Age structure of the Elephant population in the Etosha National Park, Namibia

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ABSTRACT

The age structure of the elephant population in Etosha National Park, Namibia, was determined using aerial photogrammetry and ground classification of herds into age groups. Age distributions derived from photogrammetry differed significantly between years in 1983 - 1987. Age structures derived from either method used, nevertheless did not differ drastically from year to year, indicating that age specific mortality and survival rates remained similar from 1977 - 1988. A doubling of population size from 1974 to 1983 could not have resulted from any change in fecundity, as noticeable changes in the age structure would have occurred. The similarity in age structures over this period suggests that population increases were due to immigration.

INTRODUCTION

The age structure of a population, expressed as the distribution of the number of individuals in each age group, reflects the nett result of fecundity and mortality schedules of that particular population. As such, age class structure is an important way of measuring demographical changes over time, and also for comparing different populations (Caughley 1977). Age structures, however, are difficult to obtain with precision, and are only as good as the method used for estimating the age of individuals.

While elephant populations throughout most of Africa have declined in recent years due to poaching and drought (eg. Laws 1969; Corfield 1973; Leuthold 1976; Jachmann 1986; Douglas-Hamilton 1987; Ottichilo *et al.* 1987; Wells 1989), those in southern Africa have thus far escaped intensive poaching. Populations in Zimbabwe, Botswana and South Africa are apparently increasing (Calef 1988; Dublin 1989; Cumming *et al.* 1990). The population in Etosha National Park (hereafter referred to as Etosha) also increased during the 1970's, although it is believed that the increase coincided with a period of redistribution of elephants in north-western Namibia due to drought and human interference (Lindeque 1989). The number of elephants in Etosha more than doubled in ten years (Lindeque 1989), and any changes in the population age structure could reveal the relative importance of immigration versus recruitment through breeding.

METHODS

Colour transparencies were taken of all breeding herds seen during aerial censuses after December 1983, following the procedures of 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). 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 (Laws 1969b). 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 with confidence in aerial photographs. The curve is weighted using the sex ratio at age, as males and females grow at different rates (Hanks 1972; Laws *et al.* 1975; Sherry 1978).

An unsexed weighted mean distribution of back lengths per age group was constructed using the 1985 culled sample from Etosha. Back lengths were measured over body 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 $y = 131.30\text{-}14.33x\text{-}0.59x^2\text{-}0.01x^3$ ($r^2=0.891$), 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, at an asymptotic back length of 280 cm (median of back lengths of females $\geq$ 30 years). Adult females with asymptotic back lengths were used as the reference measurement in herds, and all other elephants were measured as the ratio of back length : asymptote (Table 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. The problem of scaling is thus circumvented. In the 1985 sample, 12% of individuals were adult females at the asymptotic back length. Therefore, in theory 12% of individuals in each group photographed would be used to calculate a mean asymptotic back length for that photograph. 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 and Tsavo are generally much smaller than in Croze's (1972) study, who recommended 10% as a fixed proportion. Some groups contained adult bulls which might or might not be identified as such, especially in small groups. To overcome this source of error the ratio of the smallest individual to the largest in each group 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).

TABLE 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	0.158	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
** derived by interpolation from the polynomial:
$y = 1.3130 - 14.33x - 0.59x^2 - 0.01x^3$, where y = age of individual, x = back length.

Elephants were also subjectively classed into six age intervals following diagrams in Laws (1966) and Hanks (1979) during ground-based observations by all staff members in Etosha. Classes used were 0-1 year-old calves, calves (2-5 years), juveniles (6-10 years), intermediates (11-15 years), sub-adults (16-20 years) and adults (> 20 years), 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).

Polynomial regressions were calculated using a computer package (SuperCalc 5). Age (frequency) distributions were compared using a contingency analysis as suggested by Caughley (1966).

TABLE 2: Aerial surveys and photogrammetrical samples used in constructing age distributions of elephants in Etosha National Park and other localities in Namibia.

Date of survey	Locality	Population Size	No. of elephants measured (% of population size)	
May 1984	Etosha	1158	418	(36.1)
Dec. 1984	Etosha	2081	503	(24.2)
May 1985	Etosha	1244	535	(43.0)
Aug. 1985	Etosha	1186	374	(31.5)
Sept. 1987	Etosha	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 Namibia, including Kaudom Game Reserve.
** including Mahango Game Reserve.
*** northern part of the Kaokoveld, including Kunene River Mouth (10) Hoanib-Hoarusib River group (c.35).
**** southern part of the Kaokoveld.

RESULTS

Table 2 presents the sampling intensity of elephants measured

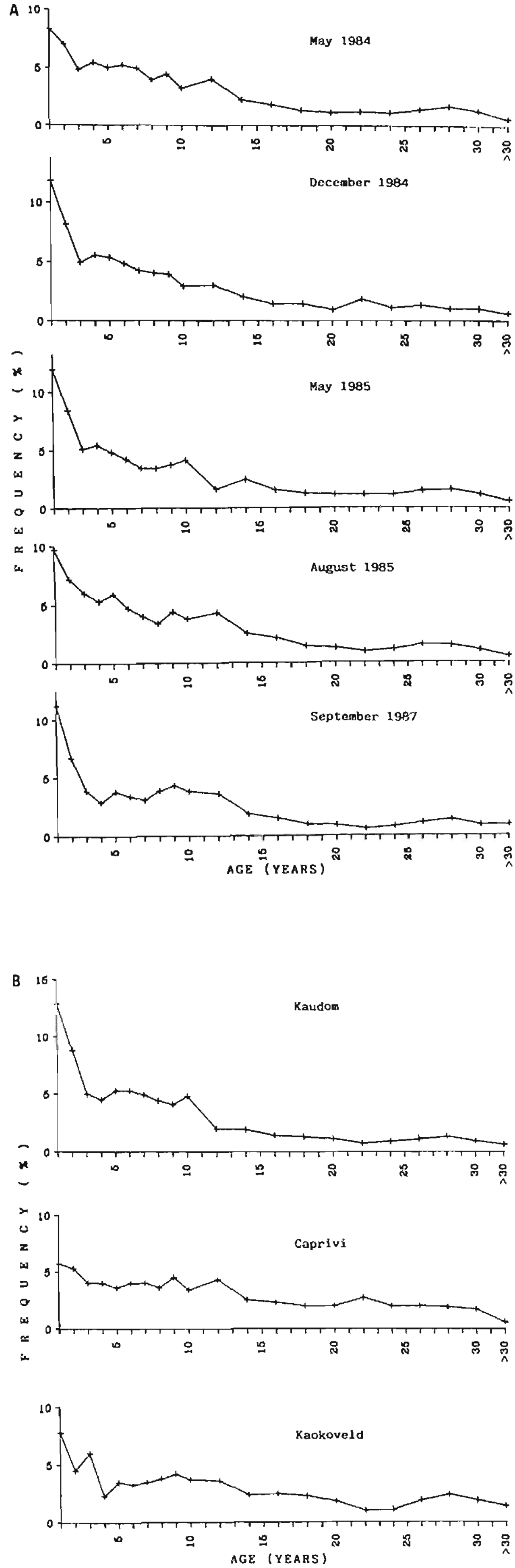

FIGURE 1: Frequency distributions in different age groups of elephants based on aerial photogrammetry in Etosha National Park from 1984-1987 (A) and elsewhere in Namibia (B).

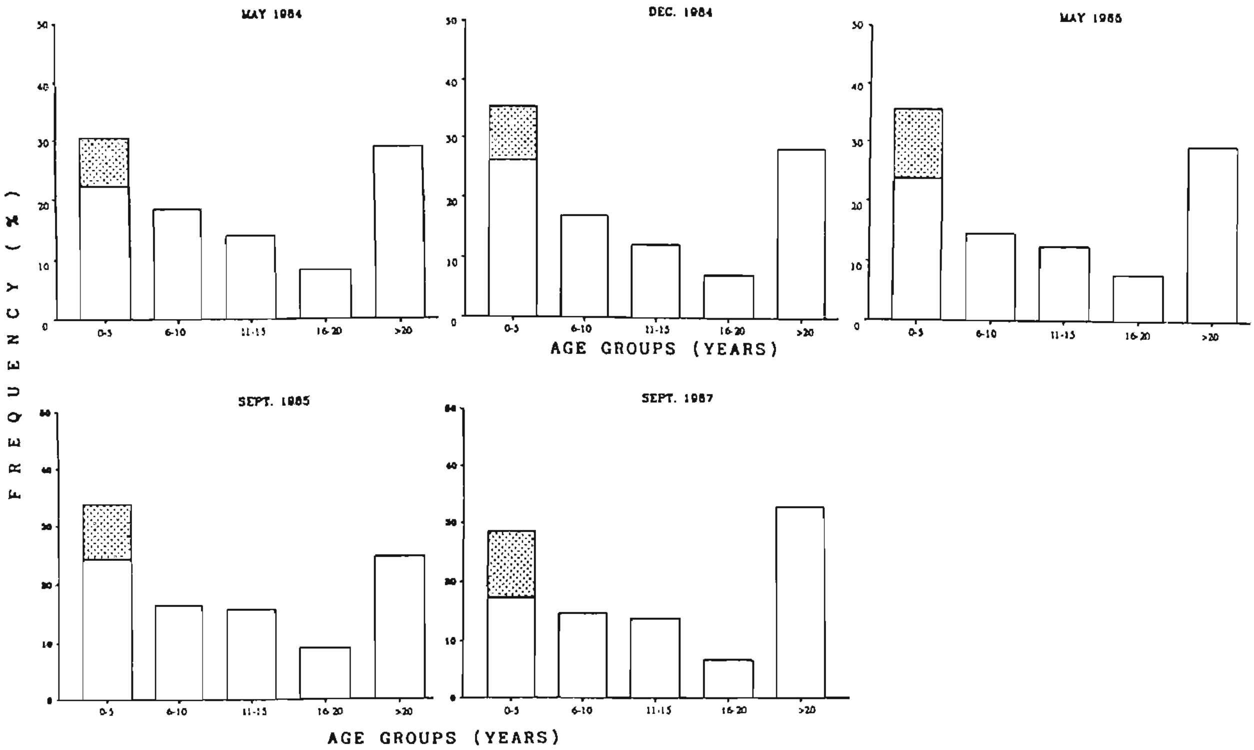

FIGURE 2: Summarized age structures based on aerial photogrammetrical surveys of elephants in Etosha National Park. Shaded areas denote elephants <1-year old.

from photographs, relative to population size. Smaller samples are also available from three other regions in Namibia for comparison. Figure 1 A & B illustrates the resulting age distributions up to 30 years of age as first-order-averages for the five surveys in Etosha and three elsewhere in Namibia. The five photogrammetrical age distributions from Etosha are significantly different from each other ($\chi^2=181.29$; $p<.05$).

Figure 2 illustrates age structures of elephants based on aerial photogrammetry in Etosha. Figure 3 illustrates age structures of elephants from 12 samples of eight populations, including three from other localities in 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 from 1977-1988 are illustrated in Figure 4. Data for 1977-1978 are from De Villiers (1981) and from 1979-1982 are from unpublished departmental records.

DISCUSSION

In the last decade, the number of elephants in Etosha changed dramatically. From 1977 to 1983 the population more than doubled, then declined from 1983 to 1986 by approximately 60 percent (Lindeque 1989). If the rapid changes in population size were mostly due to sudden changes in recruitment or mortality, the population age structure would show changes in the relative proportion of individuals in each age category. Population increases caused by rapid breeding are characterized by a reduction in the age at first conception and the mean calving interval in elephants and other large mammals (Caughley 1977; Laws 1981). Significant changes in the frequency contribution of young calves should occur in this instance. Mass mortality of elephants due to drought or disease is also likely to affect some age categories more than others. Drought mortalities in Tsavo and Amboseli National Parks showed that calves were particularly vulnerable (Laws & Parker 1968; Corfield 1973; Moss 1988) followed by senior adult elephants ($\geq$50 years). The only known mortality factor which could possibly affect all age categories is indiscriminate poaching, and no evidence could be found for large scale poaching of elephants in Etosha. Mortalities caused by anthrax and drought did occur (Lindeque 1989), and if these were responsible for the dramatic decline in population size from 1983 to 1986, changes in the population age structure would have been apparent, as both mortality factors affect selected sex and age groups more strongly than others (Lindeque 1989).

No dramatic changes in age structure could, however, be demonstrated in Etosha over the period 1977 to 1988, encompassing the period of dramatic change in population size. Age structures were significantly different between years, indicating some changes in age-specific mortality and fecundity, but were nevertheless too similar from year to year to account for eruptive breeding or mass mortality.

The use of frequency distributions of the number of individuals in each year group, or age distributions, to indicate change in the age structure of a population might, however, 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. (Figure 3). The age structure of a population furthermore does not always provide conclusive evidence of a population increase or decrease, as explained by Caughley (1977). The age structures for the Tsavo National Park (East) elephant population in Figure 3 also illustrate this point. This population would have declined in 1966, were it not for large-scale immigrations due to compression (Laws & Parker 1968, Laws *et al.* 1975), as the mean calving intervals increased and the age at first conception was delayed. After the drought in Tsavo and the population crash, the population apparently increased (Leuthold 1976) until poaching caused a further decline (Ottichilo 1986a, b, 1987). The age structure in 1974 (Figure 3), at a time when the

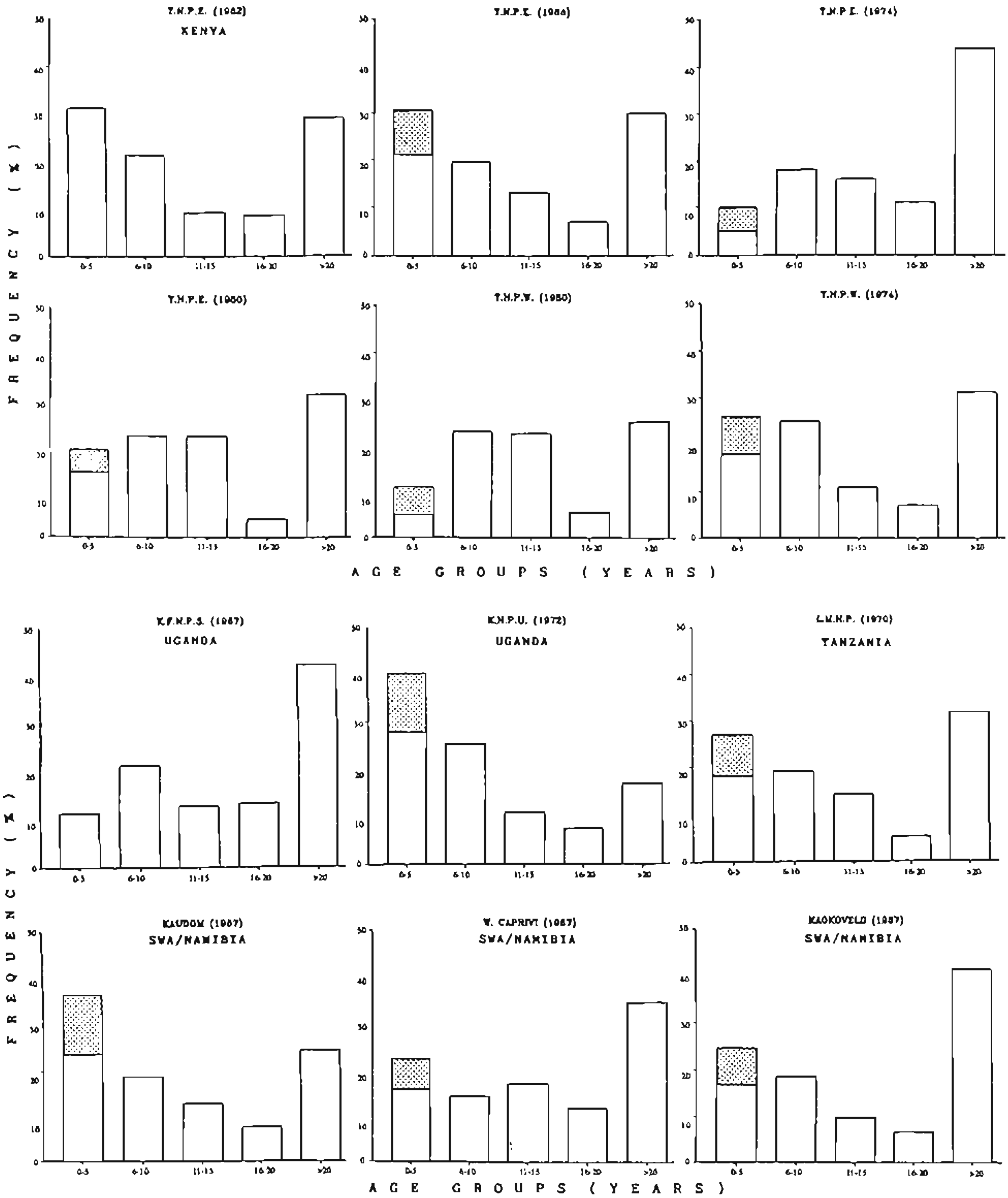

FIGURE 3: Summarized photogrammetrical age structures of 12 samples from eight populations of elephants in East Africa and Namibia. Data from references in text, all derived from aerial photogrammetry, except Douglas-Hamilton (1972 in Leuthold 1976) who used ground-based photogrammetry in Lake Manyara 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

population was increasing, still reflected the effects of the drought and mass mortality of young elephants in particular.

The age structure of the Etosha elephants from 1983 to 1987 appears similar to those from age structures from Tsavo in 1966 and Lake Manyara 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 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, as calves are undercounted from the ground while the number of adults appears to be overestimated. Calef (1988) regards the relatively high percentages of one-year-old calves reported in culled and census samples of elephants as inconsistent with the maximum rate of increase possible in elephants, namely 7% per year. He believes that confusion with older calves accounts for reported frequencies of 0-1 year old calves which are consistently greater in most studies of populations not known to be increasing rapidly. Calf mortality was nevertheless

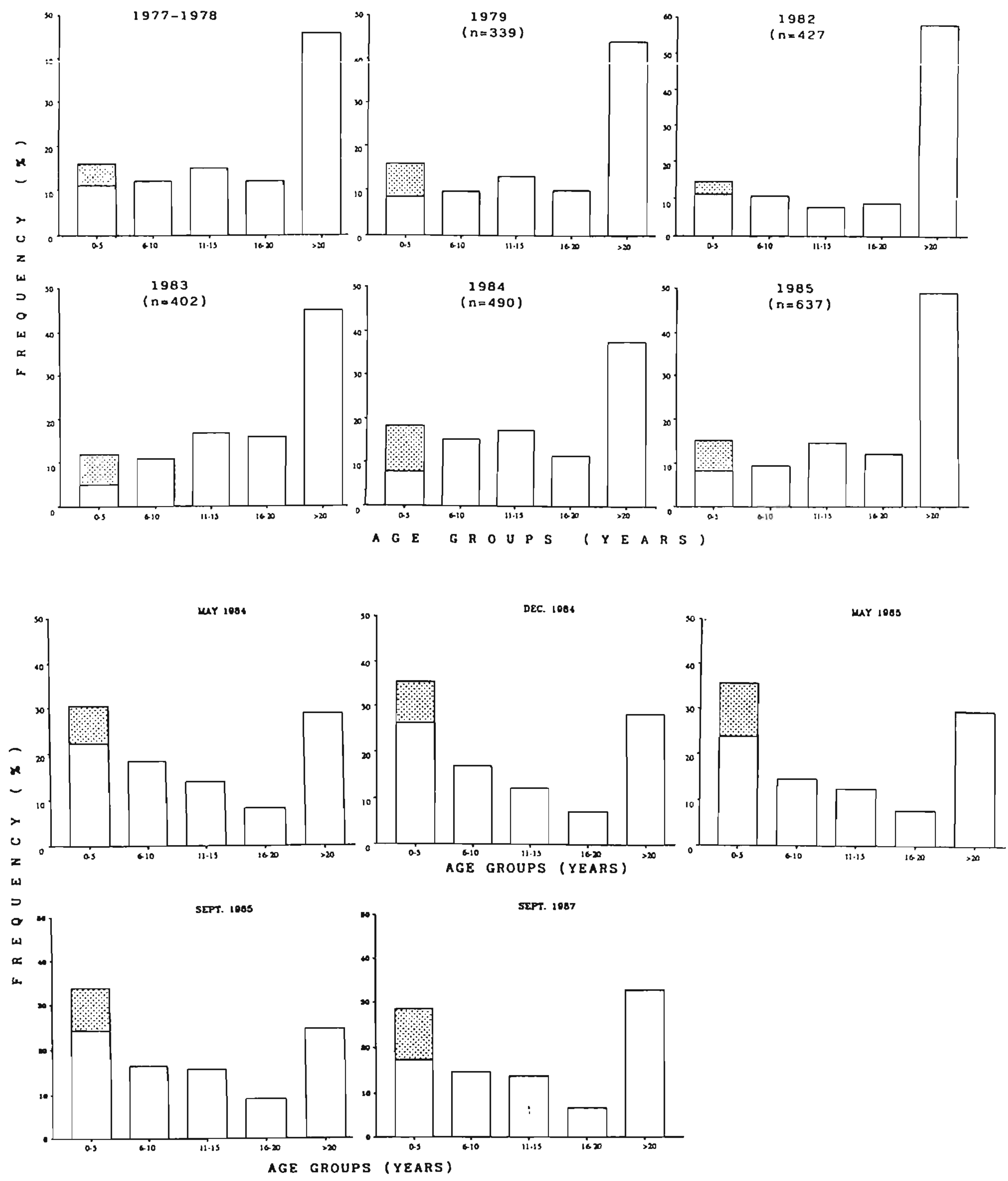

FIGURE 4: Age structures of breeding herds of elephants in Etosha National Park from 1977 to 1988, based on ground observations. The number of elephants classified per year is given in parenthesis. Shaded areas denote elephants <1 year old.

ignored in Calef's (1988) model and though this issue is still unresolved, the comparative value of age structures is not invalidated.

Annual age distributions from Etosha were significantly different, but do not prove that the population had a stable or unstable age distribution over that period, without reference to age-specific mortality and fecundity. The age distributions presented here appear remarkably similar despite major changes in population size, and were therefore not affected by such changes. The apparent stability of the age structure of elephants in Etosha therefore supports the suggestion that the observed changes in elephant abundance in Etosha from at least 1973 to 1987 were due to movements by elephants in and out of the park.

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