scale in cm, arrow indicates direction of cervix.

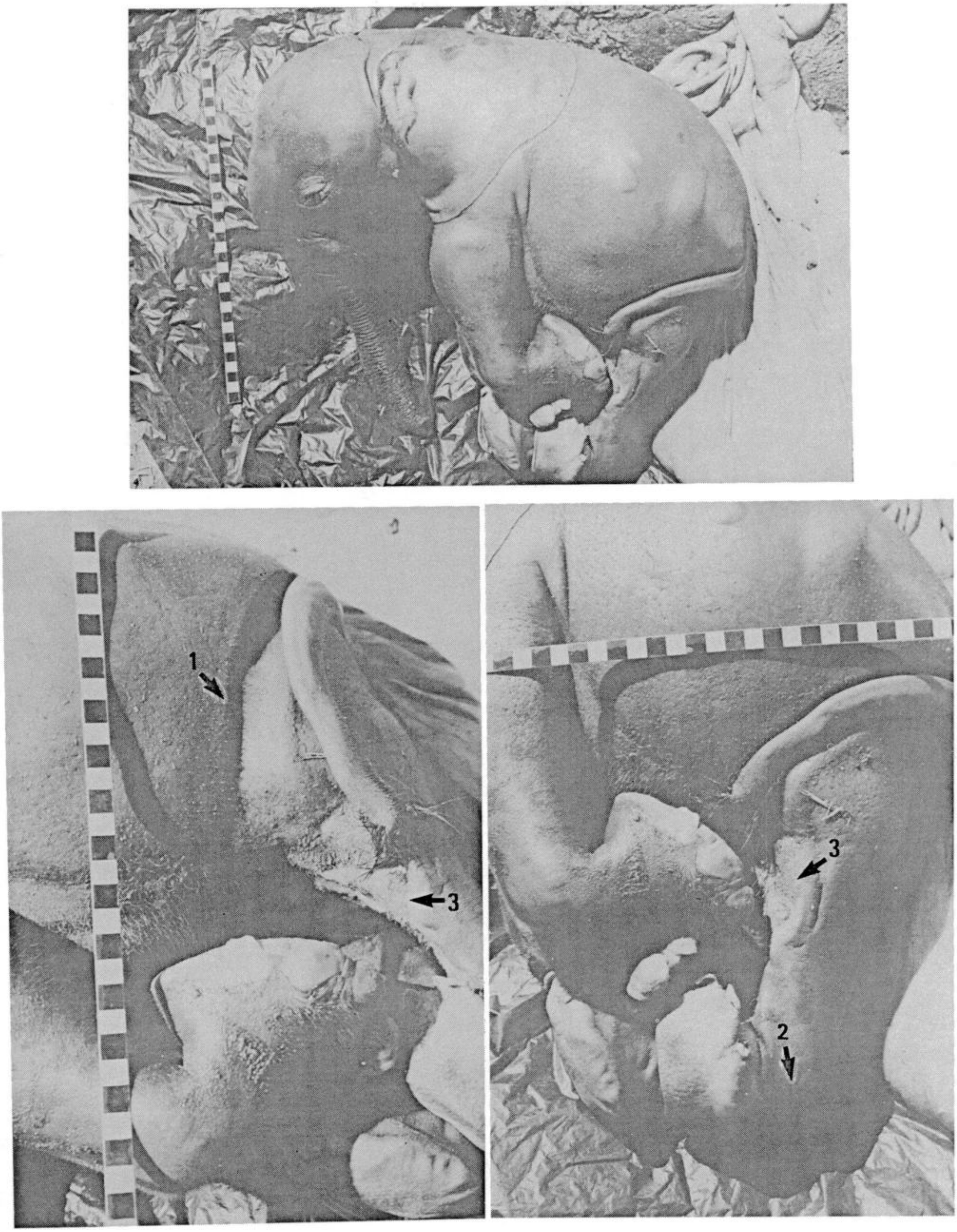


Figure 4.11 Conformational defects in a male elephant foetus caused by intra-uterine pressure, evident from the indentation on the rump by the tail (1), hyperflexure of the hindlegs (2) and abrasions caused by friction between limbs (3), collected in Etosha National Park. Scale in cm.

Table 4.11 Reproductive status of senior adult elephant cows in Etosha National Park.

	AGE IN YEARS	NO. OF ANIMALS			
		PAROUS ANOESTROUS	PAROUS PREGNANT	PAROUS LACTATING	TOTAL
1983	49 ± 6 53 ± 6	0 1 **	0 1	1 1	1 3
		1	1	2	4
1985	49 ± 6 53 ± 6 60 ± 6	0 2 ** 1 ***	3 2 0	1 2 1 *	4 6 2
		3	5	4	12

* Cow in pro-oestrus
** Cyclical anoestrous, not senescent
*** Neoplastic uterus, facultatively senescent.

was found. Figures 4.12 and 4.13 illustrate the distribution of foetuses and calves up to 10 years of age in all breeding herds culled in 1983 and 1985. The method used to estimate the age of individuals in the culled samples (Laws 1966, 1967 a) allows the distinction of 9 different age groups in the chronological range 0-10 years. If births occur randomly over time in individual cows of a breeding herd, there should be almost as many age classes represented as there are calves in a herd, if the sample size is large. Synchronization of births within an individual breeding herd was indicated by the presence of several calves in the same age group, as shown in Figs. 4.12 and 4.13. In 1985, the majority of herds showed a variable degree of synchrony in births and consequently corresponding ages of calves, while the remainder resembled the 1983 sample.

Figure 4.14 illustrates the number of calves aged 10 years and younger per herd, over the number of age groups represented by calves in this age range, in herds culled in 1983 and 1985. Herds with twice or more calves than age groups represented by calves, were considered to be synchronous, i.e. all herds on and above line A-A' in Fig. 4.14. This is merely a crude indication of possibly synchronous breeding between adult cows in a breeding herd. At least 57% of herds culled in 1985 appear to have been synchronized compared to 15% in 1983. The difference in apparent synchronized breeding between the two samples could be due to different fractions of the regional population represented in the two samples.

DISCUSSION

Foetal growth and seasonal breeding

The Etosha N.P. elephant population is the sixth population studied showing seasonality of conceptions correlated with the distribution of rainfall (Table 4.12). Peaks in conceptions are broad, lasting 5-6 months, and conceptions occur at other times as well. The coincidence of conceptions or parturitions with annual rainfall is not the result of an indisputable selection pressure. The slow-growing foetuses do not impose inordinate demands on maternal nutrition, unlike lactation prior to weaning. Weaning does not occur at a specific age (Douglas-Hamilton 1972, Laws et al. 1975) and presumably occurs usually in the second year of gestation of the next foetus. Most parturitions occur prior to or

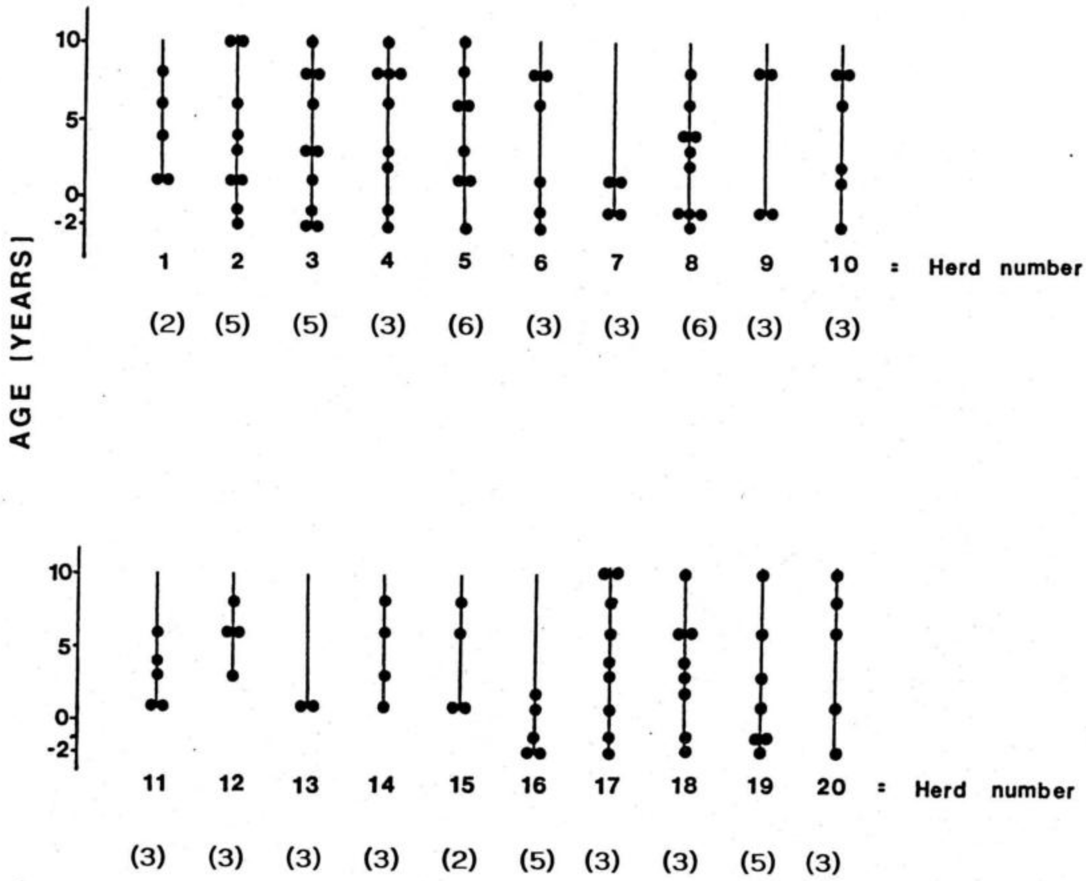


Figure 4.12 Distribution of foetuses and calves in all elephant breeding herds culled in 1983 in Etosha National Park. The number of parous cows in each herd is given in parenthesis.

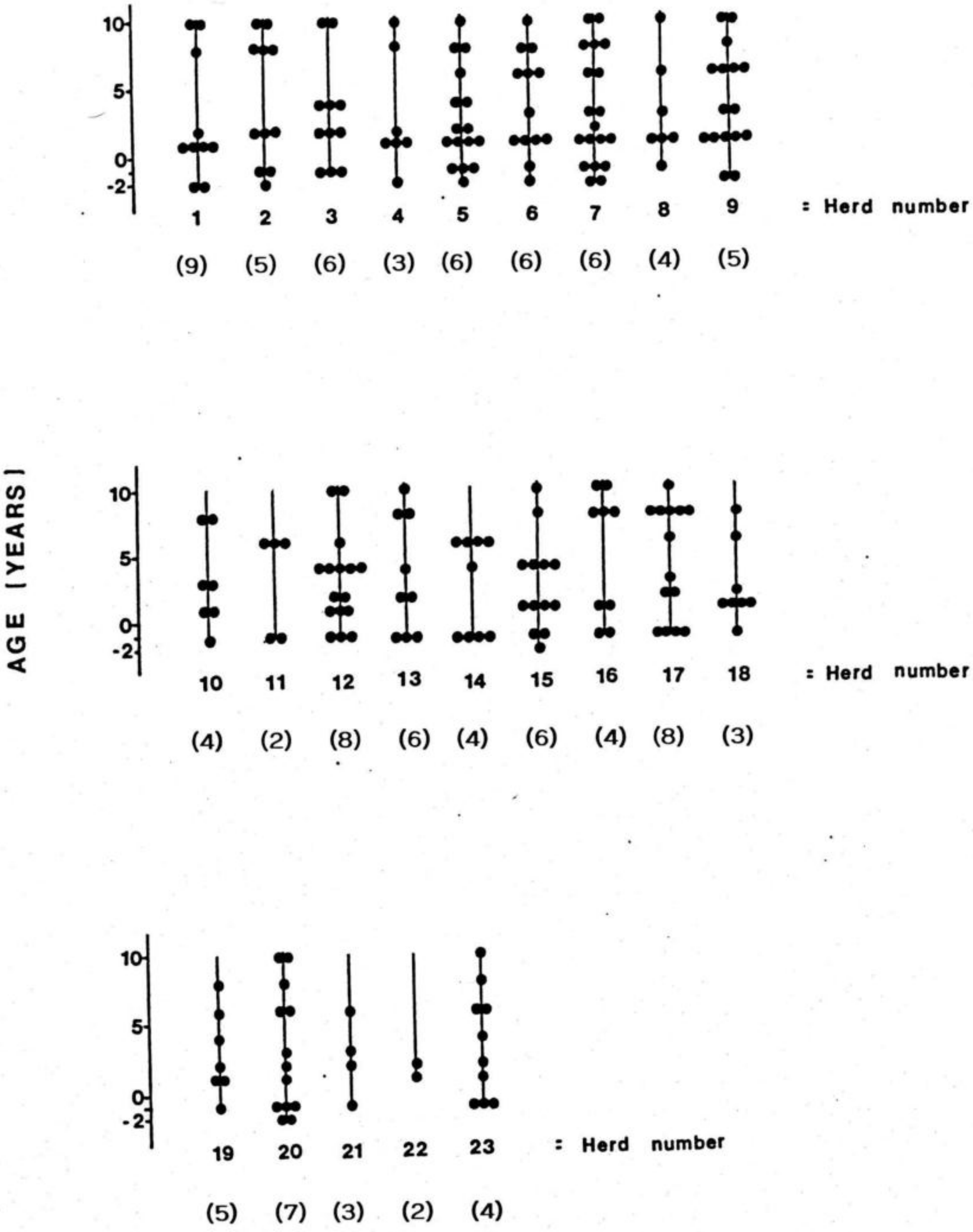


Figure 4.13 Distribution of foetuses and calves in all elephant breeding herds culled in 1985 in Etosha National Park. The number of parous cows in each herd is given in parenthesis.

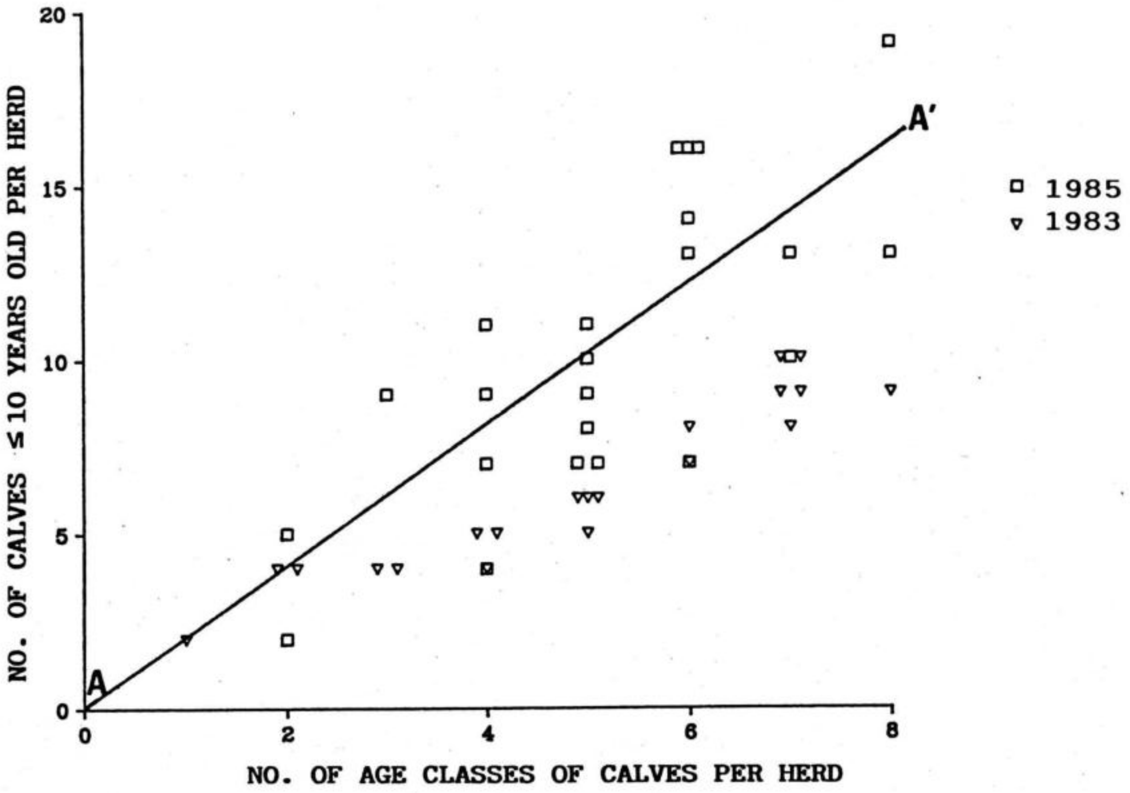


Figure 4.14 The number of calves and the number of different age groups represented by elephant calves in 43 herds culled in Etosha National Park.

Table 4.12 Seasonal breeding in African elephant populations.

LOCALITY *	BREEDING SEASON (CONCEPTION)	RAINFALL DISTRIBUTION	REFERENCE
K.F.N.P.N.	All year, peak Feb.- Jul.	All year	Laws (1969 a)
K.F.N.P.S.	All year, slight increase Sept.-Mar.	All year	Laws (1969 a)
T.N.P.	May-Jul. Nov.-Feb.	Sept.-Dec. Feb.-May	Laws (1969 a)
A.N.P.	Dec.-June peak, all year	Nov.-Dec. Feb.-May	Poole (1982)
M.R.	April-June, Nov.-Jan.	Sept.-Dec. Jan.-May	Laws (1969 a)
L.V.N.P.	Nov.-Apr. peak	Nov.-Apr.	Hanks (1969,1972 a)
M.P.N.P.	Nov.-Apr. peak	Nov.-Apr.	Kerr (1978)
H.N.P.	Nov.-Apr. peak	Nov.-Apr.	Williamson (1976)
G.N.P.	Nov.-Apr. peak	Nov.-Apr.	Sherry (1975)
K.N.P.	Nov.-Apr. peak	Nov.-Apr.	Smuts (1975)
E.N.P.	Nov.-Mar. peak	Nov.-Mar.	This study

* Abbreviations explained in Appendix 1.

early in the growing season of plants, and previous calves recently weaned would benefit from this timing of events. The incidence of calves being dependent on lactation until just prior to the birth of their next sibling is totally unknown.

A simpler explanation for seasonality of conceptions in a species where males are fertile throughout the year and oestrus may occur at any time, lies in the seasonal movements and aggregation of herds. Prior to the rains, apparently affilliated herds aggregate in larger groups ("clans" in Moss & Poole 1983) for the duration of the wet season. It is during this period that adult bulls most frequently associate with breeding herds and most matings would presumably occur at this time. At this stage, it seems premature to exclude environmental stimuli on reproduction as a cause of seasonal breeding. Oestrus occurs throughout the year, but the actual distribution of oestrous periods must still be determined for any of the seasonally breeding elephant populations in southern Africa. It was not possible to collect adequate data in this regard from the low density population in Etosha N.P.

I propose that male musth might be a cause of breeding synchrony within a population or within a herd. Poole (1982) suggests that the presence of males in musth stimulates females to come into oestrus, which would increase synchrony. If musth is more prevalent during the wet season, greater numbers of females would be affected in the large aggregations at this time of the year. Even if musth is not seasonal in incidence, synchrony within herds might be related to this phenomenon. Poole & Moss (1981), Poole (1982) and Hall-Martin (1987) found that males in musth are actively searching for breeding herds. When a breeding herd is located the presence of an oestrous cow ends the search, if not, other herds are sought. When elephant density is extremely low (0.03-0.11 /km^2) and group density even lower (0.002-0.003/km^2), as in Etosha N.P., it might be more profitable for a musth male to stay with the first herd located, regardless of female reproductive condition, and wait until oestrus occurs because of his own presence. The cue for the onset of musth, however, is totally unknown.

Other factors might be responsible for conceptions before and after the conception peak. Evidence from Etosha N.P., where 69% of females which conceived outside the breeding peak were not lactating, indicates that conceptions outside the peak period might be caused by mortalities in young calves. It would be to the advantage of a slow breeding individual to conceive again soon after a previous attempt to produce a calf has failed. This is indeed the case, as the mean calving interval of females whose previous calf died was 3.8 years against 5.4 years of females whose calves survived in Amboseli N.P. (Moss 1983). Moss (unpubl. in Bosman & Hall-Martin 1986) found that general synchrony in births occurred in Amboseli N.P. after a severe drought which caused severe calf mortalities. This phenomenon might synchronize an entire population and cause the much disputed cyclical recruitment described by Laws (1969b), but cannot explain multiple synchronized conceptions at regular intervals without the loss of the previous cohorts.

The gestation period of African elephants has yet to be determined accurately. Present estimates of 22 months are based on the semi-domesticated elephants in the former Belgian Congo (Perry 1953) which were probably forest elephants (L. africana cyclotis). Moss (1983) recorded gestation periods of 20-23 months in 42 cases. One estimate of 19 months was attributed to the observation of oestrus and mating during pregnancy. Seven births more than 24 months after mating were attributed to conception in later unobserved oestrus periods. Moss (1983) nevertheless considers it unlikely that oestrus at other times than those observed occurred in the individuals studied.

Birth mass, however, is certainly variable and indicates that the gestation period might indeed be highly variable as well. Perry's (1953) estimate of a birth mass of 120 kg is based on two 120 kg foetuses that were larger than the smallest calves collected. Three calves from Etosha N.P. less than 6 months old weighed 91, 111 and 107 kg. Smuts (1975) recorded the largest foetuses known, two males with body masses of 144.6 kg and 164.6 kg respectively. There are either substantial losses in mass after birth, or the gestation period is indeed highly variable.

No evidence was found of size differences in foetuses due to the sex of the foetus or the size and age of the mother. The apparent rate of growth in the length of the vertebral column was nevertheless different in the 1983 and 1985 samples, with the latter growing faster, when foetal age is based on foetal mass. Foetuses collected in 1983 were slightly leaner than those in 1985, and appearing younger than they should be. It would be very useful in future to assess condition and fat deposits of foetuses as well as in post-natal elephants. Although measuring the length of the vertebral column and the crown-rump distance in foetuses is standard procedure in studies on large mammals, there is surprisingly no comparable information from other elephant populations to my knowledge. Differences in post-natal growth rates and nutritional levels have been used in comparisons between populations (Laws et al. 1975) and it would be useful in future to focus on foetal growth and condition as well.

Retardation of foetal growth due to malnutrition (placental insufficiency or maternal starvation) is a well known phenomenon in humans (Hytten 1980) and sheep (Faichney & White 1987). Length at birth is far less affected than mass at birth, as is well documented from the famine in occupied Holland in 1944-1945 (Stein & Susser 1975 a,b). Duration of gestation was apparently not affected by famine and is therefore not a cause for lower mass at birth. Lean rather than fat babies were produced, showing greater perinatal morbidity and mortality (Hytten 1980). Variation in size at birth in elephants and differences in mass:length relationships in the samples from 1983 and 1985 are suggested to be equivalent to these starvation-induced effects in humans. Foetal age will have to be estimated from length rather than mass to prove this suggestion.

The incidence of twins in Etosha N.P. is the highest so far recorded (Table 4.13), and possibly higher as one set of newborn twins was almost certainly culled in 1983. The two calves were of the same size and there was only one lactating female present. Laws (1969a) however, warns that small samples of recorded pregnancies might give a biased incidence of twinning. Although small, the culled samples from Etosha N.P. represent about 7% and 14% (1983 and 1985) of the entire elephant population at the time of sampling, and are therefore regarded as being representative.

Reproductive status and mean calving interval (MCI)

The frequency distribution of females in different phases of reproduction and their mean age per class suggest that the female segments of the population in 1985 was slightly more productive than in 1983. The percentage of females which were parous but inactive declined from 1983 to 1985, as did the frequency of reproductive disorders. The improvement, however, was slight, if based on the percentage females in each reproductive class. This approach has been rightly criticized by Laws (1969a) in terms of the representation of samples taken in a limited part of the year not necessarily coinciding with the same phase of the annual cycle in successive years.

Calving intervals have been suggested to be one of the main reproductive variables operating as a homeostatic regulatory measure (Hanks & McIntosh 1973, Laws et al. 1975, Laws 1981). The estimation of calving intervals is very problematic. The most accurate estimates would come from direct observations of a representative number of females over

Table 4.13 Incidence of twins, and foetal sex ratios in African elephant populations.

LOCALITY *	NO. OF PREGNANCIES RECORDED	NO. OF TWINS (%)	FOETAL SEX RATIO M : F	REFERENCE
L.V.N.P.	223	0	1.0:1.03	Hanks (1972 a)
K.N.P.	353	2 (0.6)	1.0:0.9	Smuts (1975)
G.N.P.	254	0	1.0:1.04	Sherry (1975)
M.P.N.P.	52	0	1.0:0.45 **	Kerr (1978)
H.N.P.			1.0:1.07	Williamson(1976)
Uganda	31	0	-	Perry (1953)
T.N.P.	26	1 <1.0	-	Laws (1967 b), Laws & Parker (1968)
K.F.N.P.	46	1 ***	-	Laws & Parker (1968)
East Africa	219	3 (1.37)	1.0:0.84	Laws (1969 a)
E.N.P.	85	4 *** (4.7)	1.0:0.77 a 1.0:1.24 b 1.0:1.03 c	This study " "

* Abbreviations explained in Appendix 1.

** Considered to be erroneous by Kerr (1978).

*** Only two pairs of heterozygotic twins are known, one from East Africa and one from Etosha National Park.

a 1983 sample.

b 1985 sample.

c Total sample.

a sufficiently long period, which is not practical or feasible in most studies. (An obvious exception is the very valuable long-term study of elephants in Amboseli N.P. by Moss and co-workers). The ratio of pregnant females as first used by Perry (1953) is not likely to be representative of any period other than the year of sampling, in view of possible synchronization of conceptions, and the dubious assumption of a similar duration of lactation anoestrus in all females. The shortest recorded individual calving interval is 33 months (Laws 1969a), indicating a parturition-conception interval (= lactation anoestrus) of no more than 11 months.

The alternative method of estimating MCI by way of the regression of the number of placental scars over age generally yields estimates similar to those from the ratio method, except in Etosha N.P. A hidden assumption of this method is that young parous females accumulate scars at the same rate as older females, while there is little evidence to suggest this. Very little is known about the effect of age on reproduction in elephants other than the usual fecundity estimates, which are dependent on the ratio of parous : non-parous females. Females in Etosha N.P. accumulate scars at a greater rate than in other populations, particularly in the 10-20 year age range, but each scar does not necessarily represent a surviving calf.

Mean calving intervals, estimated from the ratio of pregnant cows, range from 2.8-9.1 years (Table 4.14) in 19 samples from 13 populations, and as estimated from placental scar regressions from 2.1-5.1 years in 12 samples from 9 populations. Four populations, based on the first method, have shorter calving intervals than elephants in Etosha N.P., but both the 1983 and 1985 estimates from Etosha N.P. are the shortest periods stemming from all the regression estimates. This would indicate that the Etosha N.P. population, during a period of population decline, is breeding at a rate faster than most others. Figure 4.15 illustrates the absence of a relationship of MCI with elephant density, for the populations in East Africa and southern Africa separately and combined (r^2= 0.03-0.11). Only in the combined regression is the slope significantly different from 0 (Fig. 4.15), but the scatter of points render a linear regression invalid.
Density-dependent effects on MCI suggested by Laws (1969a), and particularly an exponential increase of MCI with elephant density, are therefore not applicable to a direct comparison between different populations. Both indirect estimates of the MCI ignore calf mortality and compensatory breeding, and are misleading without further qualification. Moss (1983) found that the MCI was 3.8 years when the previous calf died, and 5.4 years if the previous calf survived. Compensatory breeding therefore reduces the mean calving interval, and not the opposite as suggested by Jachmann (1986). A further suggestion that young cows have shorter calving intervals than older cows (Jachmann 1986)

Table 4.14 Summary of some reproductive parameters in 24 samples from 17 African elephant populations.

LOCALITY *	PERIOD	MEAN CALVING INTERVAL (YEARS) A	MEAN CALVING INTERVAL (YEARS) B	MEAN AGE AT 1ST CONCEPTION (YEARS) C	MEAN AGE AT 1ST CONCEPTION (YEARS) B	MEAN LENGTH OF LACTATION ANOESTROUS (YEARS) A	% ANOESTRUS FEMALES/ PAROUS FEMALES	ONSET OF SENESCENCE (YEARS)	REFERENCE
B.F.	1966	7.7	-	22.4	-	5.9	-	-	Laws et al. 1975
K.F.N.P.S.	1958-64	8.6	-	7-15	-	6.8			Buss & Smith 1966
"	1967	5.6	4.9	17.8	-	3.8	28.6	40 +	Laws 1969a, Laws et al. 1975
"	1974	3.5	5.1	9.0	-	1.7	-	-	Malpas 1978
K.F.N.P.N.	1966	9.1	-	16.3	-	7.3	8.6	40 +	Laws 1969a, Laws et al. 1975
"	1974	5.1	4.6	9.6	-	3.3	-	-	Malpas 1978
M.R.C.	1969	4.2	-	12.2	-	2.4	-	-	Laws 1969a, Laws et al. 1975
M.R.E.	1968	2.9	-	12.2	-	1.1	-	-	Laws 1969a, Laws et al. 1975
R.N.P.	1973	4.5	4.2	12.3	-	2.7	-	-	Malpas 1978
T.N.P.	1966	6.8	4.0	11.7	13-14	5.0	7.9	40 +	Laws 1967b, 1969a, Laws et al. 1975
L.M.N.P.	1966-70	4.7***	-	11.0	-	2.9	-	-	Douglas-Hamilton 1972
L.V.N.P.	1965-69	3.5	3.4 ****(3.8)	14	20.1	1.7 (2.0)	2.0	40 +	Hanks 1972a
K.N.P.M.	1978	3.9***	-	-	-	2.1	-	-	Jachmann 1980
M.P.N.P.	1969-72	3.5	-	12-13	-	1.7	6.9	40 +	Kerr 1978
Zambezi Valley, Zimbabwe	1969-72	3.4	-	11-12	-		-	-	Dunham 1988
	1985	2.8	3.8	13-14	-		-	-	Dunham 1988
H.N.P.	1972	4.0	4.3	11.0	-	2.2	-	-	Williamson 1976
G.N.P.	1971-72	3.7	4.3	12-13	12.6	1.9	2.2	50 +	Sherry 1975
K.N.P.	1970-74	4.5	4.5	12.0	10.8	2.7	8.1 or 17.2**	50 +	Smuts 1975
A.N.P.	1972-80	4.9***			-				Moss 1983
E.N.P.	1983	3.8	2.1	13.5(9.1)	10.7	1.8	15.5	50 +	This study
E.N.P.	1985	3.8	2.5	11.5 (10.7)	11.9	1.8	7.6	50 +	This study

A from % pregnant females
B from placental scars
C from overlap between pubertal and parous females

* Abbreviations explained in Appendix 1
** from age structure of 15 herds
*** from direct observations
**** recalculated as (3.8) by Malpas (1978) in Eltringham (1982)

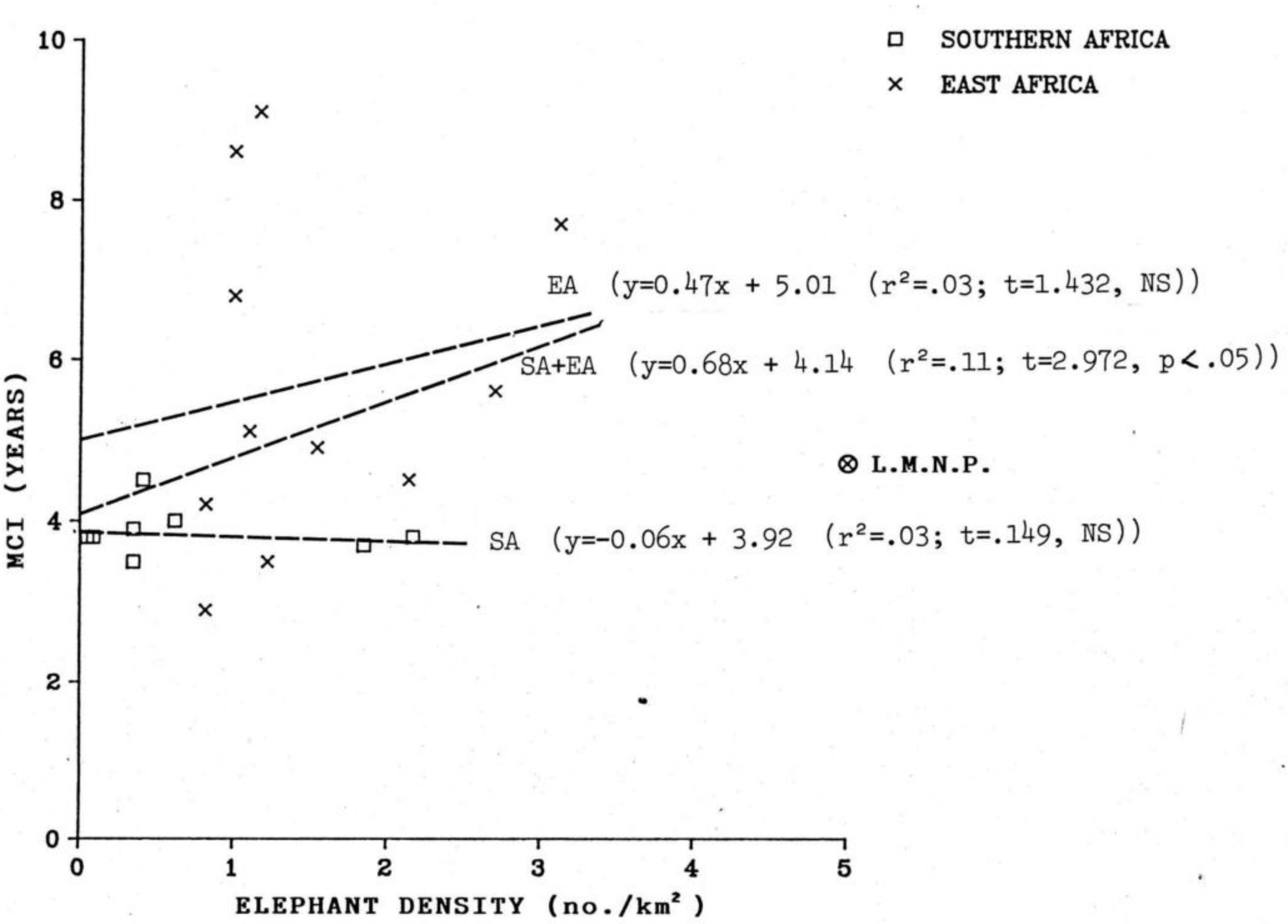


Figure 4.15 The relationship between mean calving interval (MCI) and elephant density, in southern Africa (SA) and East Africa (EA). The outlier from Lake Manyara N.P. (L.M.N.P.) is excluded from the regression.