cannot be substantiated unless the reproductive histories of females are known from evidence other than the age intervals between surviving calves. The mean calving interval as measured from indirect methods is therefore subject to calf mortality, which may even further obscure any relationship with elephant density.

Attainment of sexual maturity

Laws (1981) states that the plasticity in the age at sexual maturity in the female African elephant is unequalled in mammals. Individuals become sexually mature from 8 to 30 years of age, while population means range from 9 to 22 years (Table 4.14). It is not clear what is meant by sexual maturity in some references in Table 4.14. The appropriate definition is the age at first conception (Laws 1967b), but mean age at first ovulation or mean age at first parturition may have been implied. The estimated mean age at first conception in Etosha N.P. is at the lower end of recorded range in Table 4.14, as is the mean calving interval.

Mean age at first conception in Etosha N.P. was greater in 1983 than in 1985, accepting that the placental scar-regression estimates are inaccurate. Such an advancement of age at first conception from 1983 to 1985 corresponds with the improvement in environmental conditions after the drought, but could also be the result of different fractions of the regional population present in the two samples.

Croze (1972) considers the age at first conception to be more significant than the MCI as an indication of population increase. He argues that in a species with a litter size of one, conception at the earliest possible age would achieve greater production of calves than short calving intervals. The fecundity or sexual maturity of elephants in the pubertal age range is indeed of great importance, as so much of the female population is found in the younger age groups. Laws (1969a) regards the age at first conception as being a more long-term response to density than the MCI and his prediction of a linear relationship seems to be true. The MCI, as discussed, can be modulated quickly by a mechanism such as calf mortality.

In Fig. 4.16, significant density-dependent increases in the age at first reproduction are demonstrated for the East African populations ($r^2=0.42$, $p<0.05$; $t=8.690$, $p<0.05$) and the total sample ($r^2=0.60$, $p<0.05$; $t=24.187$, $p<0.05$). There is, however, no significant density effect on age at first reproduction in the seven samples from

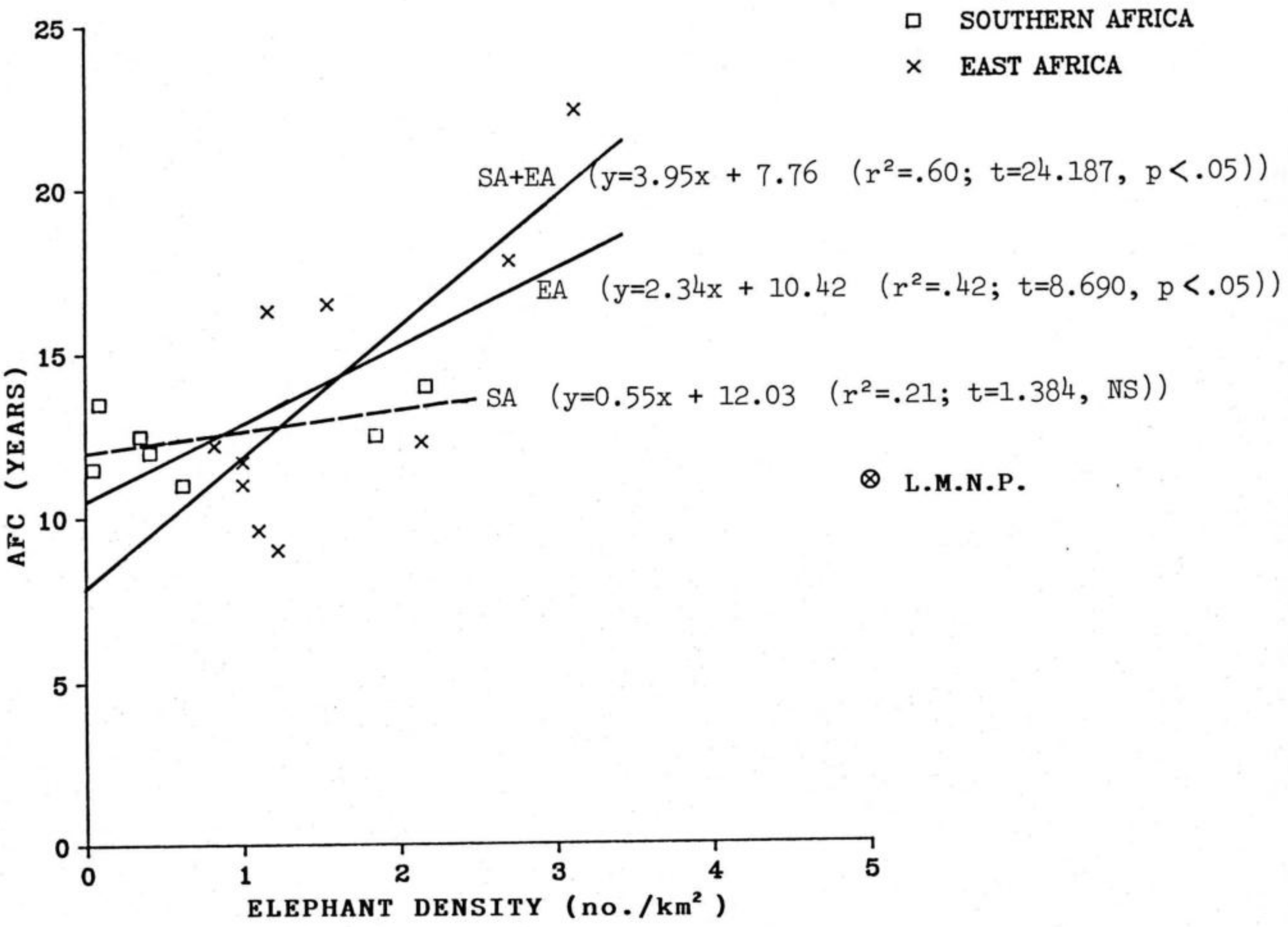


Figure 4.16 The relationship between age at first conception (AFC) and elephant density, in southern Africa (SA) and East Africa (EA). The outlier from Lake Manyara N.P. (L.M.N.P.) is excluded from the regression.

southern Africa (r^2=0.223; t=1.384, NS). Furthermore, when the contradictory Lake Manyara N.P. density and age at first reproduction are included no significant correlation can be demonstrated (East Africa r^2=0.22; $p<0.05$, total sample r^2=0.21; $p<0.05$). The highest long-term density of elephants in Africa, between 5-7.5/km^2, has no overt effect on the age at first reproduction. Elephant density, or stress from overcrowding, is clearly not the only determinant of the rate of sexual maturation, but some other factor such as nutrition could play a significant role. Comparisons between different populations are therefore biased, but long-term monitoring of the age at first conception in each population separately could reveal responses to changes in environmental conditions.

Senescence, anoestrus and reproductive disorders

The onset of senescence is the last of the homeostatic mechanisms proposed by Hanks & McIntosh (1973) and Laws et al. (1975). The cessation of breeding in some individuals as reflected in the decline in fecundity after age 40 or 50 years, has been equated to the human menopause. The latter is characterized by the cessation of ovarian function due to depletion of primary follicles, but there is no evidence that follicles are depleted in senescent elephants. Pregnant and lactating cows older than 50 years have been found in most populations, and one 60-year old cow in Etosha N.P. was approaching oestrus when culled. The only inactive cow older than 50 years in Etosha N.P. in both the 1983 and 1985 samples that could be regarded as senescent had a reproductive disorder (benign fibroidal uterus). Senior cows are poorly represented in culled samples, also in Etosha N.P., but appear to be capable of reproducing, albeit slower or more irregularly, up to the final age group.

As a homeostatic mechanism senescence has been overrated in my opinion, as only the few individuals at the apex of the age pyramid are affected. When the number of anoestrous cows is defined as the number of parous cows not lactating or pregnant, as in Table 4.14, the high incidence in some samples may be misleading and appear to be detrimental to population growth. Of all 18 non-pregnant, non-lactating females in the samples from Etosha N.P. only one had no evidence of recent ovarian activity. The rest were all cyclically anoestrous or had minor disorders occuring in pregnant and lactating females as well.

Breeding synchrony

In addition to the seasonality of conceptions and births found in most populations and particularly in southern Africa, another form of synchrony has been suggested to occur by Laws & Parker (1968) and Laws (1969a, b). This type is known as cycles in recruitment related to variation in annual rainfall, and became a much disputed issue in elephant biology (see Chapter 3). The main evidence for cycles in recruitment lies in the age structures of culled samples from populations in East Africa and southern Africa, showing a series of peaks and troughs with a wave length of about 6-8 years. Arguments against the existence of such cycles rely on the lack of correspondence between rainfall and recruitment peaks in populations from Zambia, Zimbabwe and South Africa (Hanks 1972a, Smuts 1975, Williamson 1976). Explanations have been sought in the accuracy of age estimation methods and the theory was discarded (Fatti et al. 1980).

Synchronized conceptions within herds in Etosha N.P. suggest that irregular age distributions have some biological significance other than methodological complications. The mechanism required in achieving synchronous conceptions and by implication synchronized oestrus is unknown, but may well be the result of male musth, as musth is seasonal in southern Africa (Hall-Martin 1987). Bulls in musth leave their usual home ranges, actively seek out a breeding herd with a cow in oestrus and join that herd for a variable period (Poole 1982). In the Amboseli N.P. situation with far greater elephant density, bulls may encounter several herds in a short period and are then in a position to choose to associate with a herd containing an oestrous cow. In Etosha N.P., there are possibly fewer bulls than elsewhere (see Chapter 5) and an extremely low density of herds (approximately one herd/370-550 km^2). It might be more profitable for a bull to stay with the first herd it encounters and its presence might stimulate one or more cows to come into oestrus. Although purely speculative as far as elephants are concerned, exposure to males as a cue to female hypothalamic and consequently ovarian activity is well known (Skinner & Van Jaarsveld 1987). The apparent irregularity of musth periods in bulls (Poole 1982) may give additional support to the lack of synchrony between herds.

Barnes (1982) extends the concept one step further, by theorizing that a bull in permanent association with a breeding herd has a greater chance of access to an oestrous cow, in contrast to searching for receptive cows during his musth period. Above a density of 0.4 elephants/km^2, a searching strategy would be more successful, as calculated from the probability of finding an oestrous cow per day. The herd bull strategy would even be more favourable if the distribution of cows is strongly clumped. No population intensively studied has shown the herd bull strategy, although the concept was familiar to the great ivory hunters (Sikes 1971, Barnes 1982).

In Etosha N.P., which is a semi-arid area with very low density of elephants (0.03-0.11/km^2), no evidence of strong association with breeding herds by bulls could be found although the study was not behaviourally orientated. Where seasonal breeding occurs, such as in Etosha N.P., there is furthermore little advantage to a bull in staying with a herd throughout the year. Preliminary evidence suggests that bulls associate with breeding herds during the aggregations prior to migrations and coincidental to the breeding season. This situation, however, is not evidence of the herd bull strategy.

Elephants in Etosha N.P. and elsewhere aggregate during the wet season, when breeding herds join in a higher social grouping, or clans. Musth in bulls appears to be more seasonal in southern Africa than in East Africa (Hall-Martin 1987), as are conceptions, and coincide with the wet season aggregations. More cows would presumably be affected by bulls in musth, and more conceptions would be synchronized.

From the degree of synchrony within herds in Etosha N.P., it is only a small step further to reach synchrony between herds. I postulate that greater synchrony would be evident after some perturbation such as a drought, which by postponement of breeding activity or mortality of calves, would render many herds in the same phase of calf production. This effect is likely to persist for a few years after the perturbation but would eventually phase itself out, as the age at first conception and calving intervals change in response to density and nutrition, or other factors. Regular perturbations would maintain periodic synchrony and therefore peaks in the age structure.

Cycles in recruitment have traditionally been related to rainfall, either during the year of conception or the year of birth of one or more of the ages represented by peaks in the age distribution (Laws & Parker 1968, Laws 1969a, Hanks 1972a). Synchrony, recruitment waves and the absence of either phenomenon, are the result of both reproduction and mortality. Variable numbers of calves are conceived or born in one year, presumably higher numbers in good rainfall years than in poor ones. During a drought, some calves in the 0-4 year age group would have been born prior to the drought, depending on its duration, and some would be conceived during it. Weaning of calves during a drought is likely to make calves in the 2-4 year age group particularly vulnerable. Even though rainfall might be the determining factor, age structures might not be correllated with variation in rainfall, due to the complex interaction of mortality and reproduction, both reflecting environmental conditions two years earlier as well as during a particular year.

CHAPTER 5 MORTALITY

INTRODUCTION

The central issue regarding mortality patterns of elephants is whether calf mortality is a significant mechanism in the regulation of elephant populations. Laws (1981) argues that elephants are the archetypal K-selected species, with a long gestation period, long period of growth, large parental investment and a long lifespan. High calf mortality is not a feature of K-selected species, although Hanks & McIntosh (1973) suggest early mortality to be the most important density dependent population control method. Laws (1981) maintains that adjustments in the age at first conception, and the calving interval, (and the onset of senescence in Laws 1969b) regulate population growth of elephants in a density-dependent way, the same as in other long-lived, large-bodied K-strategist mammals (Southwood 1981).

There is nevertheless substantial evidence of high calf mortality rates in some elephant populations (Hanks 1972a, Croze et al. 1981), and also in Etosha N.P. The exact cause of early calf mortality is puzzling. Only two causes come to mind which can result in large scale calf mortality before weaning, namely desertion of calves by cows and starvation through the premature termination of lactation. These possibilities again do not fit in with the stereotype picture of elephants; the large maternal investment, protectiveness of conspecifics towards calves, adoption of strange calves, caretaking by older siblings, and the low incidence of non-lactating cows. No evidence of disease or predation causing substantial calf losses has yet been presented. Malnutrition and starvation during severe droughts in Tsavo N.P. and Amboseli N.P. have nevertheless caused the deaths of almost entire cohorts (Corfield 1973, Croze et al. 1981, Laws 1981, Moss 1983). Coneybeare & Haynes (1984) and Haynes (1985) described mass mortalities of calves aged 2-8 years old during a drought in Hwange N.P., as the result of falling water tables in wells dug by elephants.

The many incidences of over-utilization of their food resources (eg. Laws 1970, Wing & Buss 1970, Laws et al. 1975, Caughley 1976) confirm that elephants might not be able to respond to temporal changes in resource abundance. Reproductive homeostasis probably operates over a period of 15-20 years (Laws 1969b), with the age at first conception even slower to change than the mean calving interval (Laws 1969a). Croze (1972) nevertheless regards the age at first conception to be the most significant short-term variable in the regulatory process. Laws' (1969a) prediction that the mean calving interval can quickly respond to environmental conditions was, however, borne out by the reduction in the MCI due to calf mortality found by Moss (1983).

Calf mortality, as discussed in Chapter 4, is therefore intimately related to at least one of the density-dependent control mechanisms, namely the mean calving interval. Calf mortality certainly has the potential to change population trend (Croze et al. 1981, Laws 1981) but whether it actually regulates populations remains unknown.

Mass mortality of elephants as in Tsavo N.P. (Corfield 1973) may be seen as proof that intrinsic controls based on reproduction are inadequate under the present limitations on large scale migrations in Africa. By evading droughts through movements, density-dependent mechanisms of control of reproductive output would probably be sufficient in maintaining stability.

In this section, the causes of elephant mortality in Etosha N.P. are examined, as well as the incidence and frequency of mortalities in each age group. Elephant mortalities in Etosha N.P. are probably not representative of mortalities occurring in the entire distribution range of the regional population in north-western SWA/Namibia. Human-related mortality factors are likely to be more prominent outside the park, but could not be investigated due to the security-imposed prohibition on access to parts of Ovambo, Kavango and the Kaokoveld.

METHODS

Elephant deaths were recorded routinely in Etosha N.P. by all research and management staff and 629 cases excluding culling are known since 1971. As anthrax is such a common cause of death in large mammals in Etosha N.P., the first step in assessing a carcase has been to determine the presence or absence of anthrax, unless the cause of death is obviously something else such as shooting. Veterinary law prohibits the dissection of even suspected anthrax-infected carcases and requires that all such carcases be destroyed by burning. As the aetiology of anthrax in elephant is not as clear as in other species, many carcases found had to be regarded as cases of suspected anthrax resulting in much loss of valuable information. Field personnel are reluctant to handle anthrax carcases, as man is susceptible to the disease. The most information collected from a carcase in this instance was an estimate of the age group (calf < 3 years old, juvenile 3-8 years old, sub-adult 9-19 years old, adult 20-49 years old and senior adult 50 years old), sex, and since 1983, shoulder height. No material could be collected, even mandibles, and the exact age at death is not known for a large part of the sample.

Anthrax is diagnosed in a fresh carcase by preparing bloodsmears and staining with a suitable stain (Giemsa, methylene blue). Prior to 1984, slides were made on site and examined by rangers after which the carcase was burnt or not. These slides and unstained duplicates were then sent to the resident veterinarian or veterinary technician for confirmation. Since the beginning of 1987, all slides were sent unstained to Okaukuejo, where a polychrome methylene blue stain (M'Fadyean 1903) was used for diagnosis (Fig. 5.1). Anthrax is also characterized by other signs which are useful when bloodsmears are inadequate or carcases too far decomposed. Bleeding from body orifices, usually nose and anus, is typical, as is the retardation of coagulation of blood after death (Fig. 5.2). Blood samples may still be collected up to 72 hours post mortem from an infected carcase, provided there is any of it left. Elephants are difficult to sample as the ears dessicate rapidly, which is the usual site for obtaining blood for smears.

Although other evidence of anthrax was usually encountered, relatively few bloodsmears showed anthrax bacilli, and were therefore not confirmed cases. M'Fadyean's stain provides superior results, allowing much better than the somewhat subjective diagnoses prior to 1987. Elephants may be extremely susceptible to bacterial toxins, and dead before massive septiceamia and very high concentrations of bacilli occur (eg. 700 x 10^6/ml in blood, Turnbull, Carman, Lindeque, Joubert, Huebschle & Snoeyenbos, in press), as in some other species (Wilson & Miles 1964). Final presentation of the disease is variable among and within species, which complicates diagnosis by non-specialist staff in particular. A large fraction of mortalities could therefore not be confirmed although anthrax was suspected. To all these must be added the carcases and

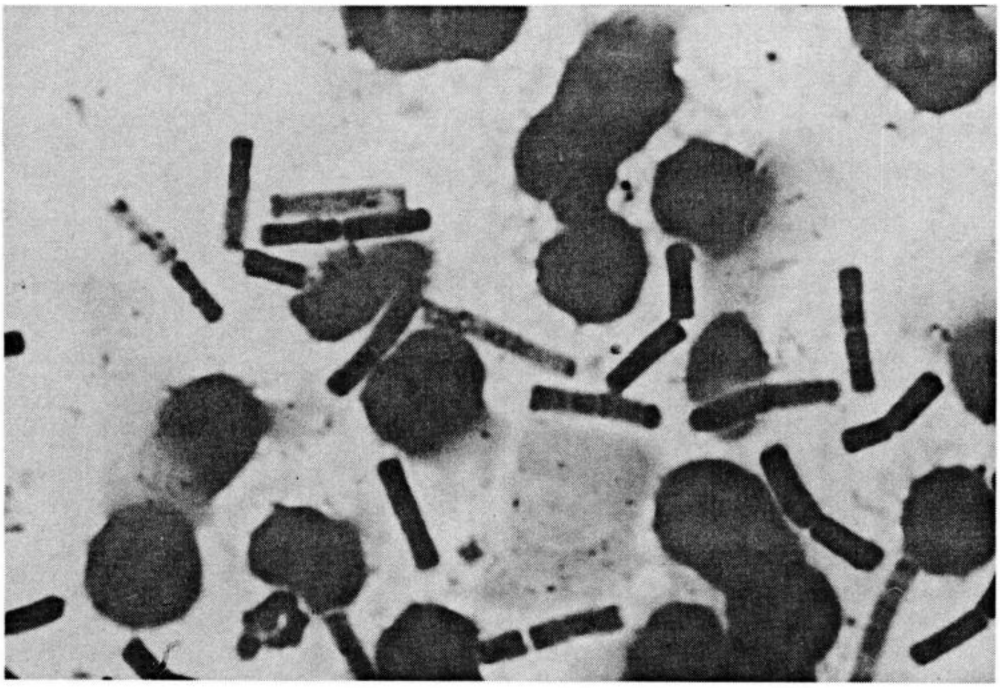
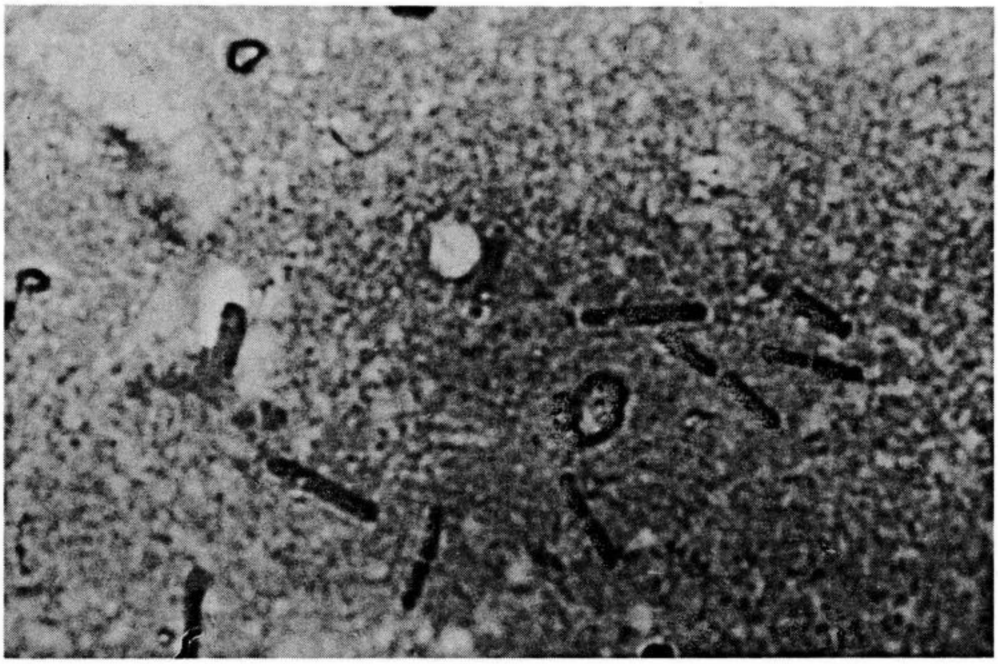
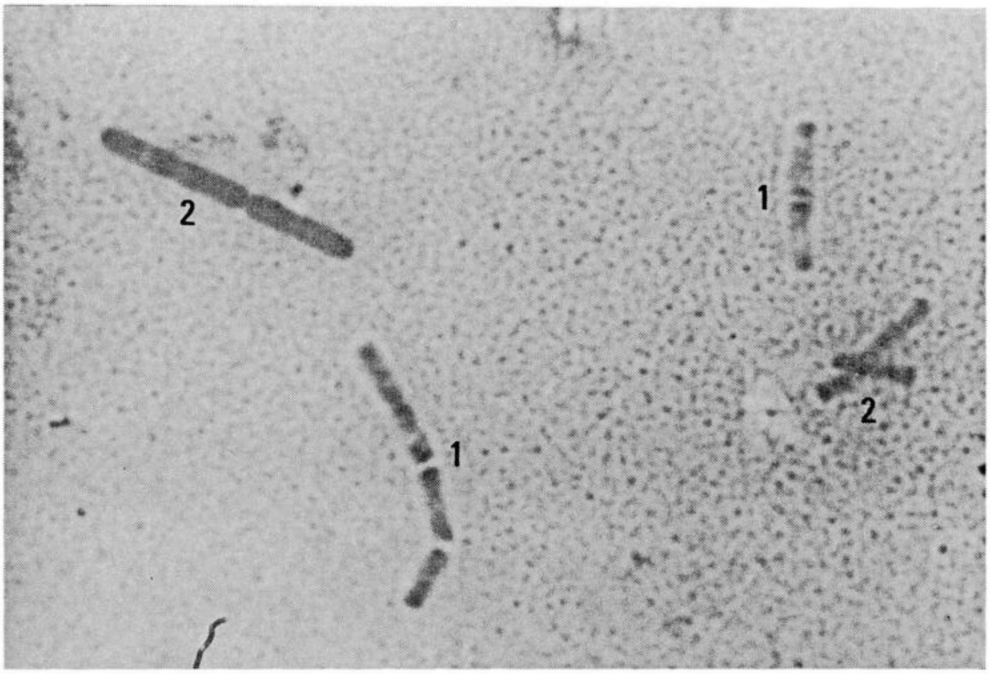


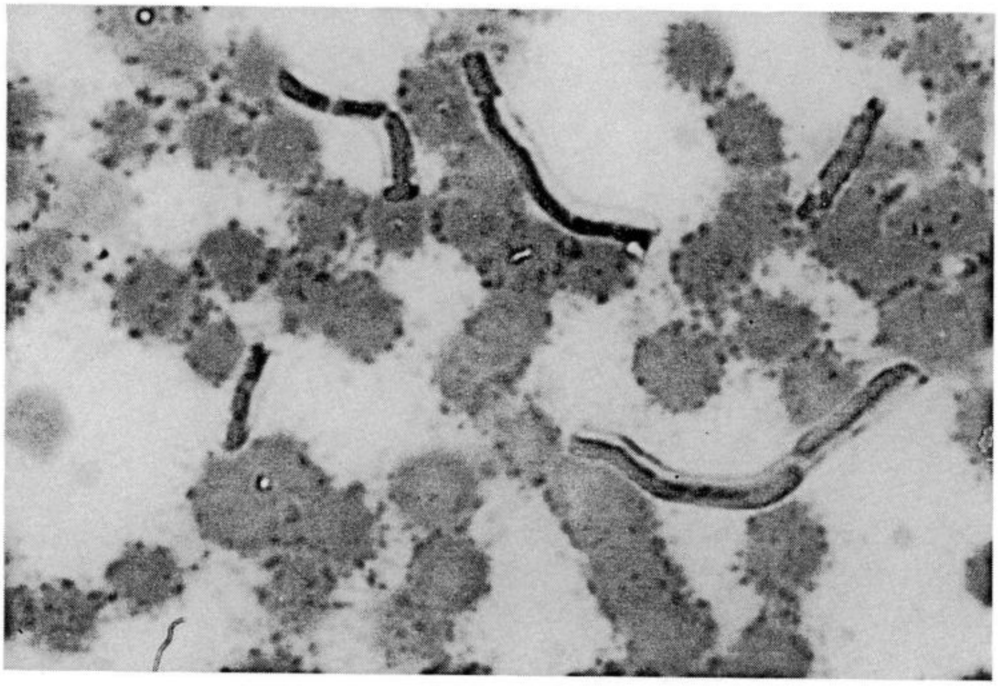
Figure 5.1 A Anthrax bacilli in elephant blood stained with Giemsa (approx. 4000 x magnification).



B. Unknown putrefaction bacteria in elephant blood stained with Giemsa, similar in shape and size to Bacillus anthracis (4000 x magnification).



C Anthrax bacilli (1) and unknown bacilli (2) in haemolized elephant blood stained with Giemsa (4000 x magnification).



D Anthrax bacilli in elephant blood stained with M'Fadyean's stain, clearly showing the diagnostic encapsulation (4000 x magnification).

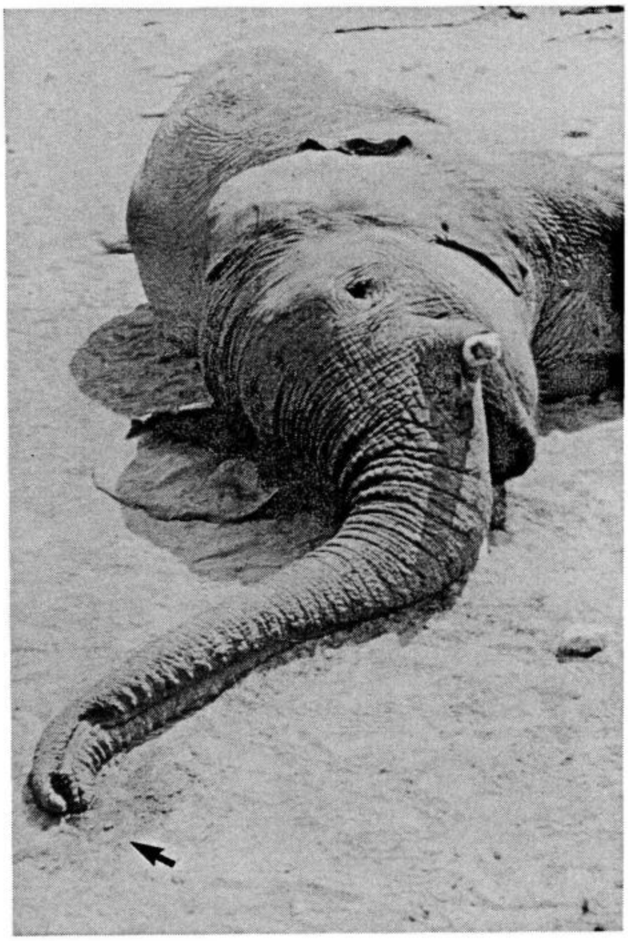


Figure 5.2 Anthrax mortality in Etosha National Park, showing characteristic bleeding (arrow) from the trunk, at approximately 24 h after death.

skeletal remains found where bloodsmears could not be collected due to decomposition, and carcases located by aircraft which could not be reached from the ground.

Up to 1986, some tissue samples from suspected and positive anthrax cases were sent to the Central Veterinary Laboratory in Windhoek for confirmation by culturing and bio-assay. Since 1987 culturing of mostly soil contaminated with carcase fluids is done in Okaukuejo by the resident veterinary technician, using PLET agar as described by Carman, Hambleton & Melling (1985) (Fig. 5.3). Final confirmation is made by a phage test (Brown & Cherry 1955) and all positive isolates are sent to Windhoek for bio-assay confirmation.

RESULTS AND DISCUSSION

Seasonal incidence of mortalities.

In Table 5.1, mortalities are grouped into the period of rapid population growth (1971-1979), the duration of the Trans-African drought (1980-1983) during which population growth peaked and declined, and the post-drought period of population decrease (1984-1987). These phases in population growth (or decline) are discussed in Chapters 2 & 6. It was only during the drought years that mortalities were markedly seasonal, with a greater incidence in the hot-dry season, which is generally agreed to be the worst time of the year for herbivores in Etosha N.P. (Berry & Louw 1982). Elephants aggregate at the end of this season prior to the rainy season dispersals, and conditions for epidemic anthrax are accordingly better than at other times.

Age-specific mortality.

Senior adults (≥50 years old)

The few cases on record (34) support the idea that few elephants reach an age older than 50 years in Etosha N.P., as shown by the culled samples (Chapter 3). More than half the cases (Table 5.2 A) were old bulls shot on farms outside the park, and the rest were

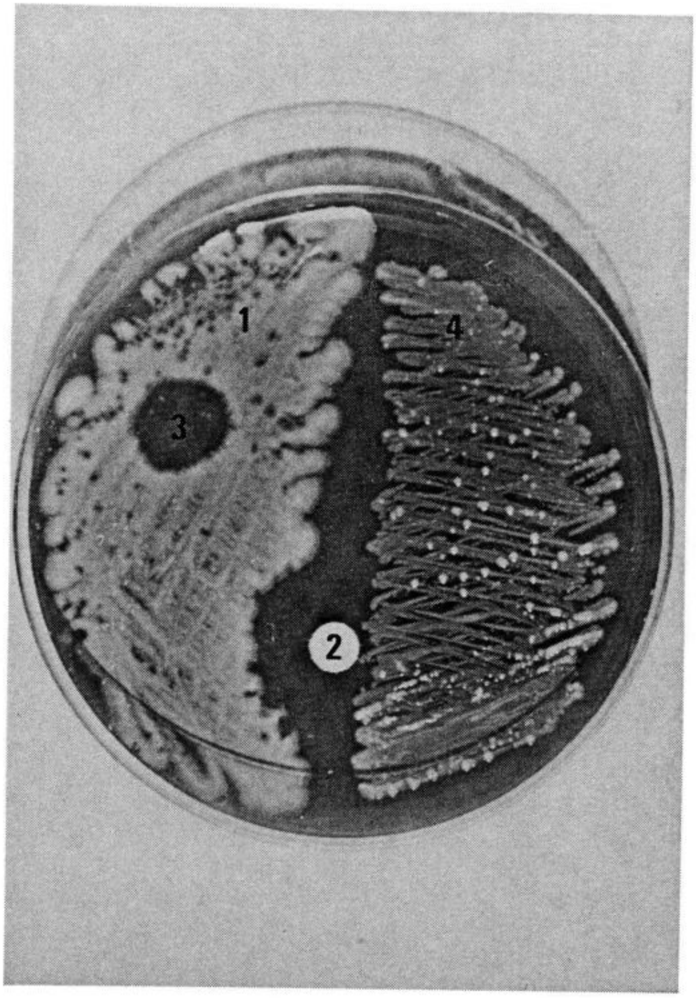


Figure 5.3 Blood-agar culture of B. anthracis (1) with a diagnostic response to penicillin (2) and the phage test (3), compared to a negative culture (4).

Table 5.1 Seasonal incidence of mortality factors of elephants in Etosha National Park.

CAUSE OF DEATH	SEASON			TOTAL
	HOT-WET (JAN-APRIL)	COLD-DRY (MAY-AUG)	HOT-DRY (SEPT-DEC)	
1971-79				
SHOT	38	26	16	80
ANTHRAX	1	4	2	7
UNKNOWN	4	6	8	18
PREDATION	0	1	2	3
POACHING	3	2	2	7
BURNS	0	0	3	3
FIGHTING (INTRASPECIFIC)	0	0	2	2
STARVATION	0	0	2	2
TRAMPLING	0	1	0	1
STRANDING	0	0	1	1
FIGHTING (INTERSPECIFIC)	0	0	1	1
TOTAL (% of grand total)	46 (36.8)	40 (32.0)	39 (31.2)	125
1980-83				
SHOT	15	28	6	49
ANTHRAX	17	6	130	153
UNKNOWN	8	9	27	44
PREDATION	0	3	3	6
POACHING	1	1	0	2
STARVATION	1	1	5	7
DROWNING	0	1	0	1
TOTAL (% of grand total)	42 (16.0)	49 (18.7)	171 (65.3)	262
1984-87				
SHOT	10	3	6	19
ANTHRAX	9	51	23	83
UNKNOWN	7	17	27	51
PREDATION	2	3 *	5	10
BURNS	0	0	5	5
DYSTOCIA	2	0	0	2
STRANDING	1	1	0	2
DROWNING	0	1	0	1
TRAMPLING	0	1	0	1
TOTAL (% of grand total)	31 (17.8)	77 (44.3)	66 (37.9)	174
TOTAL (Percent)	119 (21.1)	166 (29.6)	276 (49.2)	561

Table 5.2 Incidence of mortalities in (A) senior adult (≥50 years old) and (B) adult elephants (20-49 years old) in Etosha National Park.

A

CAUSE OF DEATH	1971-79	1980-83	1984-87	TOTAL	(% of total)
SHOT	10	2	6	18	(52.9)
ANTHRAX	1	0	6	7	(20.6)
UNKNOWN	0	1	0	1	(2.9)
STARVATION	2	6	0	8	(23.5)
	13	9	12	34	

B

CAUSE OF DEATH	1971-79	1980-83	1984-87	TOTAL	(% of total)
SHOT	57	39	13	109	(43.6)
ANTHRAX	3	47	35	85	(34.0)
UNKNOWN	11	22	14	47	(8.8)
POACHING	2	1	0	3	(1.2)
FIGHTING (INTRASPECIFIC)	2	0	0	2	(0.8)
ACCIDENTAL	1	0	1	2	(0.8)
BURNS	0	0	1	1	(0.4)
DYSTOCIA	0	0	1	1	(0.4)
	76	109	65	250	

A+B

CAUSE OF DEATH	1971-79	1980-83	1984-87	TOTAL	(% of total)
SHOT	67	41	19	127	(44.7)
ANTHRAX	4	47	41	92	(32.4)
UNKNOWN	11	23	14	48	(16.9)
STARVATION	2	6	0	8	(2.8)
POACHING	2	1	0	3	(1.1)
FIGHTING (INTRASPECIFIC)	2	0	0	2	(0.7)
ACCIDENTAL	1	0	1	2	(0.7)
BURNS	0	0	1	1	(0.4)
DYSTOCIA *	0	0	1	1	(0.4)
	89	118	77	284	

* difficult birth.

cases of death through starvation and anthrax. Only eight cases of death by starvation inside Etosha N.P. are known , and seven of these were senior adult cows and bulls with only small fragments of M6 left in their jaws (Fig. 5.4 A & B). These can all be regarded as dying at the end of their lifespan through loss of dentition. (The remaining case of death through starvation was a calf less than one year old). No other authenticated instances of death through starvation in elephants younger than 50 years of age are known in Etosha N.P., regardless of the Trans-African drought (1980-1983) and the severe drought in 1987.

Adults (20 - 49 years old)

Death by shooting and from anthrax are the most important mortality factors in adults (Table 5.2 B). Most adults were shot on boundary farms ("problem animal control"), but a few were destroyed in the park when lame or injured from unknown causes. Most of the class scored as dead due to unknown causes can be regarded as having died from anthrax owing to the difficulties in diagnosing anthrax (see above). Virtually all cases discovered weeks or months after death did not show evidence of the cause of death. After 1986, soil samples from beneath such cases could be used to determine the presence of anthrax or not.

The remaining adult mortalities include dystocia, where one cow died in giving birth after a tremendous struggle as evidenced by uprooted trees and broken branches and blood spattered over several hundred metres. The calf died as well. One pregnant cow got wedged ("accidental" in Table 5.2 B) in a trough and died when pulled out by staff. The other accidental death was a young adult who fell into a disused well (Okutamare). Only three adults were known to have been poached, all by shooting, but the incidence of poaching could be much higher, especially when elephants leave the park in the wet season. One adult cow marked with a radio-collar disappeared, and although the collar was retrieved bearing evidence that it was cut from the carcase by humans, the carcase itself was never found despite intensive aerial and ground searches. This elephant had very small tusks which shows that the indiscriminate type of poaching is present in this country as well. The poachers were clearly educated enough to know that the carcase would be found if the collar was left on.

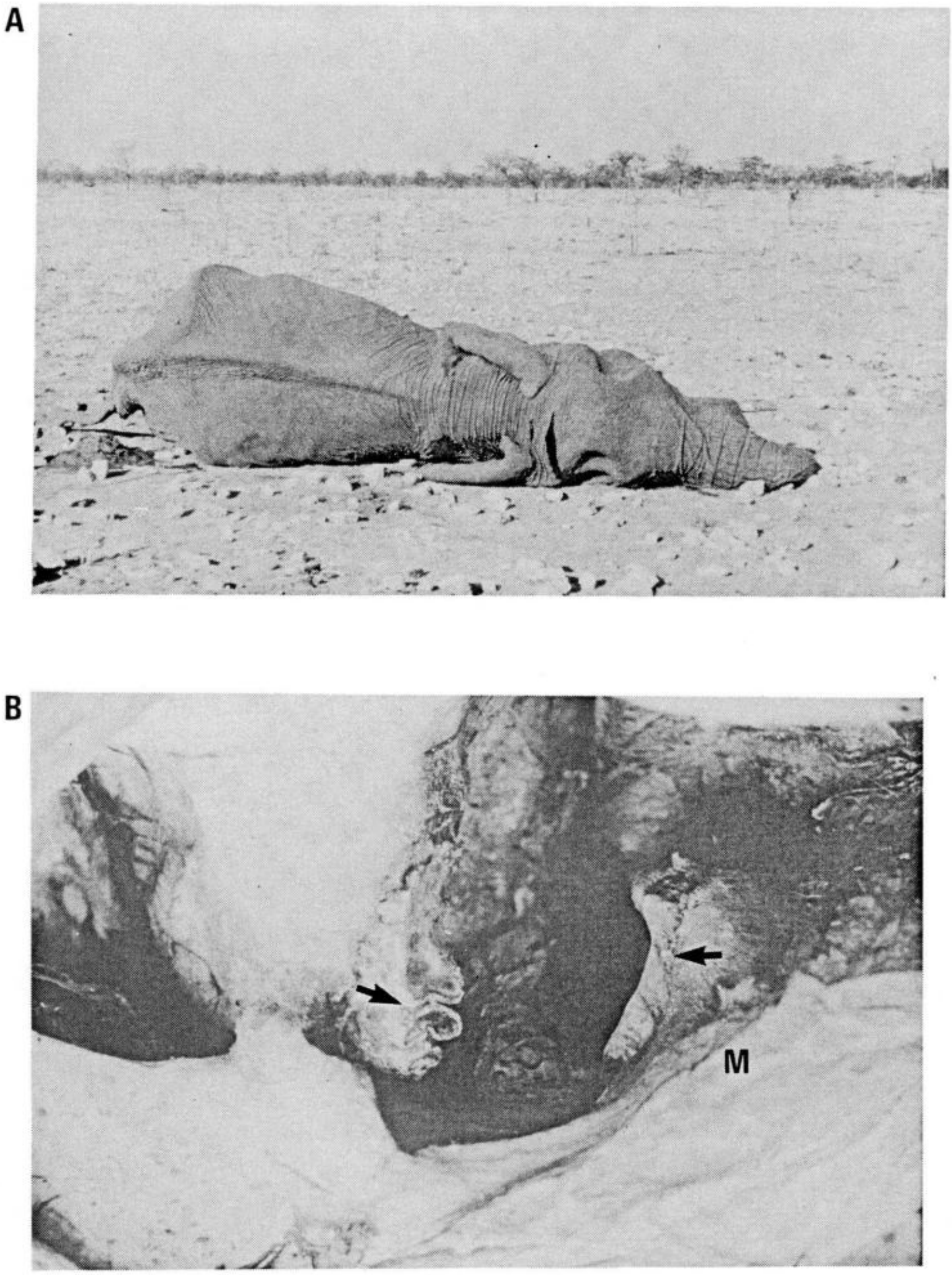


Figure 5.4 Senior-adult cow dead from starvation in Etosha National Park, showing the sunken temporal fossae of most old individuals and prominent ribs and pelvis associated with extreme loss of condition (A). Arrows indicate remnants of M6 in the same individual (B), M denotes mandible.

Two elephants died from stab wounds received from other elephants. That one was a cow is surprising, but nothing is known about the circumstances at the time. One adult with severe burns sustained in a veld fire was destroyed.

Sub-adults (9-19 years old)

Sub-adults showed a mortality pattern similar to that of adults (Table 5.3 A) except that shooting was less of a factor than anthrax. Anthrax, combined with the unknown causes suspected also to be anthrax, accounted for 74% of all cases. One sub-adult male was poached, two died when bogged down in mud ("accidental" in Table 5.3 A), and four with very severe burns from veld fires were destroyed. None of the burnt elephants had any chance to recover, as most had lost more than 50% of their skin, one or more soles from their feet, and showed advanced sepsis. All were located by following the drag marks caused by the inability to walk properly. In Etosha N.P. no elephant has ever been recorded with old scars likely to have been caused by burning, and all those burnt are regarded as likely to die.

Juveniles (3-8 years old)

Anthrax was again the most important cause of death in this age group as shown in Table 5.3 B. Not all of the unknown causes can be lumped with the anthrax cases, as lion predation could account for some. Lions are often found on elephant carcases of all sizes, but observers are reluctant to score such cases as the result of predation. One indisputable case of predation by lions on a three-year-old juvenile, as judged by skilled observers from tracks and wounds, proved to be fatally infected with anthrax as well. The oldest juvenile known to be caught by lions was approximately five years old. Although large, elephant juveniles and calves without adult protection are probably as vulnerable as the young of other species.

The two juveniles shot were destroyed on farms along with adults. One juvenile bull was gored and killed by a black rhinoceros in 1977. Conflicts as serious as this are rare between the two species; there is one other record, of an elephant killing an adult rhinoceros. Less violent conflicts occur commonly around waterholes, as elephants are usually very intolerant of other species present at the same waterhole at the same time.

Table 5.3 Incidence of mortalities in (A) sub-adult (9-19 years old) and (B) juvenile elephants (3-8 years old) in Etosha National Park.

A

CAUSE OF DEATH	1971-79	1980-83	1984-87	TOTAL	(% of total)
ANTHRAX	0	31	14	45	(52.9)
UNKNOWN	2	8	8	18	(21.2)
SHOT	7	7	2	16	(18.8)
BURNS	0	0	4	4	(4.7)
ACCIDENTAL	0	0	1	1	(1.2)
POACHING	0	1	0	1	(1.2)
	9	47	29	85	

B

CAUSE OF DEATH	1971-79	1980-83	1984-87	TOTAL	(% of total)
ANTHRAX	2	14	3	19	(43.2)
UNKNOWN	3	6	6	15	(34.1)
PREDATION	1	1	2	4	(9.1)
SHOT	2	0	0	2	(4.6)
BURNS	2	0	0	2	(4.6)
DROWNING	0	0	1	1	(2.3)
FIGHTING (INTERSPECIFIC)	1	0	0	1	(2.3)
	11	21	12	44	

Juvenile and young sub-adult bulls commonly charge nearby individuals of almost all other species and the one death must have resulted from this. Adult rhinoceros occasionally displace even several adult elephant bulls at waterholes.

One juvenile drowned in a drinking trough, which together with a younger calf suffering the same fate represent the only recorded incidents of this kind in elephants in Etosha N.P. Several other species occasionally drown in the old rectangular troughs, which was part of the reason why such troughs are currently being replaced by saucer-shaped ones.

Calves (< 3 years old)

Table 5.4 presents mortalities recorded for this group. Predation by lions is the single most important cause of death (Fig. 5.5), and was probably underestimated in the present sample due to the rapid disappearance of small carcases and the inclusion of some cases in the unknown category. Despite extensive research on lions in Etosha N.P., albeit not in the areas of relatively high elephant density, not a single case of predation on elephants was actually witnessed (H.H. Berry & P.E. Stander, pers. comm.[1]). Indisputable cases of elephant calves and juveniles killed by lions are known, often elucidated by the skills of some Heikum trackers. It is nevertheless not known whether calves are routinely caught within breeding herds. Only one case as judged from the general behaviour of the herd and signs left on the killing ground, points to a calf being caught inside a herd.

Age and sex distribution of mortalities.

Only 204 (128 males, 37 females and 39 of unknown sex) carcases out of 629 (32%) could be classified into age groups, based on molar progression or body measurements. Figure 5.6 illustrates the frequency distribution of age at death for males and females since 1971. As many records did not indicate the sex of young elephants, and the determination of sex may be difficult, 37 unsexed but known-age records of elephants younger than 15 years old were equally divided into males and females in Fig. 5.6. This is justified as the sex ratio is equal up to 15 years, as is shown below. Young elephants less than four years old represent 16.4% of male and 27.0% of female mortalities. This merely indicates that the male and female mortality patterns differ, with proportionally more males dying later in life than females. Almost four times as many males as females are represented in the

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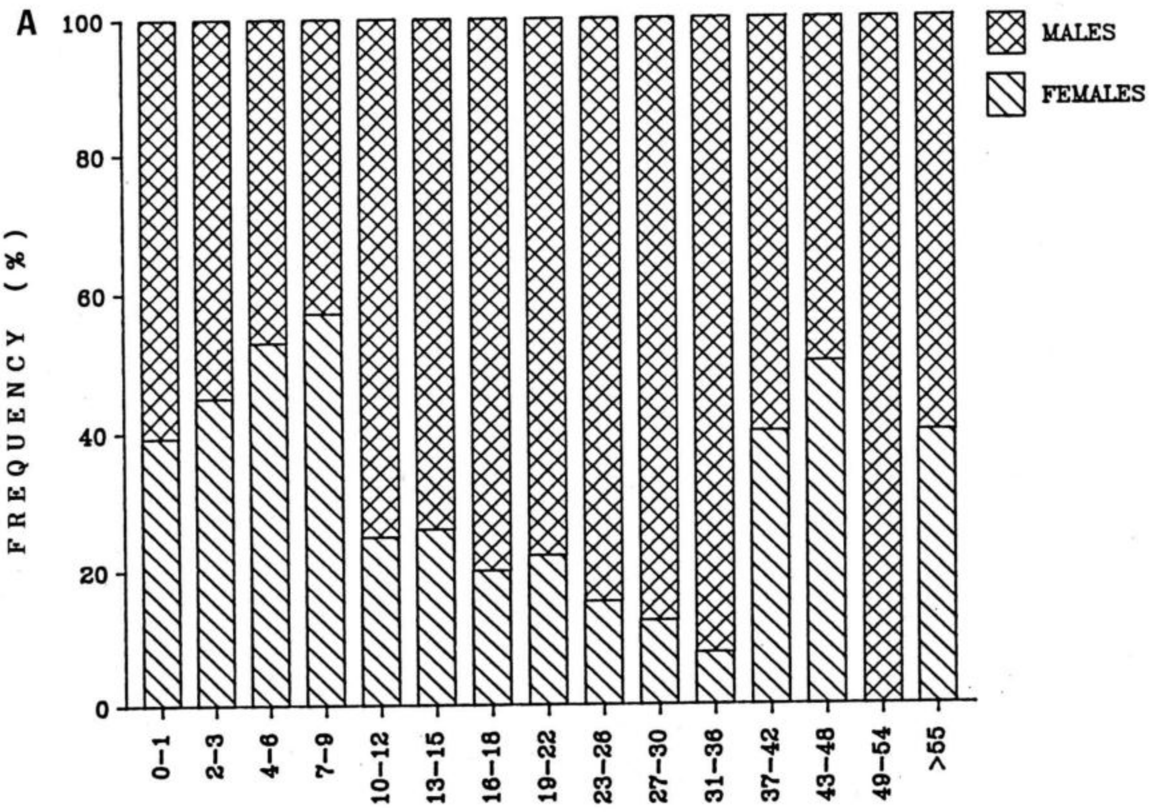
[1] Directorate of Nature Conservation, Private Bag 13306, Windhoek, SWA/Namibia.

Table 5.4 Incidence of mortalities in elephant calves (< 3 years old) in Etosha National Park.

CAUSE OF DEATH	1971-79	1980-83	1984-87	TOTAL	(% of total)
PREDATION	2	5	8	15	(31.9)
UNKNOWN	1	6	5	12	(25.5)
SHOT	5	2	1	8	(17.0)
ANTHRAX	0	6	0	6	(12.8)
TRAMPLED (ELEPHANT)	1	0	1	2	(4.3)
BURNS	1	0	0	1	(2.1)
STARVATION	0	1	0	1	(2.1)
DYSTOCIA	0	0	1	1	(2.1)
DROWNING	0	1	0	1	(2.1)
	10	21	16	47	

Figure 5.5 A. A one-year-old elephant calf killed by lions in Etosha National Park. Arrows indicate canine punctures.

B. The same carcase 18h later. Note the fresh elephant dung ball indicating, along with other evidence, that the herd returned to the site.



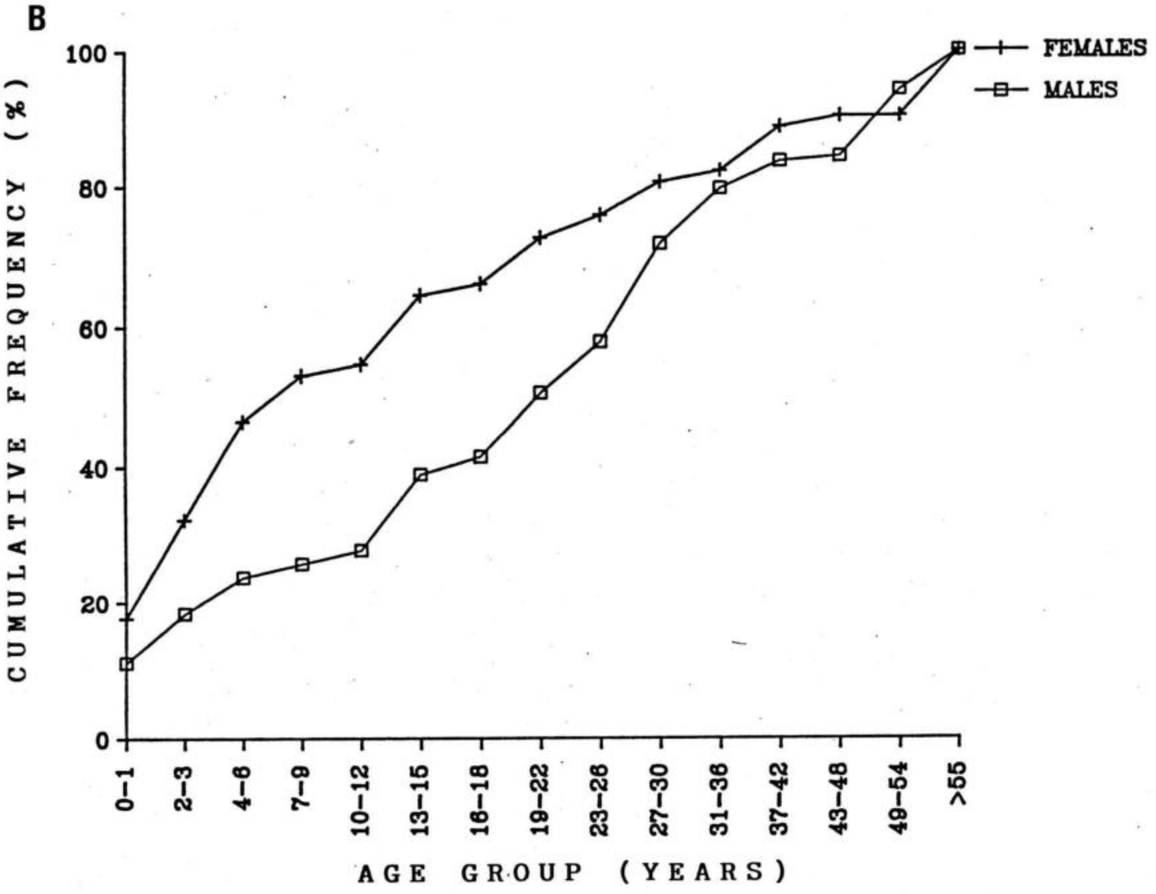


Figure 5.6 Age frequency distribution of elephant mortalities from 1971-1987 in Etosha National Park, where A illustrates the distribution of male and female mortalities in each age group, and B illustrates the cumulative frequencies of male and female mortalities per age group.

sample. What is important is that early mortality, likely to be underestimated in the sample, represents about a quarter of all carcases found.

The sample of records of known age and sex cannot be used to derive a distribution of age at death for the entire population, due to sampling bias. Elephants shot on farms, which account for many of the known-age and sex records, may have been selected for size and age. Older elephants were believed by rangers to lead younger ones on to the farms, and were therefore the prime targets.

In the total known-sex sample, and also when combined with records of unknown sex but classed into age groups, the difference in mortality pattern between males and females is less prominent (Table 5.5). Although more than three times the number of males than females appear in the sample, the relative proportion dying in each age group is very similar in males and females. Both male and female elephants in Etosha N.P. experience relatively high mortalities as sub-adults and adults, compared to other populations (Laws 1969a, b).

It was suspected that the number of elephants destroyed for various reasons might bias the sample, although these mortalities are as real in their effect on the population as the more "natural" deaths. In Table 5.6 all mortalities resulting from shooting are excluded, and no adjustments using young unsexed elephants are used, but the similarity in male and female mortality pattern persists. No statistical tests were done as the classification of age and sex is not reliable enough over such a long period and with so many observers.

Anthrax.

This disease, as elsewhere, causes mass mortality in elephants and some other mammal species in Etosha N.P., yet there are some differences in the incidence of anthrax-related deaths in elephants and other species (Turnbull 1986). Figure 5.7 illustrates that mortality from anthrax occurs throughout the year in elephants and other species, but the peak incidence in elephants (November) differs from the peak incidence in the other three ungulates in March (data from departmental records). Burchell's zebra, blue wildebeest and springbok contract anthrax during the wet season when all three species are concentrated on the plains near Okaukuejo (pers. obs.). The cause and timing of anthrax epidemics in Etosha N.P. is poorly understood. Ebedes' (1976) findings

Table 5.5 Distribution of sex and age classes in all recorded elephant mortalities in Etosha National Park.

		AGE CLASS				
	SEX	CALF (0-2)	JUVENILE (3-9)	SUBADULT (10-19)	ADULT (20-49)	SENIOR ADULT (50 +)
1971-79	M	6	3	9	60	8
	F	1	3	1	14	2
	?	3	5	0	2	0
F/M	*	0.17	1.00	0.11	0.23	0.25
(F/M)	**	(0.33)	(1.00)			
1980-83	M	3	7	22	77	2
	F	2	3	7	25	5
	?	16	11	18	13	0
F/M	*	0.67	0.43	0.32	0.35	2.50
(F/M)	**	(0.91)	(0.68)	(0.52)		
1984-87	M	1	3	15	51	10
	F	2	0	9	13	1
	?	15	3	10	2	0
F/M	*	2.00	-	0.60	0.26	0.10
(F/M)	**	(1.12)	(0.33)	(0.70)		
TOTAL	M	10	13	46	182	20
	F	5	6	17	52	8
	?	34	19	28	17	0
F/M	*	0.50	0.46	0.37	0.29	0.40
(F/M)	**	(0.82)	(0.69)	(0.52)		

* Only known-sex cases.

** Including equal allocation of unknowns to males and females.

Table 5.6 Distribution of sex and age classes in all elephant mortalities in Etosha National Park, excluding elephants shot.

		AGE CLASS				
	SEX	CALF (0-2)	JUVENILE (3-9)	SUBADULT (10-19)	ADULT (20-49)	SENIOR ADULT (50 +)
1971-79	M	3	2	3	12	0
	F	0	2	0	5	1
	?	1	5	0	2	0
F/M *		-	1.00	-	0.42	-
1980-83	M	2	6	17	38	2
	F	1	3	5	19	5
	?	16	11	18	13	0
F/M *		0.50	0.50	0.29	0.50	2.50
1984-87	M	0	3	13	39	3
	F	1	0	9	12	1
	?	15	3	10	2	0
F/M *		-	-	0.69	0.31	0.33
TOTAL	M	5	11	33	89	5
	F	2	5	14	36	7
	?	32	19	28	17	0
F/M *		0.40	0.46	0.42	0.41	1.40

* Only known-sex cases.

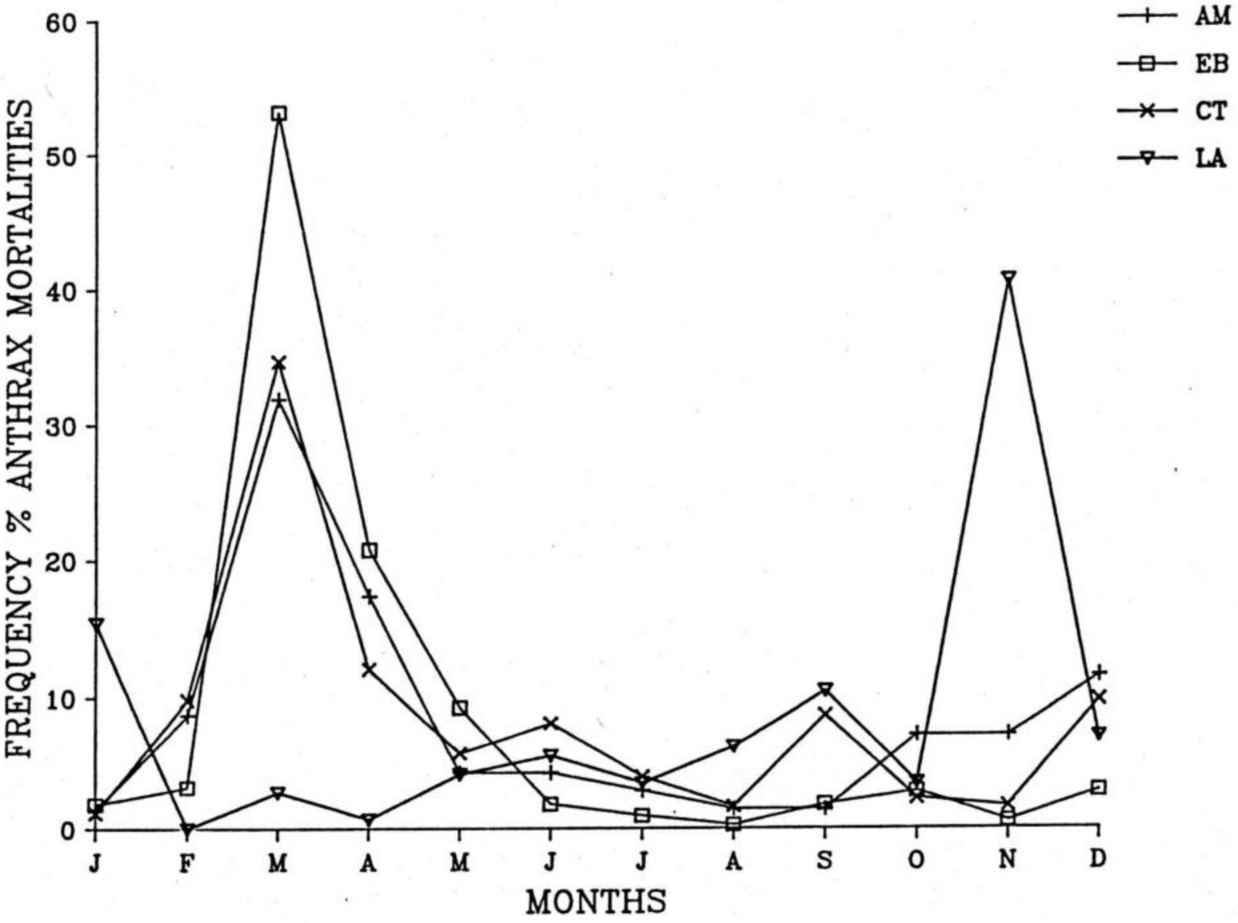


Figure 5.7 Monthly incidence of anthrax mortalities in the four major susceptible species in Etosha National Park. (AM: springbok, EB: Burchell's zebra, CT: blue wildebeest, LA: elephant).

that gravel pits, constructed for road maintenance act as anthrax reservoirs, were not supported by Turnbull, Hofmeyr, McGetrick & Oppenheim (1986) and Turnbull et al. (in press). Anthrax probably occurs in other water sources, dust, soil and vegetation as well. The one major recorded epidemic outbreak of anthrax in elephants occurred during the annual concentrations prior to the rainy season migrations.

From November 1981 to January 1982, 130 elephant carcases were found in the north-western quarter of the park. A further 54 carcases in the same area were found during the aerial census in April-June 1982 and it was felt at the time that the total number of deaths exceeded 200 (Berry 1982a). This outbreak resulted in 130 known, and possibly up to 200 deaths, or about 12-13% of an estimated 1500 elephants present in Etosha N.P. by the end of 1981. A further nine elephants also died from anthrax north of Namutoni, in a presumably unrelated outbreak in November 1981.

A similar though smaller outbreak occurred in July and August 1987 in the Namutoni area, when seven anthrax elephant carcases were found from the ground, and a further 24 during the aerial census in September. It is quite possible that many more elephants might have died, as the area is densely wooded and carcases could be easily overlooked.

In Table 5.7 the age and sex distributions of mortalities from epidemic and non-epidemic anthrax are compared. No statistical tests are used due to suspected inaccuracies in age and sex classification, but more adults and males in particular seem to die during the rest of the period than in the epidemical outbreak. The inverse seems to happen in juveniles.

Males appear to be more susceptible to anthrax than females (69.8% males:30.2% females). Adult males account for 45.0% of all anthrax cases, and together with sub-adult males for 64.4% of all cases, but adult males only represent about 10-15% of the population.

Anthrax as an epidemic or contagious mortality factor conceivably has some density dependent relationship in elephants. There is some evidence to suspect that major outbreaks are facilitated during periods of stress, such as drought. The cause of anthrax outbreaks, however, are so poorly understood that the incidence of the disease in Etosha N.P. with regard to locality and time and species affected seems spurious. There seems to be no relationship between the outbreak of the disease in elephants and in other species, as illustrated in the series of maps in Fig. 5.8 and also Fig. 5.7. There is no correllation between the number of elephant deaths from anthrax (excluding the 1981-1982

Table 5.7 Age and sex distribution of elephant mortalities during epidemic and non-epidemic anthrax outbreaks in Etosha National Park.

		AGE CLASS											
	TOTAL DEATHS	ADULT			SUB-ADULT			JUVENILE			CALF		
EPIDEMIC	86	42 (48.8)			27 (31.4)			14 (16.3)			3 (3.5)		
NON-EPIDEMIC	86	56 (65.1)			22 (25.6)			6 (7.0)			2 (2.3)		
		M	F	?	M	F	?	M	F	?	M	F	?
EPIDEMIC		20	13	9	11	5	11	5	0	9	0	0	3
	M:F	1 : 0.65			1 : 0.45				-			-	
NON-EPIDEMIC		38	13	5	14	5	3	2	3	1	0	0	2
	M:F	1 : 0.34			1 : 0.36			1 : 1.50				-	

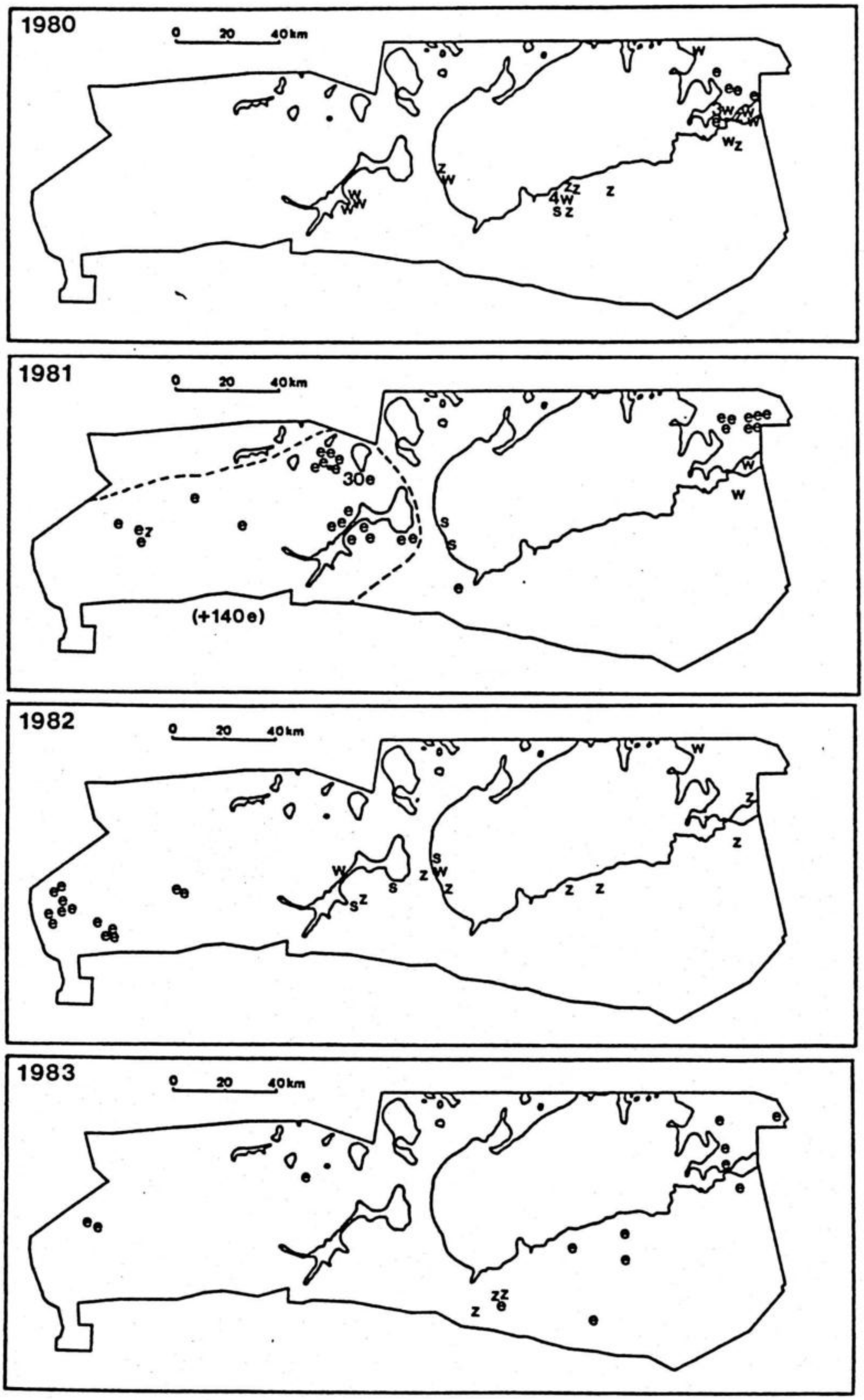


Figure 5.8 The distribution of anthrax mortalities in Etosha National Park since 1980 (e=elephant, z=Burchell's zebra, w=blue wildebeest, s=springbok). Numbers in brackets not confirmed anthrax cases.

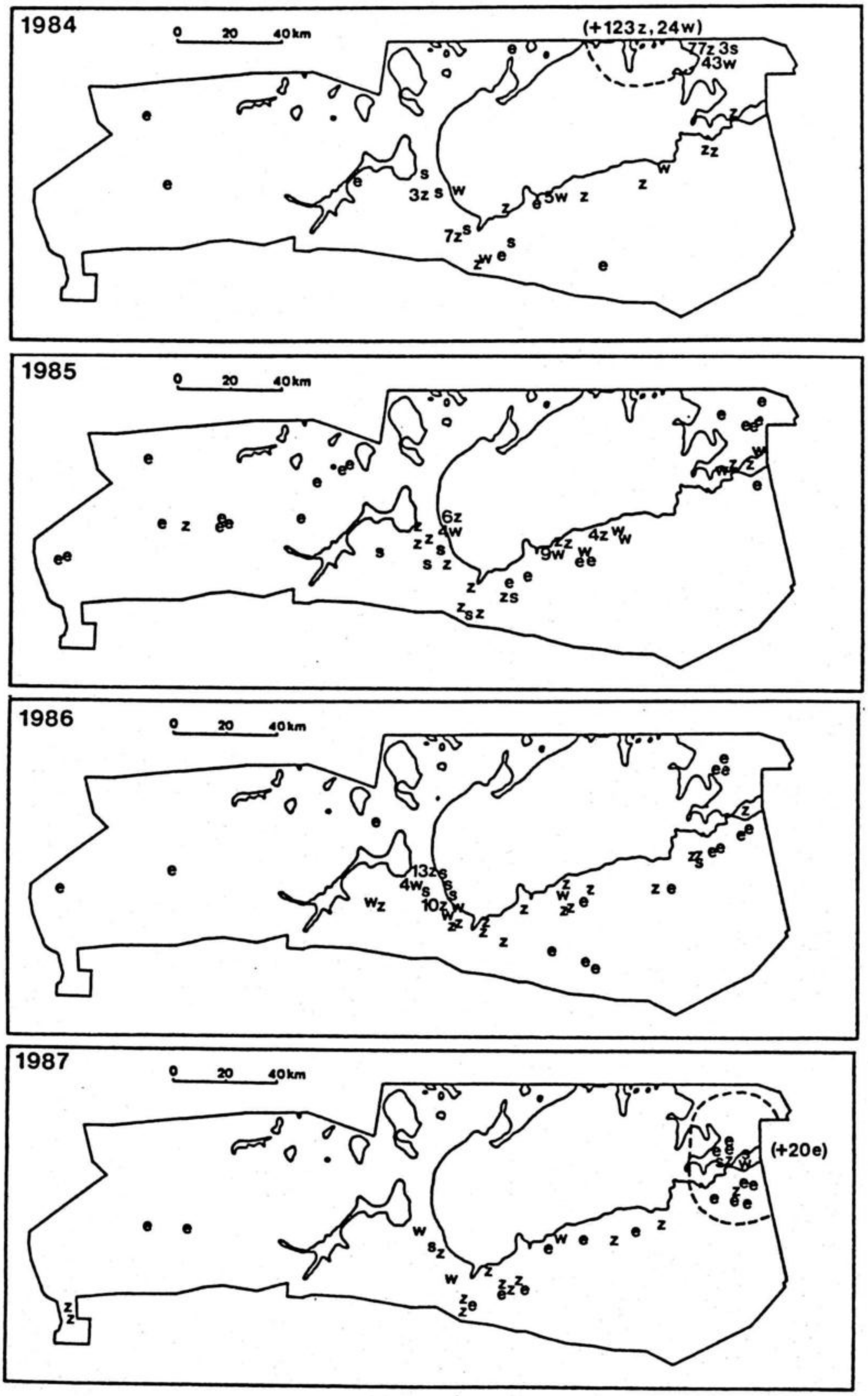


Fig. 5.8 continued.

epidemic) and the number of elephants in Etosha N.P. (r^2=0.13; NS), and no trend of increasing incidence of anthrax cases from 1971 to 1987 (r^2=0.46; NS). Non-epidemic anthrax therefore seems to be independent of density, while epidemic anthrax in elephants might have some density dependent relationships provided that the incidence is linked to stress, as in a drought.

Sex ratio

The sex ratio before birth, based on 77 foetuses collected in 1983 and 1985, was not significantly different from unity (Table 5.8 A). Equal sex ratios persist for individuals up to 20 years of age in the samples culled in 1983 and 1985 (Table 5.8 B) although males start leaving the herds from 12-15 years of age. In both culls, family herds and loosely associating bulls were herded together and culled, thus accounting for the high number of sub-adult bulls in each sample.

The secondary sex ratio is far more difficult to determine. Bull herds were not culled after 1983, and culled samples are of dubious value in estimating sex ratios of adults. Table 5.9 summarizes estimates of sex ratios in Etosha N.P. and elsewhere. Sex ratios vary considerably in different populations but methodological errors are likely to cause much of this variation. Census estimates are perhaps the best, as an entire population is sampled, but the identification of males from the air is subject to great error except in adult bulls.

One possible index of change is the proportion of adult males in the population. Adult bulls and first-year calves are perhaps the least affected by error in aerial surveys, which seem to be the only way of obtaining data regarding differential mortality in elephant populations. Adult females are not easily separated from young adult bulls or sub-adult females, especially in some populations in SWA/Namibia where large gaps in the age distribution occur within individual herds. Two estimates of adult male numbers can be obtained from an aerial census. One will be based on the number of individuals in bachelor groups (bull herds) and single bulls, but these include some sub-adult bulls, as shown in Table 5.10. The other will include adult bulls identified in breeding herds added to those not occurring in breeding herds. The latter estimate is least likely to be affected by breeding activities as males are counted within and outside breeding herds. Only bulls definitely larger than adult cows can be scored in this way, and some younger bulls might be mistaken for cows. In practice, however, bulls separate readily from breeding herds when circled overhead by aircraft, and this facilitates counting.

Table 5.8 Numbers of male and female foetuses (A) and post-natal elephants (B) in the culled samples from Etosha National Park in 1983 and 1985.

A

YEAR	SEX (MALE=M) (FEMALE=F)	OBSERVED NUMBER (O)	EXPECTED NUMBER (E)	$\frac{(O-E)^2}{E}$	P
1983	M	17	30÷2 :15	0.267	0.95 (df=1)
	F	13	30÷2 :15	0.267	
				χ^2=0.534	NS *
1985	M	21	47÷2 :23.5	0.266	0.95 (df=1)
	F	26	47÷2 :23.5	0.266	
				χ^2=0.532	NS *

B

	1983		1985	
AGE (YEARS)	M *	F *	M *	F *
0-10	49	44	89	91
0-13	62	50	107	105
0-15	72	63	120	118
0-20	76	78	128	132

* All χ^2 comparisons not significant (NS).

Table 5.9 Adult sex ratio from the number of adult females and adult males recorded in various studies on elephants in Africa.

LOCALITY *			F/M (RANGE)	AGE INTERVAL	SOURCE OF DATA	REFERENCES
R.N.P.			1.58	all ages	?	Petrides & Swank 1966
K.N.P.			1.05	all ages	census	Smuts 1975
K.N.P.U.			1.66 (1.23-2.09)	>12	census	Ross et al. 1976
K.N.P.M.			2.00	all ages	census	Jachmann 1980
Kaokoveld, SWA/Namibia			1.38-1.93	all ages	census	Viljoen 1980
L.V.N.P.			2.5	all ages	census	Lewis 1984
E.N.P.	1973		2.61	all ages	census	Joubert 1973
	1978		3.30	all ages	census	De Villiers 1978
	1983	May	2.58 x=1.92 ± .27	all ages	census	Berry & Nott 1983
		Dec	0.98 (0.98-3.30)	all ages	census	This study
	1984	May	1.07	all ages	census	This study
		Dec	2.00	all ages	census	This study
	1985	May	1.95	all ages	census	This study
		Aug	1.53	all ages	census	This study
		Dec	1.23	all ages	census	This study
K.F.N.P.N.			1.65	all ages	cull	Laws 1969 a
K.F.N.P.S.			1.42	all ages	cull	Laws 1969 a
B.F.			1.29	all ages	cull	Laws 1969 a
T.N.P.			1.14	all ages	cull	Laws 1969 a
M.R.			1.35	all ages	cull	Laws 1969 a
L.V.N.P.			1.09 (1.00-1.22)	≤ 16	cull	Hanks 1972 a
T.N.P.			8.43	≥ 20	Mass mort.	Corfield 1973
G.N.P.			1.12 (1.07-1.16)	≤ 17	cull	Sherry 1975
M.P.N.P.			0.90 (0.65-1.10)	≤ 16	cull	Kerr 1978
E.N.P.	1983		1.02	≤ 20	cull	This study
E.N.P.	1985		1.03	≤ 20	cull	This study

* Abbreviations explained in Appendix 1.

Table 5.10 Elephant bulls occurring in bull herds and singly as a percentage of the total population, of various populations studied in Africa.

LOCALITY *	% BULLS IN BULL HERDS + SINGLE BULLS/TOTAL POPULATION	REFERENCE
T.N.P.	9.2 (4.4-15.7)	Laws 1969 b
K.F.N.P.	14.6 **	Laws et al. 1970
K.N.P.U.	5.6 ± 1.4	Croze 1972
K.N.P.	15.5 (15.1-16.1)	Smuts 1975
K.N.P.	16.0 (12.4-19.1)	Joubert 1984
Kaokoveld, SWA/Namibia	21.6	Viljoen 1980
A.N.P.	26.5	Poole & Moss 1983
E.N.P.		
1973 Sept	18.0	Joubert 1973
1974 July	8.7	Berry & Hofmeyr 1974
1976 July	6.4	Berry et al. 1976
1978 Sept	10.6	De Villiers 1978
1983 May	13.0	Berry & Nott 1983
Dec	11.6	This study
1984 May	9.3	This study
Dec	13.6	This study
1985 May	17.0	This study
Aug	16.5	This study
Dec	14.5	This study
1987 Sept	11.0	This study

* Abbreviations explained in Appendix 1.

** culled sample.

Nevertheless, when sex and age classification data are not available for some of the censuses, the number of individuals present in herds ranging from 1-4 individuals which usually represent bull herds, correspond well with the actual number of adult males counted (Table 5.11).

Variation in the sex ratio or proportion of adult males recorded in Etosha N.P. might simply be determined by variation in the distribution of bull herds and consequently the number of bulls present in the park during each survey, and not temporal changes in age specific mortality patterns of the entire population. Sex ratios in elephants in Etosha N.P. therefore appear to be of limited use as a diagnostic measure of change in population status. This is unfortunate, as the two major causes of death, namely the shooting of elephants on boundary farms and anthrax, are biased towards adult males. Adult males are also the target group for utilization by trophy hunting, which may eventually be implemented in part of the distribution range of the population.

Anthrax is currently the most prevalent cause of death in all age groups except young calves, where predation by lions accounts for most deaths. Anthrax has spread throughout the park, and is no longer limited to the so-called enzootic areas on the southern edge of the Etosha Pan (Ebedes 1976, Grant 1988). The single most severe outbreak in 1981-1982 occurred in western Etosha N.P., after a virtual absence of the disease in that region. The disease seems to be well established in the west ever since, although the loci of infection are unknown. Prior to the Trans-African drought, anthrax mortalities were surpassed by elephants shot on border farms (Fig. 5.9). The decline in elephants shot probably has a dual explanation. Attitudes of farmers and local conservation staff have apparently become more tolerant of elephants crossing fences, although official policy has hardened. The other possible reason for the decline is that most of the adult bulls who wanted to return to their original range have already been shot.

Both anthrax and predation are very likely underestimated in the mortality record, as both are or were not easy to diagnose unambiguously. Predation on elephant calves is particularly enigmatic, as the reconstruction of circumstances at the time are usually not possible due to the terrain and the rapid disappearance of small carcases. In at least one case it was reasonably clear that the calf was caught in or in the vicinity of its family herd. Lions certainly show interest in elephant herds and elephant herds are particularly intolerant towards lions, which might indicate that this form of predation is more common than apparent from the data. Calves were occasionally found on their own, but not more than one or two such cases per year have occurred since 1983. Desertion by the family group due to the calf being too weak to keep up with the herd, is unlikely to

Table 5.11 Three estimates of the proportion of adult males in the elephant population in Etosha National Park based on aerial censuses since 1973.

YEAR	MONTH	A No. OF ELEPHANTS IN HERDS OF 1-4 INDIVIDUALS	B TOTAL COUNTED	A-B x 100	ADULT MALES IN BULL GROUPS AS % OF TOTAL	ALL ADULT MALES AS % OF TOTAL
1973	SEPT	153	1230	12.4	-	18 *
1974	JULY	56	835	6.7	-	8.7
1976	JULY	81	1170	6.9	-	6.4
1977	MARCH	126	836	15.1	-	-
1978	SEPT	-	1298	-	-	10.6
1982	MAY	218	2202	9.9	-	-
1983	MAY	202	2389	8.5	-	13 **
1983	DEC	145	1437	10.1	10.4	11.6
1984	MAY	81	1158	7.0	9.2	9.3
1984	AUG/SEP	257	2464	10.4	-	-
1984	DEC	181	2081	8.7	9.1	13.6
1985	MAY	111	1244	8.9	12.5	17.0
1985	AUG/SEP	110	1186	9.3	13.1	16.5
1985	DEC	71	713	9.9	10.5	14.5
1987	SEPT	207	2021	10.2	11.0	12.0

* Estimate of Joubert (1973).

** Based on waterhole counts during aerial census (Berry & Nott 1983).

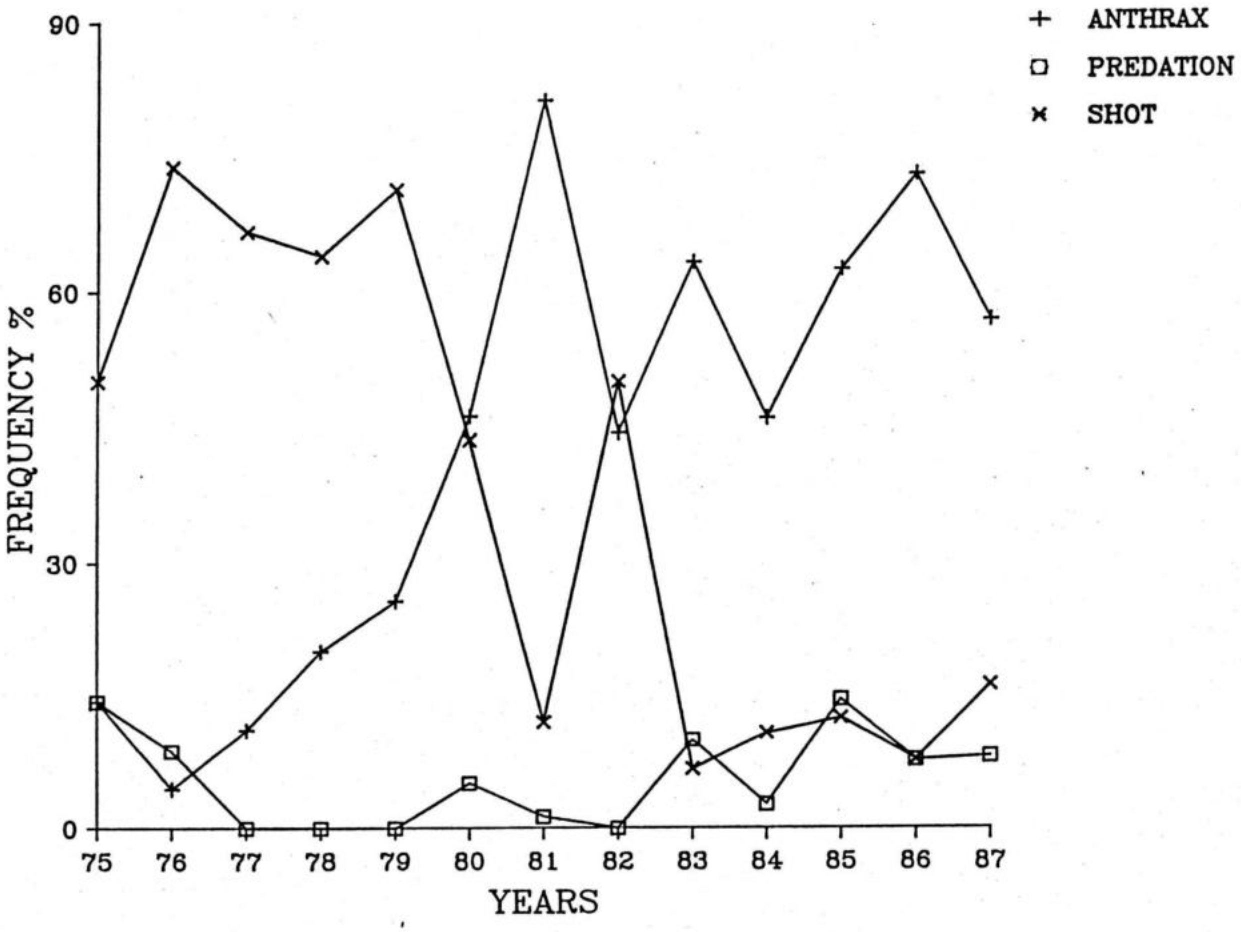


Figure 5.9 Percentage frequency distribution of elephant mortalities due to anthrax, shooting and predation since 1975 in Etosha National Park.

be the cause, as most calves were in sound condition and sometimes survived for several weeks on their own, unlike in the mass mortalities described by Haynes (1985).

Human interference is a possible cause of calves getting separated from herds as elephants, after running the gauntlet of military and farming activities in the densely populated northern part of the country during the wet season, are highly sensitive to disturbance on their return to the park in the dry season. Young calves, particularly bulls, are also inquisitive and sometimes wander out of sight of the herd. In some situations this might lead to permanent separation, and the calf might well be caught by lions eventually. Predation on elephant calves, presumably by lions, has also been recorded by Jachmann (1980) but no further details are known.

Starvation, even during severe drought, has played an insignificant role as an agent in elephant mortality in Etosha N.P., and culling operations during the drought showed that fat reserves were largely intact. Most adults lose condition as shown by the prominence of the pelvic bones at the onset of the dry season, and again when leaf-drop occurs in mopane (Colophospermum mopane) from August to October. This points towards the effect of relatively sudden dietary changes from green to dry grass and from leaves to bark and roots.

Apart from the almost proportional representation of age and sex classes in the major anthrax epidemic, as was also found in the mass mortalities in Tsavo N.P. (Corfield 1973) and Hwange N.P. (Coneybeare & Haynes 1984, Haynes 1985), strong biases are apparent in the mortality record in Etosha N.P. Female deaths exceeded male deaths in only one category and one time period, namely the number of senior adult cows dying from starvation through loss of dentition during the 1980-1983 drought. Similar rates of death have to be accepted for male and female calves and juveniles, as the sexes are not always easily distinguished, but are if anything biased towards higher mortality rates in males. Corfield's (1973) findings of greater mortalities in females than in males in the immature and adult classes are in contrast to the present findings. It is probably safest to assume similar rates for both sexes, as is also supported by the sex ratio of culled individuals up to 20 years of age (Table 5.7 B).

Disparity in the adult sex ratio in Etosha N.P. is reflected in the mortality record, where more than twice as many males than female deaths are recorded, even when known biases such as boundary shootings are excluded. This pattern is typical of sexually dimorphic polygynous mammals as reviewed by Ralls, Brownell & Ballou (1980) and predicted by Fisher's theory of sexual selection (Wilson & Pianka 1963, Emlen 1968). The way that the disparity in favour of females arises differs from species to species, from direct intra-sexual competition to more subtle forms of differential access to resources.

Adult sex ratios in different populations of African elephants have almost certainly been affected by the trophy hunting of adult bulls throughout the continent, and continuously so in most parts for at least a century. Relatively little is known, however, about determinants of the sex ratio in the pre-hunting era, and even the recorded instances of fatalities caused by bulls in musth are too rare to have been such a determinant (Poole 1982). Man could have possibly affected adult sex ratios since the earlier times. Single adult bulls are seemingly less vigilant than herds, at least so in Etosha N.P.; they are habitual users of paths and drinking places; show fidelity to one area; and are consequently more vulnerable to primitive and modern human hunting tactics than breeding herds.

In spite of the greater incidence of male deaths caused by anthrax and shooting in Etosha N.P., the sex ratio is only slightly more in favour of females than in other populations. This is possibly the result of higher than usual rates of death in adult females in Etosha N.P., also due to anthrax. If adult female anthrax deaths are excluded, the ratio of male:female deaths is 1:0.08, and if all anthrax deaths are excluded the ratio is 1:0.17. Both anthrax and the shooting of elephants on farms with their strong biases towards males could therefore have independently caused a much greater disparity in the adult sex ratio, if only males had been affected.

The reason for greater susceptibility to anthrax in male elephants is unknown, other than possibly a greater exposure to contaminated water sources. Adult bulls spend at least double the time at water holes than cows and breeding herds and if this is the source of infection, the risk of contracting anthrax will be greater. Ebedes (1976) suggested that lacerations resulting from eating Acacia nebrownii could enhance the chances of contracting anthrax, but preliminary evidence indicates no dietary difference between the sexes. More male than female deaths occur throughout the park, large portions of which contain few spiny food items for elephants.

The classic mass mortality of elephants in Tsavo N.P. in 1970-1971 when more than 10 000 elephants died out of a population greater than 40 000 (Corfield 1973, Laws 1981), has become a benchmark in elephant management history. This episode, although dramatic at the time and hotly debated in press, has paled into insignificance compared to the number of elephants poached in the subsequent 15 years. Douglas-Hamilton (1987) reports declines of 70000 in the Central African Republic alone over ten years, concommittant with equally serious declines in most countries, such as the 80-90% extermination of elephants in Uganda over a five year period. Elephant populations in most national parks, excluding those in southern Africa, are still declining, in contrast to general increases in the period 1960-1970. After a decade of research dominated by undesireable elephant-vegetation interactions in African conservation areas, the emphasis could and should shift to elephant-human interactions, and mortality patterns might get more attention in years to come.

CHAPTER 6 SYNTHESIS

INTRODUCTION

This chapter is an attempt to combine the salient features of the dynamics of the Etosha N.P. elephant population into one holistic interpretation. In some cases, this interpretation is applicable to the regional elephant population as well, as elephants in Etosha N.P. are part of the regional population (Chapters 1 & 2). Major determinants of demography, namely nutrition and particularly the effects of elephants on the vegetation, are not considered in detail in this study, as explained in Chapter 1. Other factors almost certainly have far more serious and direct effects on elephant demography in Etosha N.P. and north-western SWA/Namibia, namely movements, survival and fecundity, which are themselves under the direct control of environmental factors.

Laws (1969a, b, 1971, 1981), Laws & Parker (1968) and Laws et al. (1970, 1975) are largely responsible for the interpretation of elephant population regulation through changes in reproductive output. This output is changed according to environmental conditions by varying the age at first conception, onset of senescence, and the calving interval. Elements in the environment responsible for such variation are overcrowding or the compression effect resulting in combined social and nutritional stress, and climate. In fact, changes in reproductive output are seen as having a direct inverse relationship with elephant density (Fowler & Smith 1973). Croze (1972), Corfield (1973) and Croze et al. (1981) suggested that mortality of calves is at least as important as reproduction in the control of elephant populations, and furthermore question the density dependence of reproductive variables. The population in Lake Manyara N.P. is used as an example of the failure to explain reproductive homeostasis solely in terms of density. This population represents one of the highest recorded elephant densities, probably caused by compression, yet with no extraordinary delay in puberty, and related changes in the calving interval or onset of senescence. In conservationist literature the elephant population of Africa is often the unit referred to, yet this population occurs in an extremely variable environment, from coastal lowlands, savannas to montane woodlands. It should be more appropriate to examine density-dependent effects on population increase within each locality, as the range of variables is likely to differ from one environment to the other. Variation in some parameters, however, is probably an attribute of the species as a whole.

The demography of the Etosha N.P. population should be of some general value to the understanding of elephant populations elsewhere. Elephant habitat in Etosha N.P. is certainly different from that experienced by the majority of the remaining elephants in Africa. The population is at a comparatively low density; migratory; has not caused major changes in the vegetation (Nott 1986); and is subjected to anthrax, high juvenile mortality relative to the East African populations, and unpredictable rainfall and primary production. It is therefore of interest to find out how a K-strategist species copes in an environment perhaps more suitable to r-selected species.

RESULTS AND DISCUSSION

Fecundity

The reproductive output of a population is described by fecundity, i.e. the mean number of female offspring produced per female per year. Fecundity varies with the age of the females and environmental conditions (Hanks 1972a) which makes it a useful parameter in the modelling of population response to environmental change. Variation in fecundity is caused by variation in the onset of puberty, the duration of the calving interval, and the onset of reproductive senescence, thus the three homeostatic mechanisms suggested by Laws (1969a, b). Fecundity by the definition used here does not measure or reveal anything about the survival of female offspring produced. The number of offspring produced that survive is clearly of great importance, and prompted the inclusion of a survival term in the alternative definition of fecundity used in Leslie-Lewis matrix modelling (Leslie 1945, 1948).

Fecundity in large mammals is commonly measured by the number of females in each age class that show breeding activity, compared to the total number of females in each age class (Caughley 1977a). A shot sample of females is usually the easiest way of obtaining this information, where fecundity (m_x) is calculated as the number of pregnant or lactating females at age x (B_x) divided by the total number of females sampled at age x (f_x). This value is halved when the sex ratio at birth approaches 1:1, as only female offspring are considered. Half of all the females pregnant or lactating are therefore said to be producing female offspring. If the sample is taken prior to the season of births, the number of pregnant females would give similar results.

Gestation lasts longer than one year in elephants, and the standard formula of calculating fecundity ($m_x = B_x/2f_x$) does not apply. Hanks (1972a), followed by Sherry (1975), Williamson (1976) and Kerr (1978), constructed fecundity tables for elephants from the number of pregnant females only, and dividing the value of m_x by 2 to compensate for the 660 day gestation period. The divisor should in fact be 2.212 ($660/2 \times 365 = 0.904$; $.904/2 = 0.452 = 1/2.212$). Single samples of pregnancy rates are known to be inadequate, as breeding seasons and pregnancy rates vary from year to year (Hanks 1972a, Laws et al. 1975). A better approximation of fecundity might be obtained by averaging the number of pregnant and lactating females. If there is any measure of breeding synchrony present in the population, widely disparate estimates would result from the two methods. Where an estimate of instantaneous fecundity is required, only pregnant females should be used. Fecundity schedules for the 1983 and 1985 samples from Etosha N.P. calculated in both ways are presented in Table 6.1 A & B. Figure 6.1 illustrates the amplitude of variation in m_x when the ratio of pregnant females (P_x) are used to calculate m_x, compared to the ratio of pregnant and lactating females (B_x). Irregularities in both curves are likely due to small sample size rather than an age-related effect. Weighted mean fecundity rates were calculated following Caughley (1977a) as $m_w = n / N_{(i-n)}$, where n= the number of female offspring produced by N females from age i to n. Weighted mean fecundity rates (m_w) were calculated over the period when fecundity is approximately constant in other populations, from age 20 to 60, and are presented in Table 6.2.

If female elephants could each produce one offspring in one year, fecundity would be 1.0 offspring per year, or 0.5 female offspring per year. As gestation lasts nearly two years however, the maximum number of female offspring produced per year would be 0.25.

Table 6.1 Fecundity schedules of female elephants culled in Etosha National Park in 1983 (A) and 1985 (B).

A

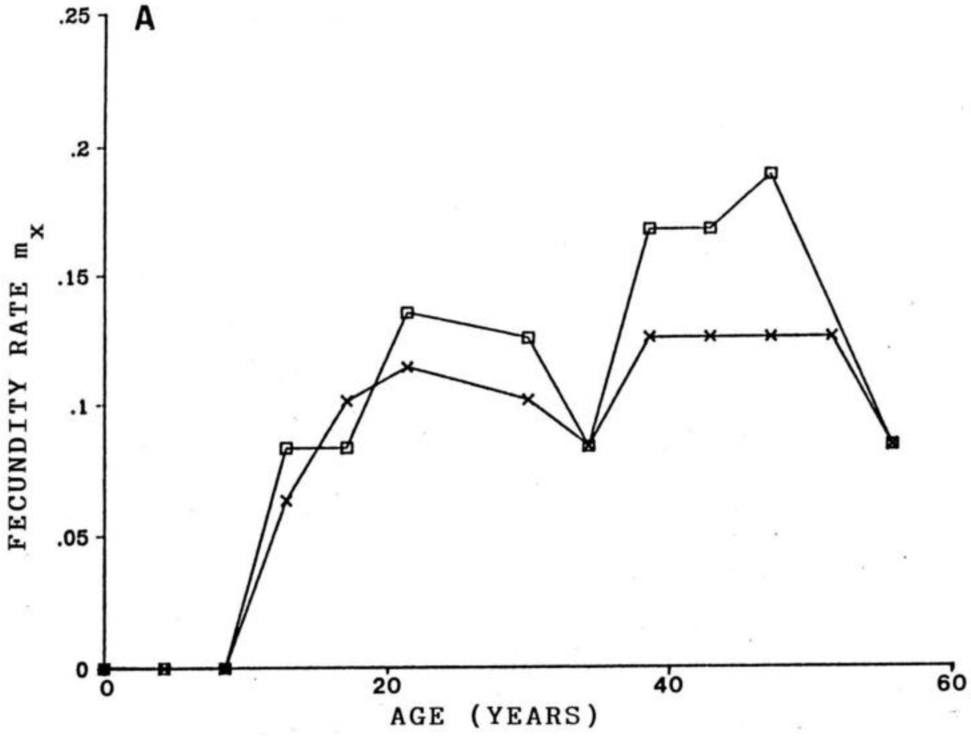
AGE (YEARS) x	NUMBER CLASSIFIED f_x	NUMBER PREGNANT P_x	FEMALE BIRTHS/ FEMALE/YEAR $(P_x/2f_x/2)$ m_x	NUMBER PREGNANT OR LACTATING B_x	FEMALE BIRTHS/ FEMALE/YEAR $(\frac{1}{2}B_x/2f_x/2)$ m_x
0-4	22	0	0.000	0	0.000
5-8	10	0	0.000	0	0.000
9-12	6	0	0.000	0	0.000
13-16	18	6	0.083	9	0.063
17-20	12	4	0.083	10	0.104
21-24	11	6	0.136	10	0.114
25-28	0	-	-	-	-
29-32	6	3	0.125	5	0.104
33-36	3	1	0.083	2	0.083
37-40	3	2	0.167	3	0.125
41-44	3	2	0.167	3	0.125
45-48	4	3	0.188	4	0.125
49-52	1	0	0.000	1	0.125
53-56	3	1	0.083	2	0.083
57-60	0	-	-	-	-

$m_w(20-60) = 0.132$ $m_w(20-60) = 0.110$

B

AGE (YEARS) x	NUMBER CLASSIFIED f_x	NUMBER PREGNANT P_x	FEMALE BIRTHS/ FEMALE/YEAR $(P_x/2f_x/2)$ m_x	NUMBER PREGNANT OR LACTATING B_x	FEMALE BIRTHS/ FEMALE/YEAR $(\frac{1}{2}B_x/2f_x/2)$ m_x
0-4	45	0	0.000	0	0.000
5-8	30	0	0.000	0	0.000
9-12	16	4	0.063	4	0.031
13-16	27	12	0.111	15	0.069
17-20	14	5	0.179	14	0.125
21-24	26	15	0.144	25	0.120
25-28	9	3	0.083	9	0.125
29-32	10	4	0.100	10	0.125
33-36	3	2	0.167	3	0.125
37-40	13	5	0.096	13	0.125
41-44	1	1	0.250	1	0.125
45-48	8	1	0.031	7	0.109
49-52	4	3	0.188	4	0.125
53-56	6	2	0.083	4	0.083
57-60	2	0	0.000	1	0.063

$m_w(20-60) = 0.110$ $m_w(20-60) = 0.117$



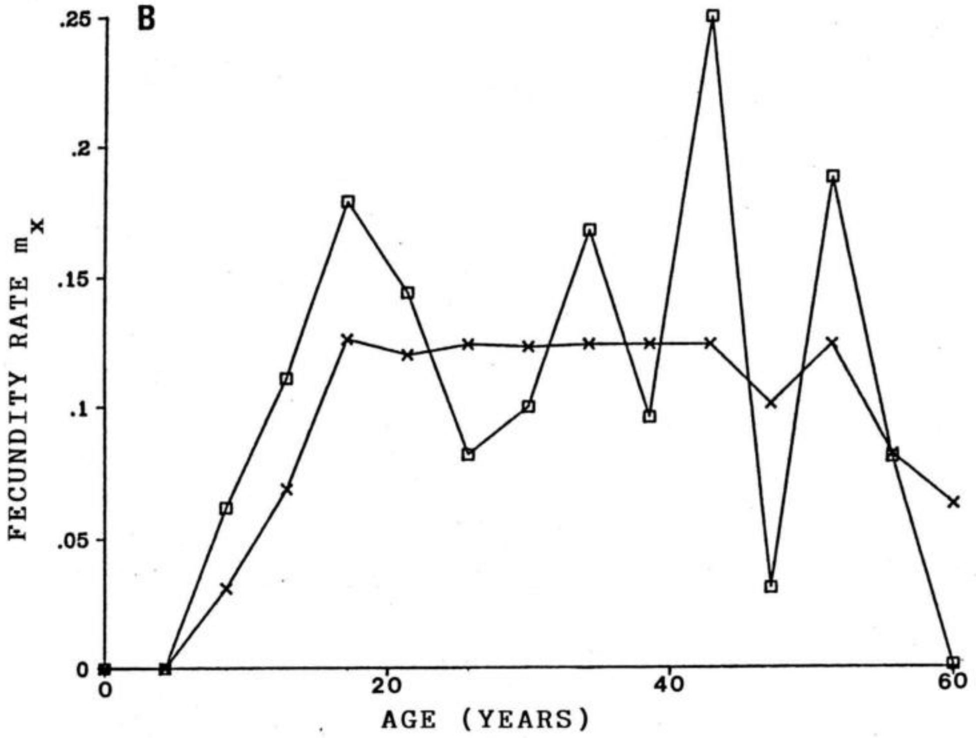


Figure 6.1 Fecundity schedules of female elephant culled in 1983 (A) and 1985 (B) in Etosha National Park calculated from the ratio of pregnant to non-pregnant individuals (□) and pregnant and lactating females to non-pregnant and non-lactating individuals (x).

Table 6.2 Weighted mean fecundity (m_w) calculated from pregnant and pregnant plus lactating females older than 18-20 years in 10 populations of African elephants.

LOCALITY **	No. of cows sampled f	No. of cows pregnant P	No of cows lactat. L	No. of cows preg. or lact. P+L=B	m_w from preg. cows P/2f /2	m_w from preg. or lact. cows ½B/2f /2	Reference
K.F.N.P.N.	100	39.6	51.8	91.4	0.099	0.114	Laws (1969a)
K.F.N.P.N.	100	20.2	67.3	87.5	0.051	0.109	Laws et al. (1975)
K.F.N.P.S.	100	39.6	31.8	71.4	0.099	0.089	Laws (1969a)
K.F.N.P.S.	100	32.6	50.2	82.8 *	0.082	0.104	Laws et al. (1975)
T.N.P.	100	26.9	65.2	92.1	0.067	0.115	Laws (1969a)
T.N.P.	100	26.9	68.8	95.7	0.067	0.120	Laws et al. (1975)
M.R.E.	100	63.3	36.7	100.0	0.158	0.125	Laws et al. (1975)
L.V.N.P.	386	184	192	376	0.119	0.122	Hanks (1972 a)
G.G.R.	383	171	196	367	0.110	0.120	Sherry (1975)
H.N.P.	390	169	–	–	0.112	–	Williamson (1976)
M.P.N.P.	68	36	28	64	0.132	0.118	Kerr (1978)
K.N.P.	587	181	352	533	0.077	0.114	Smuts (1975)
E.N.P. 1983	34	18	12	30	0.132	0.110	This study
E.N.P. 1985	82	36	41	77	0.110	0.117	This study
					0.101 (0.051-0.158)	0.114 (0.089-0.125)	

* Laws (1969a) and Laws et al. (1975) only provide percentages of all parous females.
** Abbreviations explained in Appendix 1.

If the calving interval is known from an independent estimate, fecundity can be estimated. For example, a calving interval of 4 years means that one offspring, or 0.5 female offspring is produced every four years or 0.125 female offspring per year. The only way that an elephant can produce 0.25 female offspring per year, is if the cow becomes pregnant very soon after giving birth, after a period of lactation anoestrous lasting only a few months. Pregnancy and lactation overlap commonly in elephants and for much of the reproductive cycle. A cow lactates from giving birth, throughout the lactation anoestrus period, while conceiving the next calf, and throughout most of that pregnancy.

A fecundity of 0.25 is therefore not impossible. This fecundity would be recorded as a 2 year calving interval, which is shorter than any real calving interval recorded or estimated. It is possible that such high fecundity, if it occurs, results from calf mortality, where a female conceives again soon after the death of a calf. The theoretical fecundity of 0.25 female offspring per year is therefore a maximum value only when very high calf mortality and compensatory breeding occur.

The evidence needed to show maximum fecundity rates due to compensatory breeding in a culled sample would be some females that are pregnant with very recent placental scars still visible in the uterus. Endometrial changes during pregnancy obscure scars and therefore the recent reproductive history of an individual. In the 1985 sample from Etosha N.P., one pregnant female with a conceptus in the pre-implantation stage was found with also one recent placental scar. This cow was not lactating, and as it was unlikely to be a first or second pregnancy because of the age of the cow, the existing scar is likely to represent calf mortality shortly before or after birth. So at least some individuals can breed again shortly after the loss of a calf. Even more significant would be to find proof of a pregnant and also lactating cow with a recent placental scar, implying that the first calf is still alive (because the cow is lactating). This was not apparent from the Etosha N.P. samples, and no evidence of this feature was found in other studies. Moss (1983) determined that the MCI of females in Amboseli N.P. was 5.4 years if previous calves survived, and 3.8 years if they died. Calf mortality could therefore reduce the birth to conception interval by at least 45% and the MCI by 30%. The age at death of calves is not known, but were presumed to be less than one year (Croze et al. 1981). The mean fecundity rate of the Amboseli N.P. cows changed therefore from 1/2(5.4) = 0.093; to 1/2(3.8) = 0.132.

In conclusion, fecundity as indicated by minimum calving intervals is the maximum fecundity, approaching 0.25 female offspring per year. The shortest recorded calving interval in East Africa is 2.75 years with no indication if the previous calf survived (Laws 1969a), which translates into a fecundity of 0.182 female offspring per year. Scar-based estimates of the mean calving interval in Etosha N.P. indicate even shorter intervals of 2.1 to 2.5 years, or fecundities of 0.238 to 0.200 female offspring per year (Chapter 4), which renders the Etosha N.P. population the most fecund of all populations studied. There is nevertheless some indication that substantial calf-neonatal mortality was prevalent during the sample periods.

Mean fecundity rates in Etosha N.P. as derived from the traditional distribution of pregnant and lactating females in an age group, are, however, not substantially greater than in other populations, although above the average of 14 samples from 10 populations (Table 6.2). These fecundity values can be regarded as instantaneous, or applicable to the sample time only, while fecundity derived from calving intervals as shown by the rate of accumulation of scars with age is the average over a much longer period of up to 20 years or more. The scar-based estimates should furthermore be greater than the values in Table 6.3 and Table 4.8, if some degree of perinatal-neonatal mortality occurs, as a scar does not reveal the fate of its associated calf. The absence of lactation in pregnant or non-pregnant cows in some cases, however, does (Laws 1969a).

A different type of fecundity schedule is used in conjunction with the projective population matrix commonly used in modelling populations and defined by Leslie (1945, 1948). Leslie-type fecundity (F_x) is described as the number of female offspring born in interval t to t+1 per female in age class x at time t, which survive to begin the next time interval at which time they will be in the zero age class. A measure of survival is therefore added to the usual fecundity m_x where:

$$F_x = m_x l_o$$

and

$m_x =$ number of female offspring born in interval t to t+1 per female in age class x at time t.

$l_o =$ average survivorship into the zero age class of m_x newborns.

The crucial parameter is l_o, which is difficult to measure, as Caughley (1977a) warned. Survivorship into the zero age class has been estimated by comparing the number of

Table 6.3 **Mean calving intervals (MCI) and mean number of placental scars per female in 17 African elephant populations.**

YEARS STUDIED	LOCALITY *	$\bar{x}$ PLAC. SCARS/ FEMALE (RANGE)	$\bar{x}$ AGE FIRST CONCEPTION	MCI FROM $\bar{x}$ AGE OF FEMALES WITH 1 OR 2 SCARS	MCI FROM PLACENTAL SCARS	MCI FROM RATIO OF PREGNANT FEMALES	ELEPHANT DENSITY (NO. ELEPHANTS/ km^2)	REFERENCE
1946-50	K.F.N.P.S.	-	-	-	-	3.8		Perry (1953)
1958-64	K.F.N.P.S.	-	7-15	-	-	8.6	1.00	Buss & Smith(1966)
1967	K.F.N.P.S.	-	17.8	-	4.9	5.6	2.70	Laws et al. (1975)
1974	K.F.N.P.S.	-	9.0	-	5.1	3.5	1.22	Malpas (1978)
1966	K.F.N.P.N.	-	16.3	-	-	9.1	1.16	Laws et al. (1975)
1974	K.F.N.P.N.	-	9.6	-	4.6	5.1	1.10	Malpas (1978)
1966	B.F.	-	22.4	-	-	7.7	2.12-4.12	Laws et al. (1975)
1968	M.R.E.	-	12.2	-	-	2.9	0.82	Laws et al. (1975)
1969	M.R.C.	-	12.2	-	-	4.2	0.82	Laws et al. (1975)
1966	T.N.P.	3.6(1-9)	11.7	6.7	4.1	6.8	0.88-1.11	Laws et al. (1975)
1965-69	L.V.N.P.	3.9(1-10)	14.0	3.7	3.4	3.5(3.8)[1]	2.17	Hanks (1972a)
1971-72	G.N.P.	3.0(1-10)	12-13	5.2	4.3	3.7	1.85	Sherry (1975)
1972	H.N.P.	2.6(1-8)	11.0	6.7	4.3	4.0	0.62	Williamson (1976)
1969-72	M.P.N.P.	-	12-13	-	-	3.5	0.35	Kerr & Frazer (1975) Kerr (1978)
1970-74	K.N.P.	3.7(1-11)	12.0	4.3	4.3	4.5	0.41	Smuts (1975)
1966-70	L.M.N.P.	-	[11.0][3]	-	-	[4.7]	5.00	Douglas-Hamilton (1972)
1973	R.N.P.	-	12.3	-	4.2	4.5	2.14	Malpas (1978)
1978	K.N.P.M.	-	[7 +][3]	-	-	[3.9(2.2-5.3)]	0.35	Jachmann (1980) Martin (1986)
1970	K.N.P.U.	-	[10-12][3]	-	-	[2.2-3.3]	0.62	Croze (1972)
1972-80	A.N.P.	-	-	-	-	[4.9][2]	0.2-1.54	Moss (1983)
1983	E.N.P.	6.6(1-13)	13.5	3.0	2.1	3.8	0.07-0.11	This study
1985	E.N.P.	5.0(1-12)	11.5	2.8	2.5	3.8	0.03-0.07	This study

1. Recalculated by Malpas (1978, in Eltringham 1982).
2. From direct observations.
3. From age distributions derived from age-length keys.

* Abbreviations explained in Appendix 1.

placental scars to the number of foetuses or size of litters in foxes (Michod & Anderson 1980) and foetal and post-weaning litter sizes in feral cats (Van Aarde 1983). Placental scars in elephants might similarly give an indication of the value of l_0, as the ratio of fresh placental scars to the number of young calves. How long after birth a scar remains "fresh" is not known, but a period of one year is probably not unreasonable. Allen (1983) mentions that recent scars remain identifiable as recent for at least 10 months in red foxes (Vulpes vulpes).

A minimum number of 56 cows in the 1985 sample had fresh scars and there were 50 calves younger than one year of age. This gives an estimate of $l_0 = 0.893$, or an early calf mortality of 10.7%. Twenty-five cows in 1983 had fresh scars but only 16 calves less than one year of age were counted, giving a $l_0 = 0.640$. Any of the high proportion of pregnant females that were lactating but with a surviving calf would lower the l_0 estimate in both samples. It was, however, assumed that all pregnant-and-lactating cows had older calves, except those with foetuses younger than 100 days. This group might have included some females with calves less than one year old. Multiparous cows pregnant for less than 100 days that were not lactating can be regarded as having lost a previous calf, but these calves would not have been counted as scars (the scars are obliterated by endometrial changes during pregnancy). The latter group increases the number of females which gave birth in 1985 to 59 and to 28 in 1983. At least two pregnant and lactating cows must have had one year-old calves in 1985 according to the number of one year-old calves and the number of lactating females in at least two herds. In 1985, 50 calves were therefore produced by 61 cows, and 16 calves by 28 cows in 1983, which gives estimates of $l_0 = 0.820$ and $l_0 = 0.571$ in 1985 and 1983 respectively.

A smaller sub-sample of herds with one year-old calves and no confusion over individuals which escaped or samples lost is available to derive more accurate estimates of calf mortality, when individual calves can be related to individual cows in each herd. In 1985, 18 cows produced 15 calves, therefore $l_0 = 0.833$, and in 1983 18 cows produced 12 calves, therefore $l_0 = 0.667$. Both these estimates correspond with that from the total samples used before.

Laws (1969a) regards the incidence of multiparous pregnant cows in the first half of gestation that were not lactating as indicative of calf mortality. This incidence, however, cannot be used as a precise estimate of l_0, as pregnancy obscures the exact reproductive history of a female. In 1983 and 1985, 37.5% and 30.0% of females in the first half of pregnancy were not lactating, which gives estimates of l_0 as 0.625 and 0.700 respectively. These estimates may however be included in the range of l_0 estimates used in modelling, as 0.893 - 0.820 - 0.700 and 0.640 - 0.625 - 0.571 in 1985 and 1983 respectively.

If the high incidence of placental scars in females in Etosha N.P. is regarded as the result of early mortality of calves, the incidence of females with two recent scars might be used to indicate calf mortality over an earlier period. In 1983 56.5% of females had more than one recent scar, indicating an l_0 estimate of 0.435, and likewise in 1985 the incidence of 45.5% yields $l_0 = 0.555$. Both estimates however, refer to perhaps a two-year period previously, 1980-1982 and 1982-1984. These estimates are largely conjectural but nevertheless interesting.

Calf survival can vary greatly over a short interval, as in Amboseli N.P. where only 24% of calves less than one year old survived in 1977, against the majority that survived in subsequent years (Moss unpubl. in Croze et al. 1981). The probable range of calf survival therefore extends from at least $l_0 = 0.24 - 0.95$.

The measurement of annual recruitment as the function of fecundity and survival over the first year is potentially a useful index of population trend. The number of yearling calves counted prior to the breeding peak represents that fraction of the cohort to be recruited into the second year, while the number of calves present after the breeding peak represents natality minus neonatal mortality. In practice, however, accurate counts of young calves at the appropriate part of the breeding cycle are difficult to obtain. The elephant population in Etosha N.P. is not restricted to the park and actual counts could therefore not be used, but rather the number of calves relative to the number of adult cows, as given in Table 6.4. Counts of adult cows, or parous cows, are equally biased, as smaller cows also produce calves, and sub-adult bulls are sometimes scored as cows.

Table 6.4 presents the estimates of abundance of newborn and year-old calves in Etosha N.P. since 1982, as based on ground observations and aerial surveys. These estimates are clearly not adequate as estimates of recruitment, because of inadequate sampling and misclassification, as also found by Eltringham (1977). Similar estimates in Jachmann (1986) are used to estimate recruitment, but are in fact estimates of fecundity.

Table 6.4 Relative abundance of newborn and year-old elephant calves relative to the breeding season and the number of adult cows in Etosha National Park.

BIRTH SEASON B	% NEWBORN AFTER B	% YEARLINGS BEFORE B+1	SAMPLE SIZE (NO. OF ELEPHANTS CLASSIFIED)
1981-82	3.4	6.9	293
1982-83	3.4	9.6	372
1983-84	11.9	4.7	397
1985-86	6.1	6.5	334
1986-87	12.7	9.0	1062
1987-88	8.6	8.2	1522

	NO. OF ADULT COWS/ NO. OF NEWBORN AFTER B	NO. OF ADULT COWS/ NO. OF YEARLINGS BEFORE B+1
1981-82	11.0	7.5
1982-83	12.7	3.4
1984-85	3.4	5.7
1985-86	8.3	6.3
1986-87	3.4	5.2
1987-88	4.8	5.2

AERIAL SURVEY	% YEARLINGS IN POPULATION (COUNTED)	% YEARLINGS IN POPULATION (PHOTOGRAMMETRY)
DEC 1983	8.0	-
MAY 1984	6.8	8.3
AUG 1984	5.9	7.1
DEC 1984	9.6	11.8
MAY 1985	10.1	11.9
AUG 1985	8.0	9.7
DEC 1985	12.0	11.1
SEPT 1987	8.1	11.2

Rate of increase

A simple measure of population change when several estimates of population size at different times are available, is the observed rate of increase r (Caughley & Birch 1971, Caughley 1977a). This is simply the slope of the natural log of population size estimates over time, and is calculated for several intervals from census estimates given in Table 6.5. Original estimates are used in Table 6.5, as corrections based on area coverage or method used are impossible with the information available on each estimate.

The present elephant population in Etosha N.P. was founded in the early 1950's after a local extinction of 70 years. Figure 6.2 A shows an initial period of slow increase from 1951-1970, followed by a rapid eruption from 1972-1984, and a decline from 1984-1986. An increase occurred in 1987 again. The pattern is superficially very similar to a classic ungulate eruption or colonization sequence (Fig. 6.2 B) (Caughley 1970, 1979, 1981a, 1983, Riney 1982). It is also tempting to say that the population increased rapidly during the accelerated growth stage, overshot its carrying capacity, decreased and should from 1987 onwards fluctuate around its carrying capacity. Points are not connected in Fig. 6.2 A, however, as at least part of the population increase is surely attributable to improvements in census methods. The dramatic increase in elephant numbers has nevertheless been attributed to the rate of reproduction (Berry & Nott 1983) regardless of abundant evidence of large-scale elephant movements in and out of the park, such as the incidence of breaks in the fence around the park.

Dramatic changes in elephant numbers from season to season and between consecutive years, such as 1983-1984, illustrate this effect, which is impossible to reproduce through births and deaths only. The currently accepted maximum rate of increase achieved by elephants anywhere is seven per cent per year in Addo Elephant N.P. (Hall-Martin 1980). Rates of increase substantially higher than 7% can be calculated for the different phases in elephant population growth in Etosha N.P., or over the entire period (Table 6.5). Immigration must have contributed substantially to population increase, and likewise, emigration played a part in the decline. The study of movements of the elephant population is still in progress, but it appears that there is a strong relationship between rainfall and elephant numbers in Etosha N.P. (Chapter 2). Regional rainfall outside the park has an inverse effect on numbers of elephant inside the park. The observed rates of increase of the number of elephants in Etosha N.P. therefore refer to

Table 6.5 Estimates of elephant numbers in Etosha National Park since 1950 and observed rates of increase (r).

YEAR	DRY SEASON	WET SEASON	REFERENCE
1881- 1950	0 (or vagrants)		Fischer 1914, Shortridge 1934 Joubert & Mostert 1975
1951	20	-	Departmental report
1952	60	-	Departmental report
1954	200	-	Departmental report
1958	160	-	Bigalke 1958
1960	300	-	Departmental report
1966	200	-	Departmental report
1967	500	-	Departmental report
1968	450	-	Ebedes 1970
1969	300	-	Ebedes 1970
1970	490	-	Ebedes 1970
1972	690	-	Joubert 1973
1973	1230	480	Joubert 1973
1974	840	900	Berry & Hofmeyr 1974
1976	1170	-	Berry, Hofmeyr & De Villiers 1976
1977	-	840	Berry 1977
1978	1300	820	De Villiers 1978
1979	-	1880	De Villiers 1979
1982	2200	-	Berry 1982a
1983	2390	1440	Berry & Nott 1983. This study
1984	2460	1160	Berry 1984 a, b. This study
1985	1590[*]	700	This study
1986	1150[**]	650[**]	This study
1987	2020	1100[**]	This study

[*] 350 culled in June-July plus 1240 counted in August.
[**] Estimates based on incomplete aerial survey, ground surveys and waterhole counts.

DRY SEASON

r 1951-72 : 0.116
1951-84 : 0.117
1951-87 : 0.103
1967-83 : 0.116
1967-85 : 0.100
1973-84 : 0.088
1982-83 : 0.083
1984-85 :-0.436
1984-87 :-0.092

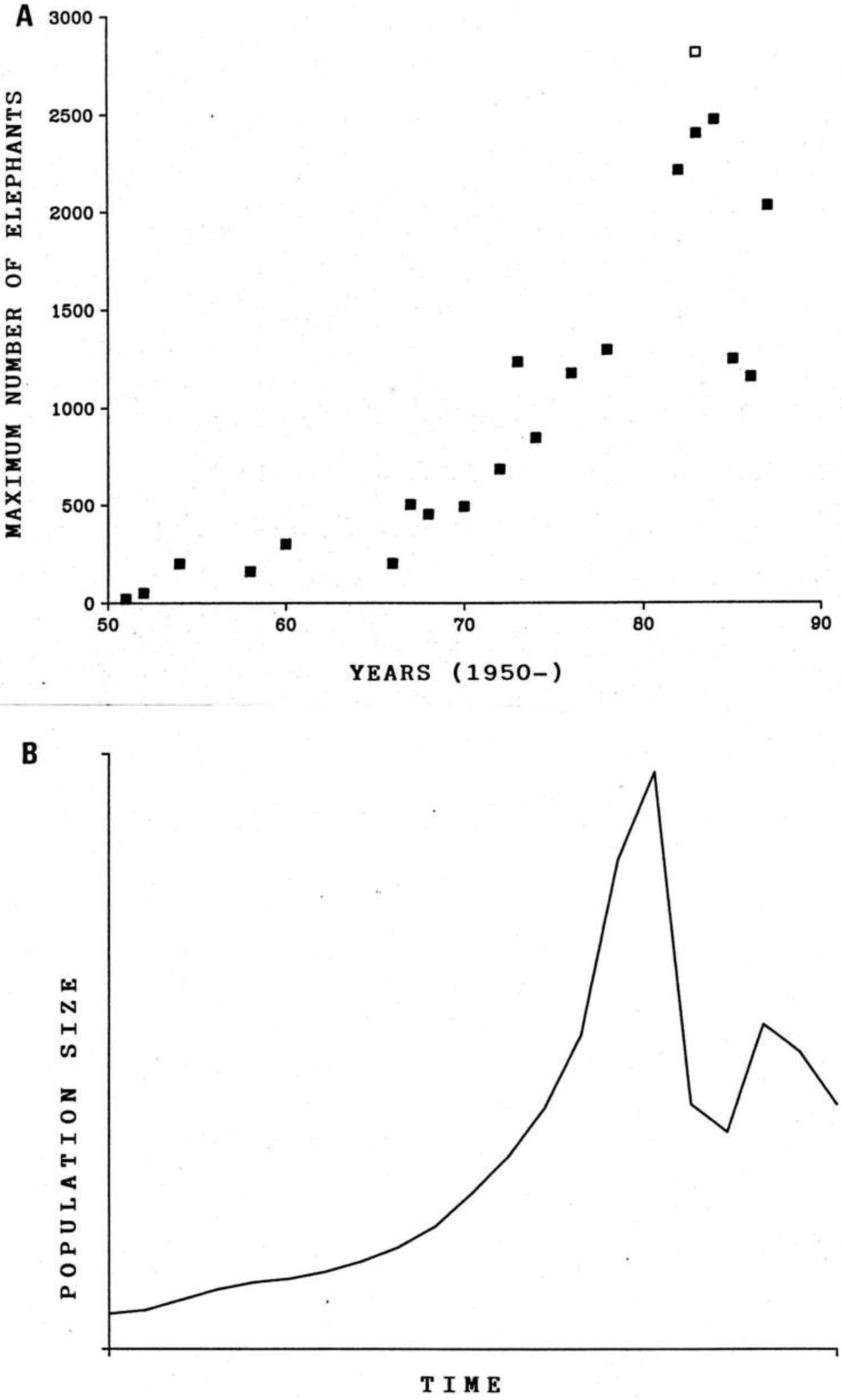


Figure 6.2 Elephant population trend in Etosha National Park from aerial surveys (A) and a theoretical eruption sequence (B).

trends in the abundance of elephants in the park, or changes in the relative portion of the regional population present in the park over a specific period.

Observed rates of increase, or the informal equivalent of comparing annual census totals, is therefore of limited use when further insight is sought into the more recent effects of environmental constraints on the elephant population in Etosha N.P., or similar "open" populations. Another rate of increase is calculated from the current survival and fecundity schedules as a measure of the population's current capacity to increase (Caughley 1977a). This parameter r_s or the survival-fecundity rate of increase is calculated from a stable age distribution resulting from constant rates of survival and fecundity in each age class. No one has yet managed to prove a stable age distribution over two or three generations in elephants, and few likewise in other species. This concept is possibly a cul-de-sac in large mammal population dynamics, particularly elephants, where generation lengths exceed environmental periodicities. The theorists will have to find a way around the impracticality of classical Lotka population dynamics. Such a new way may be found in Fryxell (1986), were it not that the type of data required once again excludes most wild populations.

The increase in elephant numbers in Etosha N.P. until 1984 has great local significance. To prove that this increase was due to immigration and not explosive breeding, is difficult if circumstantial evidence is ignored. One of the few retrospective approaches that can answer this question is the comparison of observed rate of increase and the "intrinsic rate of natural increase" at the time. The innate ability to increase through current survival and fecundity is described by the survival-fecundity rate of increase r_s. In total ignorance of the occurrence of a stable age distribution, this process is marginally acceptable if used to roughly indicate the sign of r, and no more (Caughley 1977a).

The rate r_s was calculated from a discrete-time Leslie-model equivalent (Michod & Anderson 1980) where

$$\lambda = \Sigma N_x/N_o{}^{*} F_x \qquad \text{and} \qquad r_s = \ln \lambda$$

N_x = number of females in age class x
N_o = number of females in age class 0
F_x = Leslie-type fecundity ($F_x = m_x l_o$)

In 1983 and 1985 r_s was calculated as -0.417 and -0.340 respectively. This indicates that the population in 1983 would probably have declined, in contrast to the observed trend. To say that age and fecundity schedules would be changing close to the end of the accelerated growth phase in anticipation of the decline is to ignore that both schedules are the result of past influences on the population. In a true eruption, r_s would have remained positive after the actual crash had started due to exactly this time-lag affect. It therefore appears that the elephant numbers in Etosha N.P. would have declined in 1983 were it not for immigrations into the park. If, as I believe, the elephants in Etosha N.P. represent an annually and seasonally variable fraction of the regional population, demographic parameters based on features other than the number of elephants counted in the park, also apply to the regional population of elephants in north-western SWA/Namibia. The survival-fecundity rates of increase calculated for 1983 and 1985 suggest that the regional population was declining from at least 1983 to 1985.

Caughley & Birch (1971) and Caughley (1977a) regard another rate of increase (r_m) to be important. This is the rate at which a population will increase when no resources are limiting, such as during colonization or after a perturbation from an asymptotic level. Although potentially useful in harvesting strategies, the maximum rate of increase has no utility in Etosha N.P. as long as elephants are free to leave and enter the park. Caughley & Krebs (1983) suggest that a population's intrinsic rate of natural increase, or r_m, is approximated by average body mass, as $r_m = 1.5\ W^{-0.36}$, with W in kg. Jachmann (1986) has used this general trend to calculate $r_m = 0.111$ for elephants in Kasungu N.P., but this can hardly be valid as the relationship between elephant mass and r_m is based on Hall-Martin's (1980) maximum observed rate of increase. Although Caughley & Birch (1971) defined the more esoteric concepts of r_s and r_m, they conclude that all one is really required to know is the observed rate of increase, which is just as well as r_s and r_m are nearly impossible to measure in practice (Tait & Bunnell 1980). In Etosha N.P., however, as discussed in the previous section, observed rates of increase have little relevance to the balance of births and deaths in the elephant population. This is a clear example where an estimate of the survival-fecundity rate of increase (r_s) would have been most helpful, were it not that r_s is nearly impossible to measure accurately.

Yet another estimate of population increase linked to generation length was defined by Andrewartha & Birch (1954, in Caughley 1977a, May 1981). It was used by Hanks & McIntosh

(1973) as

$$r = \log R_0/T_c$$

where

$T_c = \Sigma l_x m_x x / l_x m_x$ and $R_0 = \Sigma l_x m_x$

Hanks & McIntosh (1973) and for example Melton (1983) assumed that they were dealing with a stationary age distribution, although probably meaning a stable age distribution, as $r=0$ in the former. Caughley (1977a) shows that the definition of generation length (T_c) is not appropriate in populations with overlapping generations, as in Hanks & McIntosh (1973) and Melton (1983) and defines the rate of increase per generation (R) as

$$R = e^{rT}$$
$$= \exp (r \Sigma S_x m_x x)$$

where S_x = stable age distribution F_x/F_0 and r is calculated from $\Sigma l_x m_x e^{-rx}=1$. R is therefore not a new or independent measure of population increase, but might be a convenient expression in models when stable age distributions are developed.

Mortality and survival

The standard way of expressing mortality and survival patterns is the life table, which either contains the recorded history of a single cohort from birth to death, or is a simplified abstraction of the transitional probabilities of dying at any particular age based on a sample of dead or live animals of all ages. Few cohort life tables have been produced for long-lived animals, and none for elephants. The alternative is therefore a life table based on a sample of the number of individuals alive in each age group when sampled, or a sample of ages at death.

The former is typically derived from a culled sample and the latter from a collection of mortality records. The mortality record of elephants in Etosha N.P. cannot be used to construct a life table due to biases in the record, such as the faster rate of disappearance of small carcases compared to big ones, and inadequate data collected from anthrax carcases in particular, as discussed in Chapter 5.

Life tables constructed from an instantaneous sample of the number of individuals alive in different age intervals, i.e. a standing age distribution (Caughley 1977a) have important restrictions, namely that the rate of increase must have been constant over at least 2-3 generations, and the age distribution should be stable. The age distribution of a population converges to stability for as long as the survival schedule and the rate of increase remain constant. This is a basic axiom in population dynamics with sound theoretical and factual backing (Caughley 1983). The proximity of a standing age distribution to a stable age distribution is usually unknown, and is usually the objective of studies of the dynamics of populations. Phrased differently, the question is how long the current observed schedules of fecundity and mortality have been operating in the population, and therefore how much of the recent population trend can be explained by these schedules. Evidence of the existence of a stable age structure is usually obtained from successive estimates of rate of increase and age structures of a population.

Few studies, mine included, are done over a sufficiently long period to generate the information needed in this assessment. For elephants, a study over 2-3 elephant generations or about 30 years with frequent estimates of population size, age specific fecundity and mortality, is required. It is also unlikely that such a study would confirm stability over such a long period, particularly in semi-arid environments. A life table based on the assumption of such stability in the absence of either evidence or a logical reason for stability, is therefore worthless. Elephants, however, should be candidates for stability even in fluctuating environments, if the classical reproductive homeostatic mechanisms are so well expressed in this species as Laws (1981) believes. Evidence of over-utilization of their food resources argues against stability, but elephants have probably never been faced with anything like the enormous human pressure on their habitat as in the second half of this century. Caughley & Krebs (1983) furthermore predict that elephants should not have evolved intrinsic regulation for purely allometric reasons.

Standard life tables based on Caughley's (1977a : 92-95) method 6 are presented in Tables 6.6 and 6.7, using the observed rates of increase from 1967 to 1983, and 1985 respectively. Age intervals of four years were used to condense the life table, thereby resulting in 15 age intervals. The sampled frequencies (f_x) are multiplied by e^{rx} as

Table 6.6 Life table for female elephants in the 1983 culled sample from Etosha National Park.

AGE INTER-VAL (4 YRS)	SAMPLED FREQ. f_x	CORRECT. FACTOR e^{rx}*	CORRECT. FREQ. F_x	SMOOTHED FREQ	l_x	d_x	q_x	p_x
0	22	1.000	22.000	18.998	1.000	.167	.167	.833
1	10	1.123	11.230	15.834	.833	.103	.124	.876
2	6	1.261	7.567	13.869	.730	.065	.089	.911
3	18	1.416	25.492	12.629	.665	.042	.064	.936
4	12	1.590	19.085	11.826	.623	.030	.048	.953
5	11	1.786	19.647	11.265	.593	.025	.042	.958
6	5	2.006	10.029	10.796	.568	.026	.046	.954
7	2	2.252	4.505	10.297	.542	.033	.061	.939
8	4	2.530	10.118	9.669	.509	.044	.086	.914
9	1	2.841	2.841	8.842	.466	.056	.119	.881
10	3	3.190	9.570	7.788	.410	.066	.161	.839
11	4	3.582	14.329	6.536	.344	.072	.209	.791
12	1	4.023	4.023	5.170	.272	.064	.263	.737
13	3	4.518	13.553	3.812	.201	.072	.320	.680
14	0	5.073	0.000	2.593	.137	.000	.000	.000

* $r_{(1967-83)} = 0.116$

Table 6.7 Life table for female elephants in the 1985 culled sample from Etosha National Park.

AGE INTER-VAL (4 YRS)	SAMPLED FREQ. f_x	CORRECT. FACTOR e^{rx} *	CORRECT. FREQ. F_x	SMOOTHED FREQ	l_x	d_x	q_x	p_x
0	45	1.000	45.000	42.998	1.000	.151	.151	.849
1	30	1.105	33.155	36.491	.849	.121	.142	.858
2	16	1.221	19.543	31.293	.728	.097	.134	.867
3	27	1.350	36.446	27.117	.631	.078	.124	.876
4	14	1.492	20.885	23.744	.552	.064	.115	.885
5	26	1.649	42.867	21.008	.489	.052	.106	.894
6	15	1.822	27.332	18.783	.437	.042	.097	.903
7	6	2.014	12.083	16.969	.395	.034	.087	.913
8	9	2.226	20.030	15.491	.360	.028	.078	.923
9	5	2.460	12.298	14.290	.332	.023	.068	.932
10	1	2.718	2.718	13.321	.310	.018	.058	.942
11	8	3.004	24.034	12.547	.292	.014	.048	.952
12	4	3.320	13.281	11.942	.278	.011	.038	.962
13	6	3.669	22.016	11.485	.267	.008	.028	.972
14	2	4.055	8.111	11.162	.260	.000	.000	.000

* $r_{(1967-85)} = 0.100$

a correction factor for a value of r other than zero, and the corrected frequencies (F_x) are smoothed using a log-polynomial model. The survival schedule (l_x) or the probability of survival from birth to age x is formed by dividing each smoothed frequency by the frequency in the 0 age interval. The probability of dying (d_x) during age interval x, x+1, is calculated from the difference between consecutive values of l_x. The mortality rate (q_x), or the proportion of animals alive in age x that die before reaching age x+1, is calculated as d_x/l_x. The survival rate (p_x) is the complement of q_x (or $1-q_x$).

Both life tables can be rejected on grounds other than the unproved stable age distribution. The rate of increase resulting from the survival and fecundity schedules is unknown, and certainly not the observed rates of increase used in Tables 6.6 and 6.7. The smoothed version of the observed age distribution is also by necessity very different from the observed age distribution. Not all variation in age frequencies from one interval to the next is caused by inadequate sampling, as other mechanisms such as synchronous breeding might produce such variation. Peaks in the age distribution might also form a stable pattern if the causes for such peaks are stable.

Life tables can also be constructed over 60 years using the relatively smooth age distributions in Fig. 2.11, assuming a stationary population. Table 6.8 presents an example of such a life table over 60 years, but as the assumptions cannot be empirically proved, it is as invalid as Tables 6.6 and 6.7. One important aspect is nevertheless apparent from the two life tables for 1985. The survival schedules (p_x) differ dramatically, and in the opposite direction than expected from the two different r values used. The survival rate in Table 6.7 represents the cumulative probability of survival from one age interval of four years to the next age interval. P_x values in Table 6.8 represent probabilities of surviving from one year to the next. The problem comes in the calculation of yearly survival probabilities from four-year intervals, as $p_1 \cdot p_2 \cdot p_3 \cdot p_4 \neq p_0$. The fourth root of p_0 or $p_0^{.25}$ is an approximate value of the probability of surviving from year to year over the first four years of life. This problem was not recognized in Croze et al. (1981) who used interval probabilities as equivalent to yearly probabilities.

Michod & Anderson (1980) proposed an alternative method of calculating a life table without having to assume any value of r, which is valid if the age distribution is stable. The l_x schedule is calculated as

Table 6.8 A life table over 60 years based on the 1985 culled elephant sample in Etosha National Park assuming r=0.*

AGE (YRS)	SAMPLED FREQ. f_x	SMOOTHED FREQ.	l_x	d_x	q_x	p_x
1	19.00	12.131	1.000	.057	.057	.943
2	10.70	11.436	.943	.054	.057	.943
3	10.10	10.785	.889	.050	.057	.944
4	9.60	10.175	.839	.047	.056	.944
5	9.10	9.604	.792	.044	.056	.944
6	8.60	9.069	.748	.041	.055	.945
7	8.20	8.567	.706	.039	.055	.945
8	7.80	8.096	.667	.036	.055	.945
9	7.40	7.654	.631	.034	.054	.946
10	7.00	7.240	.597	.032	.054	.946
11	6.60	6.850	.565	.030	.053	.947
12	6.30	6.485	.535	.028	.053	.947
13	6.00	6.141	.506	.027	.053	.947
14	5.70	5.818	.480	.025	.052	.948
15	5.40	5.515	.455	.024	.052	.948
16	5.10	5.229	.431	.022	.051	.949
17	4.90	4.960	.409	.021	.051	.949
18	4.70	4.707	.388	.020	.051	.949
19	4.40	4.469	.368	.019	.050	.950
20	4.20	4.244	.350	.017	.050	.950
21	4.00	4.033	.332	.016	.049	.951
22	3.80	3.833	.316	.016	.049	.951
23	3.70	3.646	.301	.015	.049	.951
24	3.50	3.468	.286	.014	.048	.952
25	3.30	3.301	.272	.013	.048	.952
26	3.20	3.143	.259	.012	.048	.953
27	3.00	2.994	.247	.012	.047	.953
28	2.90	2.853	.235	.011	.047	.953
29	2.80	2.720	.224	.010	.046	.954
30	2.60	2.594	.214	.010	.046	.954
31	2.50	2.475	.204	.009	.046	.955
32	2.40	2.362	.195	.009	.045	.955
33	2.30	2.256	.186	.008	.045	.955
34	2.20	2.155	.178	.008	.044	.956
35	2.10	2.060	.170	.008	.044	.956
36	2.00	1.969	.162	.007	.044	.957
37	1.90	1.884	.155	.007	.043	.957
38	1.80	1.803	.149	.006	.043	.957
39	1.75	1.726	.142	.006	.042	.958
40	1.70	1.653	.136	.006	.042	.958
41	1.60	1.583	.131	.005	.042	.959
42	1.50	1.518	.125	.005	.041	.959
43	1.47	1.455	.120	.005	.041	.959
44	1.40	1.396	.115	.005	.040	.960
45	1.35	1.340	.110	.004	.040	.960
46	1.30	1.286	.106	.004	.040	.961
47	1.25	1.236	.102	.004	.039	.961
48	1.20	1.187	.098	.004	.039	.961
49	1.15	1.141	.094	.004	.038	.962
50	1.10	1.098	.091	.003	.038	.962
51	1.06	1.056	.087	.003	.038	.963
52	1.02	1.016	.084	.003	.037	.963
53	0.98	0.979	.081	.003	.037	.963
54	0.94	0.943	.078	.003	.036	.964
55	0.90	0.909	.075	.003	.036	.964
56	0.87	0.876	.072	.003	.036	.965
57	0.83	0.845	.070	.002	.035	.965
58	0.80	0.815	.067	.002	.035	.965
59	0.77	0.787	.065	.002	.034	.966
60	0.74	0.760	.063	.000	.000	.000

* As $r=0$, $e^{rx}=1$

$$l_x = \frac{l_0 f_x \lambda^x}{f_0} \quad (x=1,2 \;.......n-1)$$

where λ is calculated as

$$\lambda = \sum \frac{f_x}{f_0} l_0 m_x \quad \text{and } r = \ln \lambda$$

The growth multiplier λ (or e^r) is equivalent to the e^{rx} correction in Caughley's (1977a) method. Two completely different values for λ are calculated when the same age distribution is indexed in four-year intervals and in yearly intervals, and l_x always increases with age in the life tables with 60 intervals. The method of Michod & Anderson (1980) was therefore discarded.

Caughley (1966) suggests that although the l_x schedule might be biased by invalid assumptions of a zero rate of increase, the mortality schedule q_x can be calculated directly from age frequencies, where

$$q_x = (f_x - f_{x+1})/f_x$$

which although not based on constant rates of survival and fecundity, represents the current pattern. Such mortality schedules and the complementary survival schedules (p_x) are presented in Table 6.9 A & B for the 1983 and 1985 samples in 15 age intervals and 60 years respectively. The mortality pattern is characterized by high mortality during the first four years of life, followed by a constant low mortality with a steep increase towards the end of the lifespan. This pattern is similar to the general large mammal mortality pattern as in Caughley (1966, 1977a).

Only three life tables for elephants have been published, and all three would have been rejected according to the criteria of Caughley (1966). Jachmann's (1980) life table for elephants in Kasungu N.P. is based on only 52 mandibles collected over a number of years. Petrides & Swank (1966) developed a life table from relative sizes and not age, and avoided the question of population increase or stability. Laws (1969a) produced the most comprehensive life table for elephants to date, from the Tsavo N.P. population, but rejected his own l_x schedules and calculated mortality rates from age frequencies.

Table 6.9 Mortality (q_x) and survival (p_x) schedules for elephants in Etosha National Park in 1983 and 1985 in (A) four year intervals and (B) yearly intervals.

A. (Age intervals of 4 years)

AGE CLASS	q_x 1983	q_x 1985	p_x 1983	p_x 1985
0	.467	.393	.534	.607
1	.189	.196	.811	.805
2	.190	.183	.810	.817
3	.181	.176	.819	.824
4	.169	.165	.831	.835
5	.172	.186	.828	.814
6	.170	.157	.830	.843
7	.159	.187	.841	.813
8	.162	.188	.838	.812
9	.129	.180	.871	.820
10	.148	.156	.852	.844
11	.170	.158	.830	.842
12	.195	.200	.805	.800
13	.221	.250	.779	.750
14	1 *	1 *	0 *	0 *

* all elephants are assumed to die at 60 years.

Table 6.9 (continued)

B. (60 year groups)

AGE CLASS	q_x 1983	q_x 1985	p_x 1983	p_x 1985
1	.339	.248	.661	.752
2	.099	.107	.901	.893
3	.054	.048	.946	.952
4	.053	.050	.947	.950
5-8	.051	.053	.949	.947
9-12	.051	.049	.949	.951
13-16	.049	.047	.951	.953
17-20	.045	.044	.955	.956
21-24	.046	.050	.954	.950
25-28	.045	.042	.955	.958
29-32	.042	.050	.958	.950
33-36	.043	.051	.957	.949
37-40	.034	.048	.966	.952
41-44	.039	.042	.961	.958
45-48	.046	.042	.955	.958
49-52	.053	.054	.947	.946
53-56	.061	.069	.939	.931
57	.079	.083	.921	.917
58	.099	.091	.901	.909
59	.111	.100	.889	.900
60	1 *	1 *	0 *	0 *

* all elephants are assumed to die at 60 years.

Croze et al. (1981) used this mortality schedule, but their version is completely different from the original, presumably due to an arithmetic error. Figure 6.3 illustrates the published survival and mortality schedules and those calculated from age frequencies of elephants in the Etosha N.P. The shape of the q_x and p_x curves is at least similar with the exception of those of Croze et al. (1981). It seems that survival after about 8 years was more or less constant up to age 40 in the Tsavo N.P. and Rwenzori N.P. populations at the time they were studied, and up to 50 years in Etosha N.P.

An alternative approach to estimate the mortality rate, is the 'catch curve' of fisheries biologists (Beverton & Holt 1957, in Laws 1971). A plot of the natural log of age class abundance over age yields a linear relationship if there is an equilibrium between recruitment and mortality. The instantaneous mortality rate (z) is estimated by the slope of the regression, and estimates from other populations range from 0.052 to 0.066 in the age range 20-50 years in East Africa (Laws 1971), and 0.08 in Kasungu N.P., Malawi (Jachman 1986).

Figure 6.4 illustrates the plot of ln year class abundance over age in four-year intervals for the 1983 and 1985 culled samples. The slopes, or z values of the set of regressions are not significantly different (Fig. 6.4 A: t_{25}=-.572; $F_{1,25}$=.328; NS), and the culled samples yield estimates of 4.1-4.9% annual mortality over the entire age range. Over the first 10 years, the annual mortality rate in 1983 is estimated as 19.6% compared to 12.9% in 1985, but the two values are not significantly different (t_2=1.388; $F_{1,2}$=1.926; NS).

Figure 6.5 A-E illustrates plots of ln class abundance over age of the age distributions derived from aerial photogrammetry, using two-year class intervals in the range 0-24 years. The consistent increase over the last few age classes is probably an artifact of the method, and regressions were only done up to 24 years. Values of z range from 9.5-13.1%, with only the slopes of the first and last surveys significantly different (t_{20}=2.136; $F_{1,20}$=4.562; $p<0.05$). Annual mortality rates over the first five years are estimated as 12.1-31.5%, but linear models do not provide the best fit to the data over the early years, as demonstrated in Fig. 6.6, as also found by Laws (1971). This is attributed to annual variation in mortality and fecundity, or could be due to synchronized breeding.

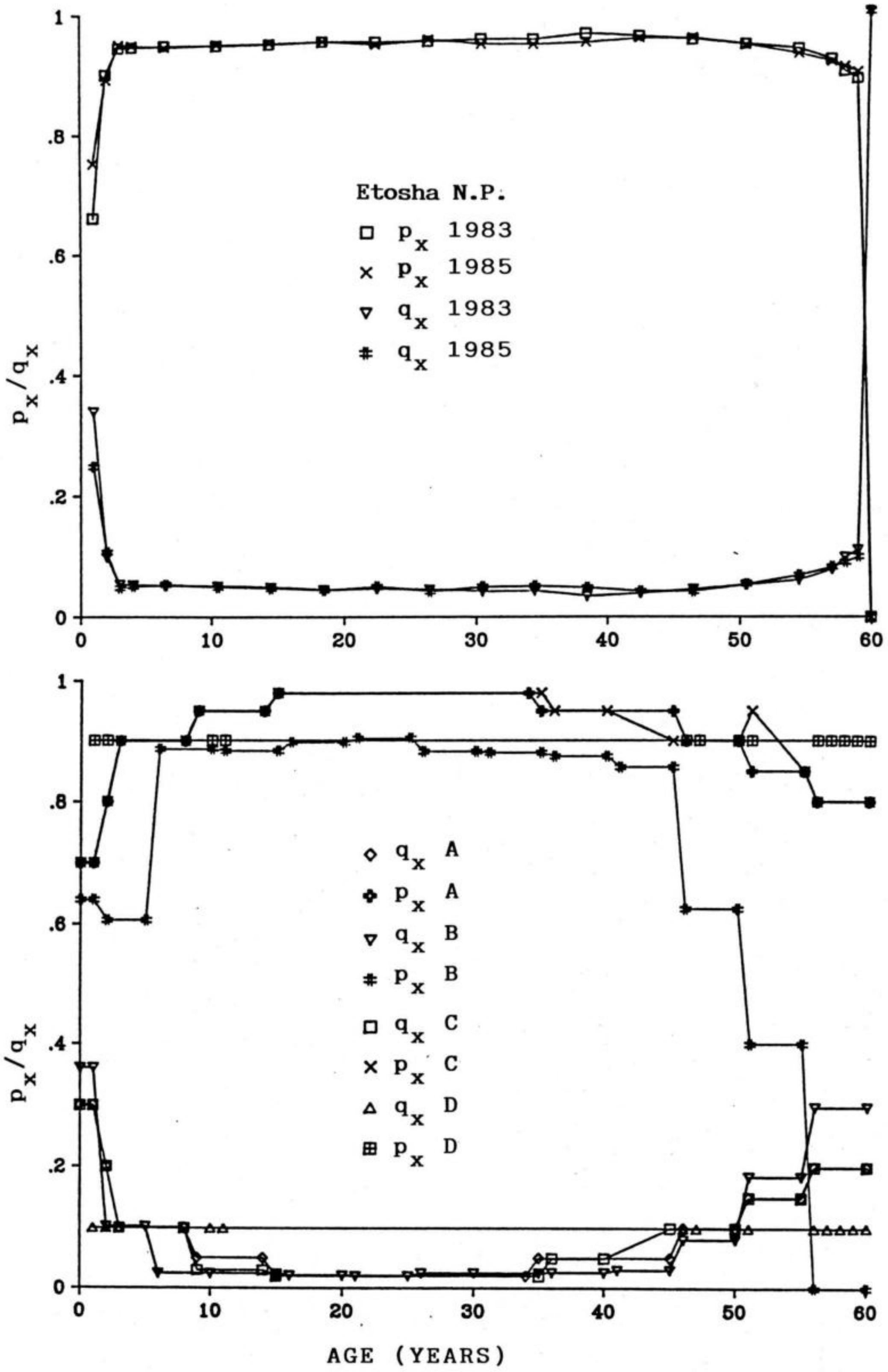


Figure 6.3 Mortality and survival pattern of elephants in Etosha National Park in 1983 and 1985 and published schedules of Petrides & Swank (1966): A; Laws (1969 b): B; Fowler & Smith (1973): C; and Croze et al. (1981): D.

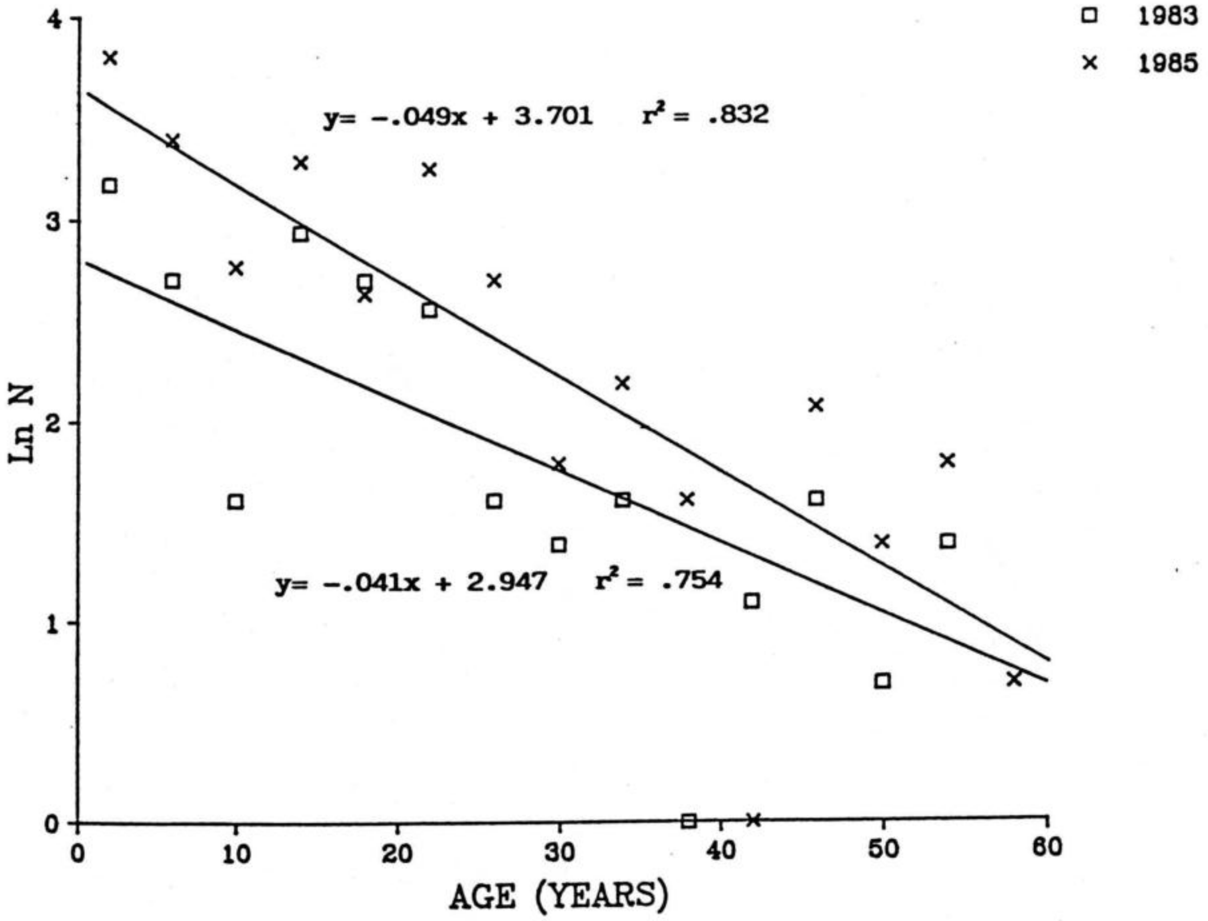


Figure 6.4 Plot of natural log year class abundance and age of culled elephant samples in 1983 and 1985 in Etosha National Park, using age intervals of four years.

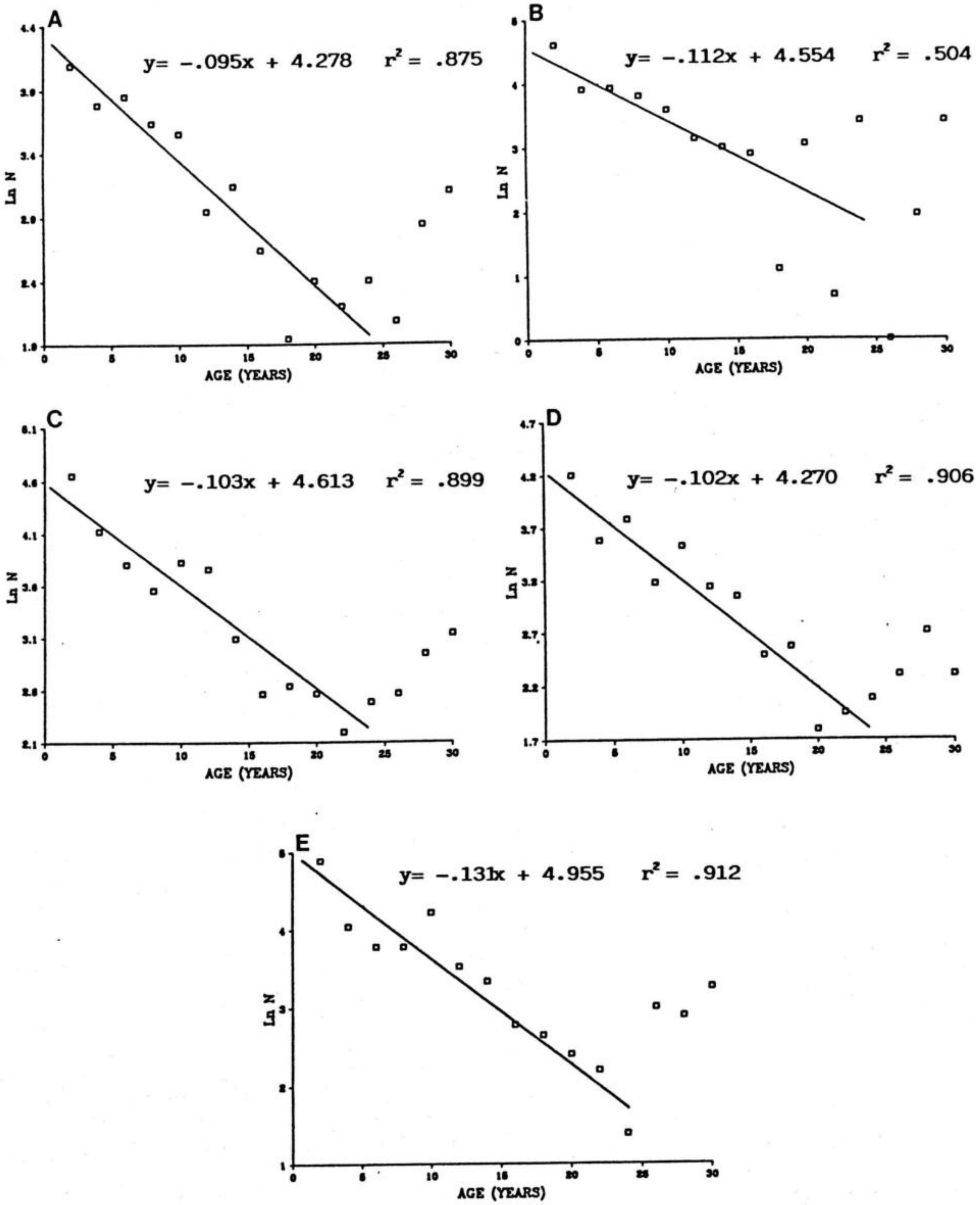


Figure 6.5 Plot of natural log year class abundance and age in two-year intervals of photogrammetrical age distributions in May 1984 (A), December 1984 (B), May 1985 (C), August 1985 (D) and September 1987 (E) of elephants in Etosha National Park.

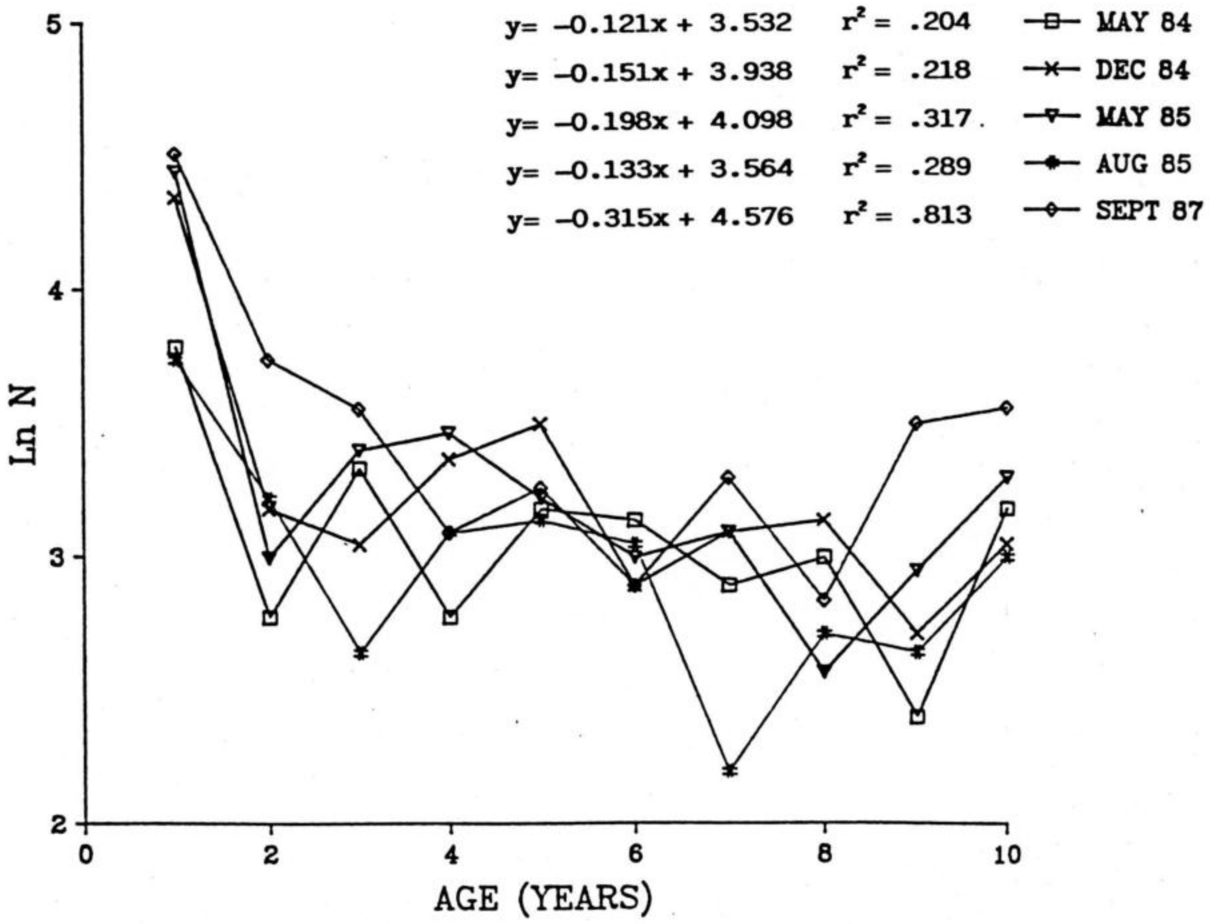


Figure 6.6 Plots of ln age class abundance and age up to 10 years, using photogrammetrical age distributions (regressions from year one to five) of elephants in Etosha National Park.

Estimates of mortality rates using age frequencies following Caughley (1966) and Beverton & Holt (1957) correspond in pattern, but are not directly comparable to each other, as linear regression of pooled and transformed age frequencies in the latter method smooth the data even further. Again it seems important to leave the data as raw as the method allows, or early mortality rates will be biased. The elephant population in Etosha N.P. is characterized by high rates of juvenile mortality which vary from year to year, and a more consistent adult mortality rate, and all estimates should be questioned. Mortality rates derived from the culled samples will be used in modelling, in favour of the instantaneous rate of mortality and photogrammetrical age distributions, as the age estimation procedure is at least more precise if not exact in the former. Survival and mortality schedules not based on standing age distributions should eventually result from long-term studies, such as those of Moss in Amboseli N.P. and Douglas-Hamilton in Lake Manyara N.P. The forefront of the attempt to estimate survival and mortality rates free of any assumptions regarding population increase or stability lies, however, in North America (Siler 1979, Bart & Robson 1982, Eberhardt 1985, Polacheck 1985, Fryxell 1986). The resolution achieved in demographical analyses of elephant populations based on culled samples, photogrammetrical age structures and even direct observations, is limited by uncertainties in age estimation methods, intra- and interpopulation variation in growth rates, and the longevity of elephants, and cannot compare to some recent studies on seals and cervids (in eg. Fowler & Smith 1981). It is a dubious consolation that the dynamics of intensively studied populations of common large mammals in North America are still not perfectly understood (Caughley 1981b, Eberhardt 1985, Fryxell 1986).

MODELS

As approximations of the real world, models differ with regard to the various parts of a system used or ignored, and consequently in the accuracy, precision, resolution and utility of their results (Starfield & Bleloch 1986). The bewildering array of models of large mammals, or systems containing large mammals can be whittled down rapidly by the constraints imposed by the data available. Few models are applicable to elephants, as most do not cater for populations with overlapping generations, unfortunately including some of the more promising models incorporating a measure of environmental instability.

The first models applied to elephants were logistic (Laws 1969b, 1971), which ignore the effect of age-specific fecundity and mortality, but predict the outcome of trends reasonably well. Caughley's (1976) stable limit cycle of elephants and trees made use of a logistic interpretation, as in some more recent models of elephant-vegetation interactions (Barnes 1983, Van Wijngaarden 1985, Swart & Duffy 1987). Barnes (1983) also developed a single-species logistic model for elephants incorporating an immigration term.

Lewis (1942) and Leslie (1945, 1948) developed matrix models incorporating the effects of age-specific fecundity and mortality. These models, commonly known as Leslie matrices, deal with one species in isolation, but reveal possible outcomes in age structures and population size due to the internal characteristics of a population. Caughley (1981a, b) criticizes the single-species approach, but also admits that little progress has been made in multi-species models. Starfield & Bleloch (1986) demonstrated that a matrix model can be made to interact with environmental changes.

Fowler & Smith (1973) used a Leslie matrix on data from Petrides & Swank (1966), Laws (1969a) and Laws & Parker (1968) to predict equilibrium age distributions for an imaginary elephant population. The same approach was followed by Croze et al. (1981), using data from Laws (1969 a) and Smuts (1975). Pilgram & Western (1986a, b) likewise used matrix models of both sexes to simulate ivory harvesting and population trend. None of these studies, however, refer to a particular existing population, other than Pilgram & Western (1986a, b) who modelled the entire elephant population in Africa.

The Leslie matrix consists of a top row and subdiagonal row of elements, namely age-specific fecundities (F_x) and a survival schedule (p_x) respectively. It is essentially a mathematical formulation of the addition of births and the subtraction of deaths in the appropriate frequencies and intervals in which births and deaths occur in a real population. No assumptions are made regarding the rate of increase or the presence of a stable age distribution, in fact the use of real unsmoothed observed values in the model has great appeal. The model is easy to manipulate and a variety of effects can be incorporated, such as immigration or emigration, density dependence in any parameter, catastrophes and harvesting. Advanced matrix models for elephants proposed by Wu & Botkin (1980) and Botkin, Mellilo & Wu (1981) also incorporate environmental perturbations, notably rainfall. The entire universe can in fact be relegated to the level of probabilities which can be as accurate as the data available, and can be incorporated in modelling one event in terms of its effect on another.

Several models have been produced on elephant-vegetation interactions, which is a reasonably complex system if judged from the copious and conflicting literature on the subject. Caughley (1979, 1981b) argues that even the simplest herbivore-plant system is not fully comprehended, but the work of Barnes (1983), Pellew (1983a, b) and Van Wijngaarden (1985) are significant advances in the study of elephants interacting with vegetation.

Hanks & McIntosh (1973) constructed a model of an elephant population to determine the relative importance of the reproductive homeostatic mechanisms in population regulation. Their model is essentially a life-table model as in Sinclair (1973), and has been criticized for some of its assumptions (Caughley 1977a, Laws 1981).

The model that best fits the type of information available and is best suited to answer the questions which led towards the study of elephant dynamics in Etosha N.P. and north-western SWA/Namibia, is the matrix model. Such a model was accordingly constructed following Starfield & Bleloch (1986 : 194-196), and simulations were performed analagous to those of Fowler & Smith (1973) and Croze et al. (1981). Two forms of the elephant matrix model written by P.M. Lindeque are presented in Appendices 3 & 4.

The initial population used in the matrix is based on the 1985 culled sample from Etosha N.P., adjusted to a size similar to the estimated total female component of the regional elephant population in SWA/Namibia at the time. The number of elephants in each age group was used as observed, as well as the age-specific fecundity values (Table 6.1 B). A schedule of survival probabilities derived from age frequencies as in Table 6.9 B, was likewise used, and for the purpose of the model, it was assumed that no elephant lives longer than 60 years.

When the fecundity and survival schedules are kept constant, the model population achieved a stable rate of increase and a stable age distribution. The initial age structure is shown to be near the stable form, as only 2 years are required to show no significant difference between the age structures in year 1 and 2 ($\chi^2 = 48.702$ NS). A modest decline results from the observed schedules of survival and fecundity, with r= -0.0053 ± .0006 in the first 10 years. To eliminate all irregularities in age frequency, the model was made to simulate a total of 60 years (Fig. 6.7 A & B), after which parameters were changed to determine their effect on population trend.

Individual parameters are changed, in isolation of the rest, and are sufficient to change the model population's course. In a real life situation, changes in single parameters only will probably be rare, and changes in other parameters are therefore gradually introduced in various combinations. Projections for an arbitrary 30 years are used to facilitate illustration of the effects of manipulations on population trend, although it is most unlikely that a parameter once changed, will remain at the new level for that long. No density-dependence in any relationship is assumed in any simulation. The results of simulations apply to a model population similar to a sample of elephants taken from Etosha N.P., which is also seen as a sample of the regional population of elephants. If a part of the regional population eventually becomes isolated in Etosha N.P. due to the disruption of movements in and out of the park, the simulations from the present model will be more accurate. Nobody knows exactly how big the regional population really is, or how different the portion of it studied in Etosha N.P. is from the rest.

Changes in survival

Table 6.10 presents six survival schedules used in the simulations, including the observed schedule in 1983 and 1985. Across-the-board changes in survival were achieved by additions or subtractions of 0.01 or 0.02 to the age specific survival probability in 1985. Increases in the probability of survival results in a population increase (Fig. 6.8) and the minimum increase necessary to achieve an increasing population is in the order of 0.005. Changes between 0.002 and 0.005 will result in a stationary population. What is significant is that minute changes in the overall survival schedule are sufficient to change the population's course from one of eventual extinction to an increase or rapid decline.

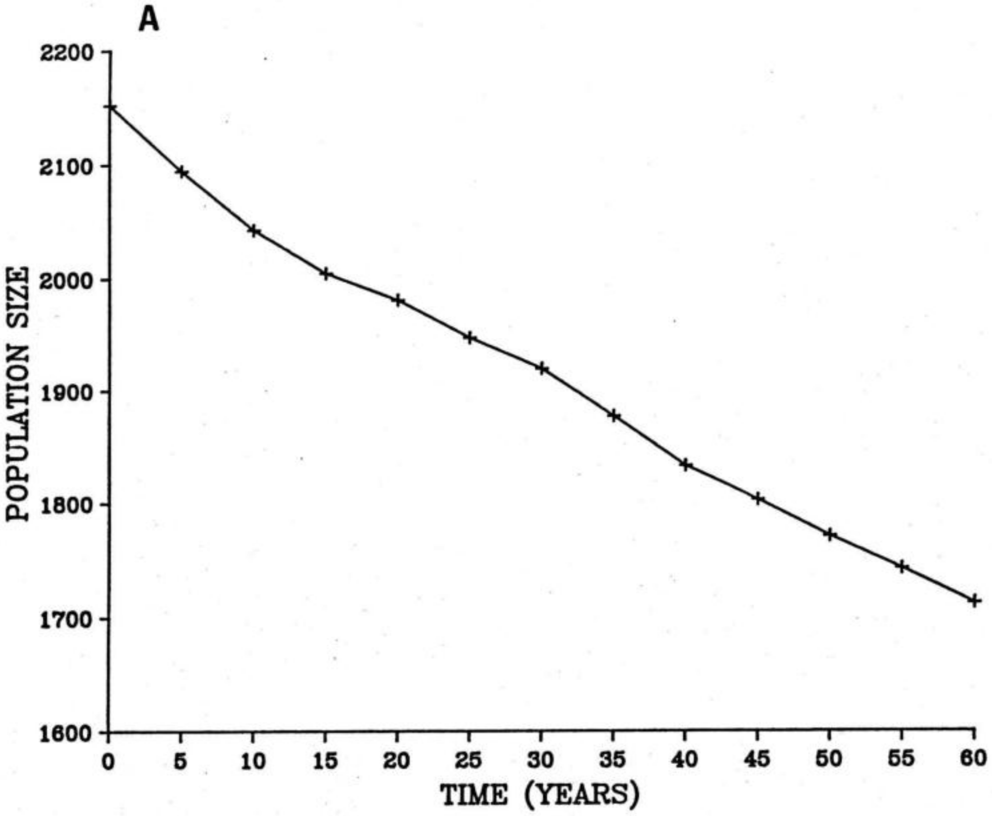


Figure 6.7 Projection for 60 years using the initial survival (p_x) and fecundity (m_x) schedules (A) and resulting age distributions in 1, 5, 15 and 60 years time (B) of female elephants in a model population.

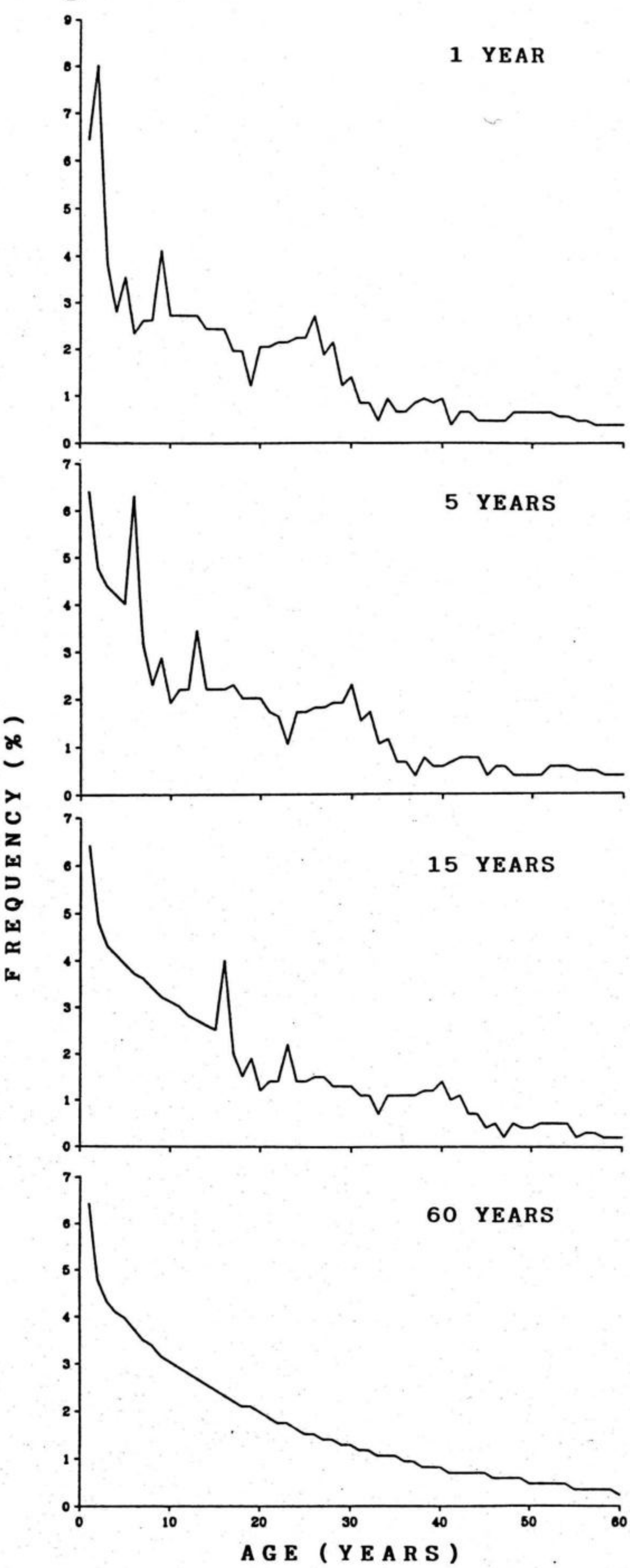


Figure 6.7 (continued).

Table 6.10 Observed and theoretical survival schedules used in models for elephants in Etosha National Park.

	p_x					
AGE	+ .02	+ .01	1985 OBSERVED	1983 OBSERVED	- .01	- .02
1	.772	.762	.752	.661	.742	.73
2	.913	.903	.893	.901	.883	.87
3	.972	.962	.952	.946	.942	.93
4	.970	.960	.950	.947	.940	.93
5-8	.967	.952	.947	.949	.937	.92
9-12	.971	.961	.951	.949	.941	.93
13-16	.973	.963	.953	.951	.943	.93
17-20	.976	.966	.956	.955	.946	.93
21-24	.970	.960	.950	.954	.940	.93
25-28	.978	.968	.958	.955	.948	.93
29-32	.970	.960	.950	.958	.940	.93
33-36	.969	.959	.949	.957	.939	.92
37-40	.972	.962	.952	.966	.942	.93
41-44	.978	.968	.958	.961	.948	.93
45-48	.978	.968	.958	.955	.948	.93
49-52	.968	.958	.946	.947	.936	.92
53-56	.951	.941	.931	.939	.921	.91
57	.937	.927	.917	.921	.907	.89
58	.929	.919	.909	.901	.899	.88
59	.920	.910	.900	.889	.890	.88
60	0.000	0.000	0.000	0.000	0.000	0.00
Code used in simulations	++	+	o		-	--

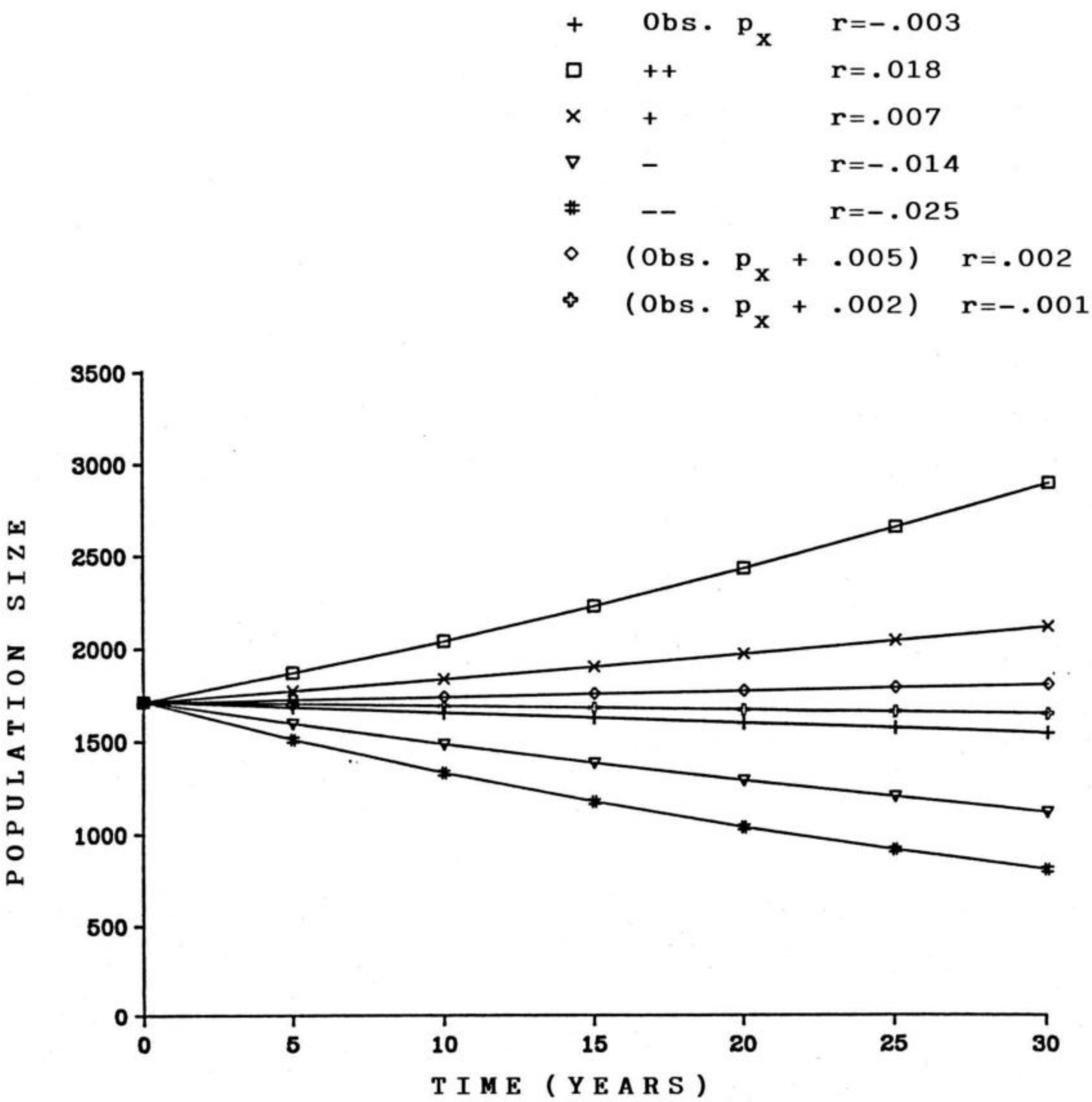


Figure 6.8 Simulated trends of a model elephant population resulting from proportional changes in the survival schedule (p_x). The starting figure and observed trends (Obs) refer to the estimated total number of female elephants in the regional population in north-western SWA/Namibia in 1985. (r=rate of increase; +, 0, - p_x schedules in Table 6.10).

It is probably more realistic to consider that conditions causing changes in the survival schedule will not have a proportional effect as in Fig. 6.8 or Table 6.10. The survival of one-year-olds for example, could respond more dramatically to environmental change, than adult survival. When such changes are simulated by changing first year survival (p_1) by one order of magnitude greater than the other age groups in Table 6.10, the resulting trends in Fig. 6.9 are similar to those in Fig. 6.8, but more dramatic. Survival, and particularly juvenile survival, is therefore clearly a potential key parameter affecting population trend.

Juvenile and yearling survival can be manipulated in the model by changing the probability of survival of individual age groups, or by changing the survival coefficient of the Leslie-type fecundities used in matrices, where $F_x = m_x l_0$. Although both parameters represent the same characteristic, they are measured in different ways, as shown previously. The various estimates of l_0 derived from the 1983 and 1985 samples are used in the model (.893, .820, .700, .640, .625, .571), as well as a theoretical maximum of .950, an intermediate theoretical low of .400, and the minimum estimate of .240 from Amboseli N.P. (Croze et al. 1981). From Fig. 6.10, it is clear that any change in l_0 to a value lower than 0.893 results in a population decrease. The regional population can be said therefore to be within 90% of the target value of l_0 to maintain a stationary population. The current fecundity schedule is therefore potentially effective in maintaining a stationary population (zero growth rate), were it not that the number of offspring produced are reduced by peri-neonatal mortalities to less than the level required to maintain the population. The population could respond to compensate for pre-natal losses by producing more units, which can be achieved in a number of ways.

The l_0 estimates do not refer to the total number of concepti produced, but to those surviving up to the stage when the uterus is visibly gravid. There is little evidence that prenatal deaths are directly affected by environmental conditions and such deaths are usually regarded as a constant factor in populations (Caughley 1977a, Michod & Anderson 1980). Where adverse environmental effects influence concepti, as in the foetal starvation recorded in Etosha N.P. (Chapter 4), actual mortalities should possibly occur after birth rather than before.

The survival of individuals in the first year (p_1) is therefore of great importance as well, especially as this class usually contains the largest number of individuals of all the year groups. It is difficult to estimate p_1 in a wild population, other than using

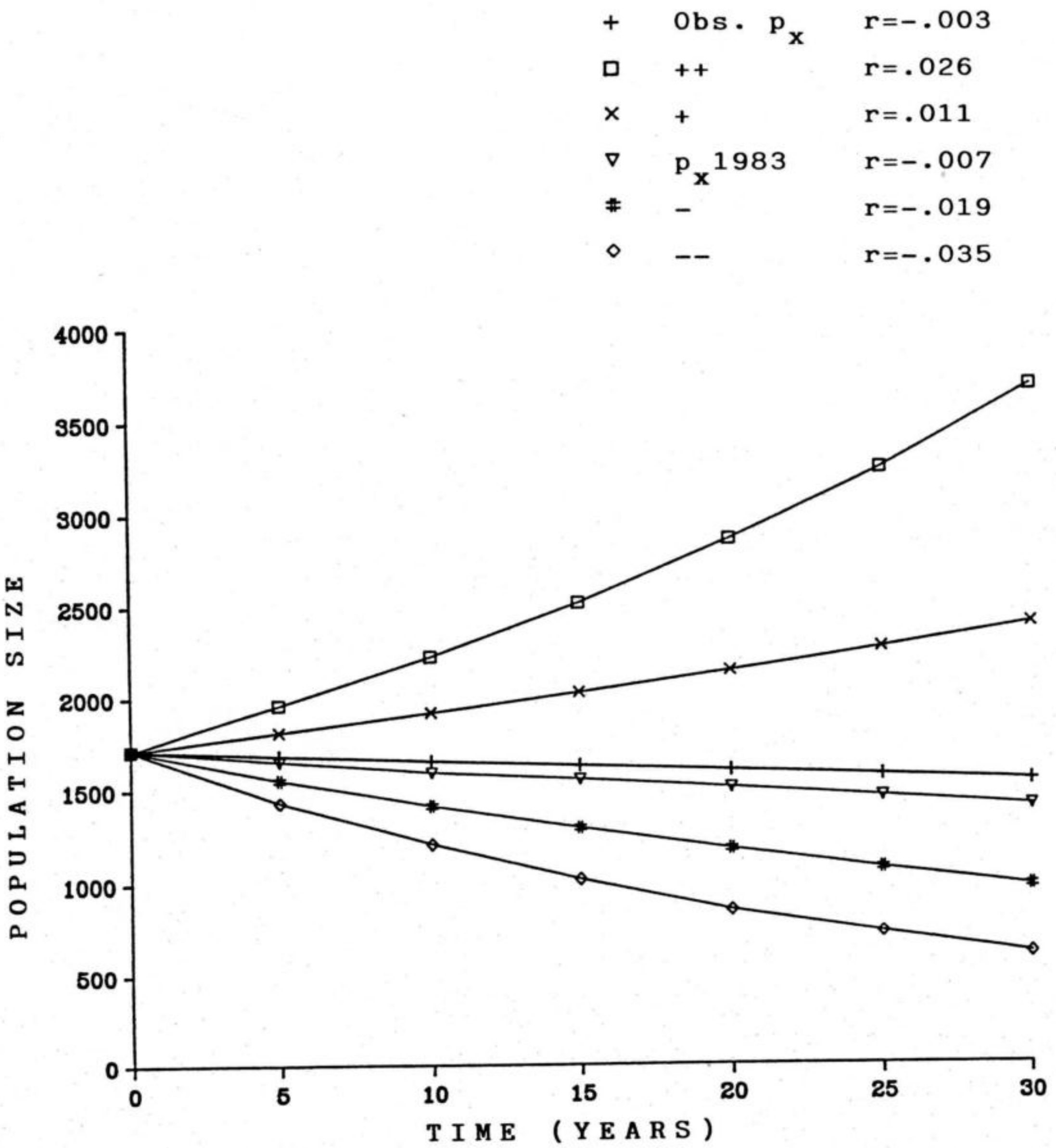


Figure 6.9 Simulated trends of a model elephant population resulting from disproportionate changes in the survival schedule (p_x) where the probability of survival over the first year is changed by one order of magnitude greater than p_{2-60}.

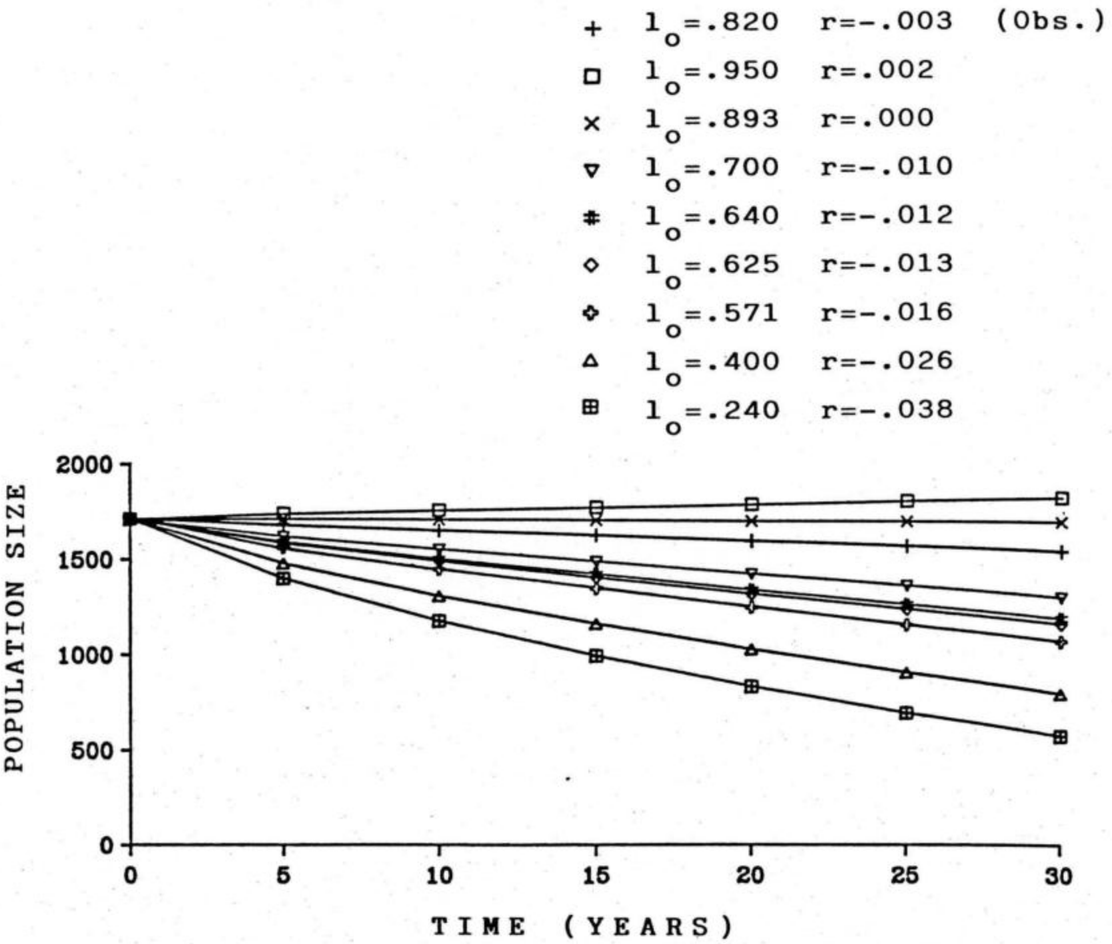


Figure 6.10 Simulated trends of a model elephant population, resulting from changes in the survival coefficient (l_o).

age frequency distributions with their corollary assumptions, because the number of newborn counted is affected by both survival and natality. Such a count just after the birth peak and again just before the next birth peak should however indicate first year survival, were it not that it is so difficult to estimate the exact age of a calf (aggravated in elephants by the variation in size and mass at birth, see Chapter 4). In lieu of precise estimates of p_1, theoretical values have to be used in simulations. These were derived by changing p_1 by .1 and .2, while keeping p_{2-60} the same as the observed values in Table 6.10. Figure 6.11 illustrates the effects of changes in p_1 on population trend. A p_1 value of 0.852, or 0.1 greater than the observed $p_1 = 0.752$, is sufficient to maintain the population.

Changes in fecundity

The three reproductive homeostatic mechanisms of Laws (1969 a, 1981), namely the mean calving interval (MCI), age at first conception (AFC) and the onset of senescence (SEN), find expression in the fecundity of a population. These homeostats might very well be dependent on population density, although this effect is not very clear in all populations (Chapter 4). Once a population has reached a critical level in numbers, its density might affect its growth through the homeostatic mechanisms, but this threshold density would have to be determined for each population. There is no hard evidence from Etosha N.P. that the elephant population is currently under the influence of a density feedback system. Changes in the reproductive rate can be interpreted in terms of short-term responses to drought as well. The purpose of simulating changes in fecundity is therefore limited to illustrating the potential effect of each parameter on the population trend, and to reassess the simulations of Hanks & McIntosh (1973).

It was previously demonstrated that the mean calving interval can be equated to a mean fecundity by 1/(2 MCI) in years = m_x, as also in Hanks & McIntosh (1973), and Table 6.11. Figure 6.12 illustrates simulated population trends at different values of MCI and mean fecundity rate. A MCI of between 3 and 4 years should be sufficient to maintain the population at the current schedule of survival.

The second homeostat is the age at first conception (AFC). The simulation of AFC in Fig. 6.13 was simplified by using a standardized value for m_x in all post-pubertal females, including the primiparous groups which in practice always has a lower fecundity than

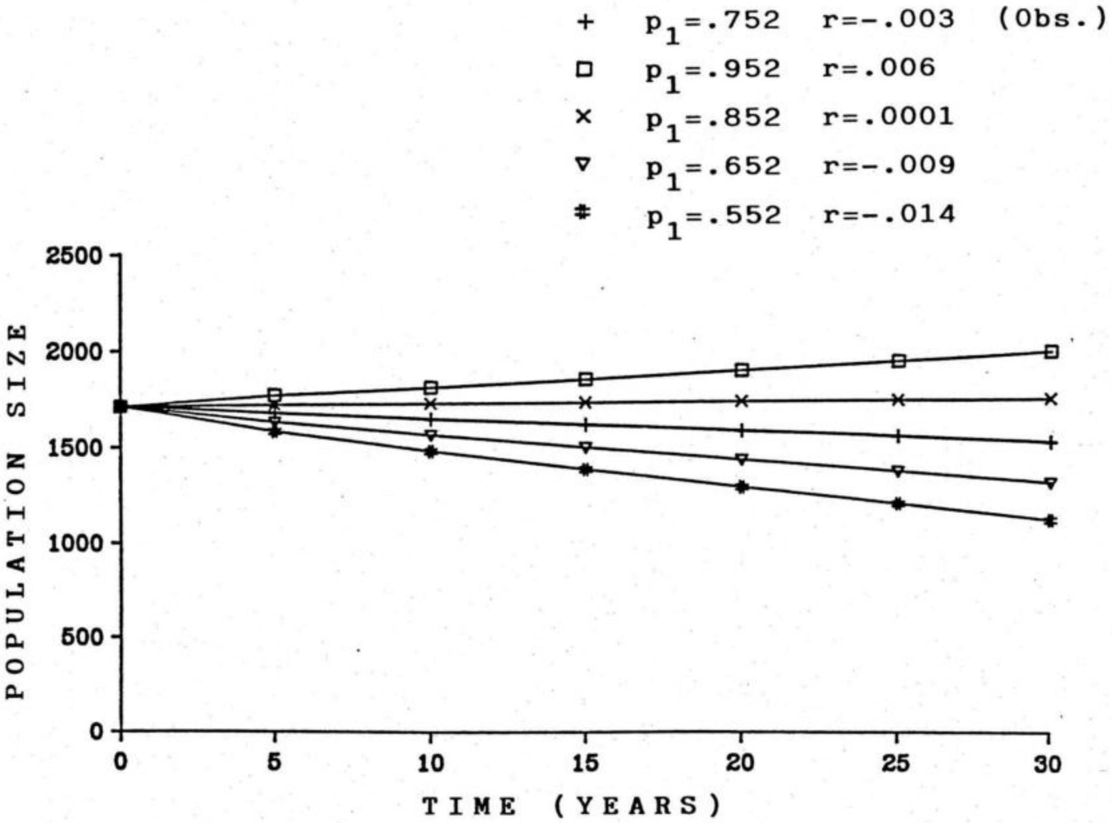


Figure 6.11 Simulated trends of a model elephant population by changes in first-year survival (p_1) only.

Table 6.11 Theoretical mean calving intervals (MCI) for elephants translated into mean fecundity rates (m_x).

MCI (YEARS)	m_x
2	.250
(2.1)	.238
(2.5)	.200
3	.167
(3.8)	.132
4	.125
5	.100
6	.083
7	.071
8	.063
9	.051
10	.050

( ) = estimates for Etosha National Park.

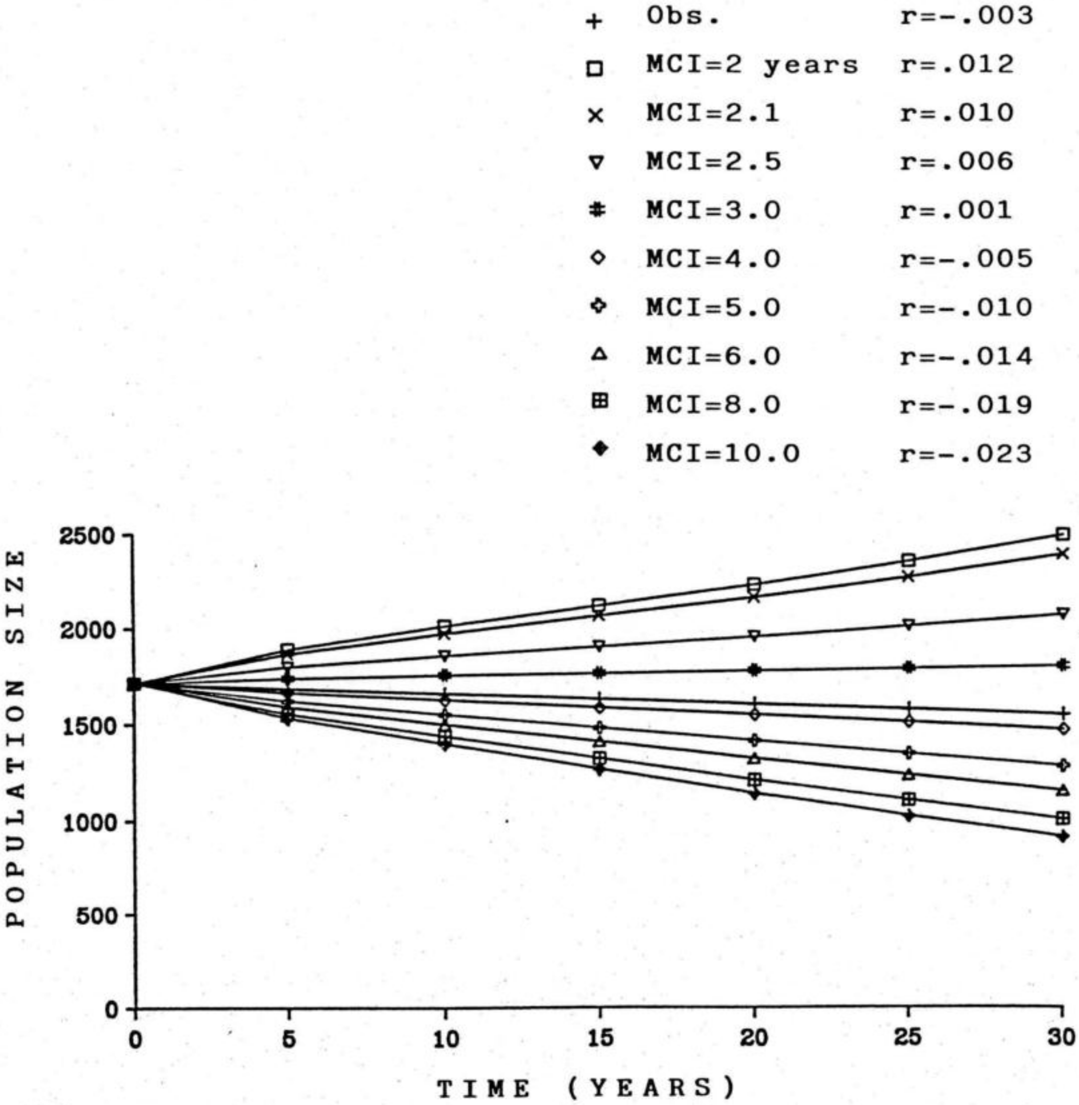


Figure 6.12 Simulated trends of a model elephant population by changes in the mean calving interval (MCI).

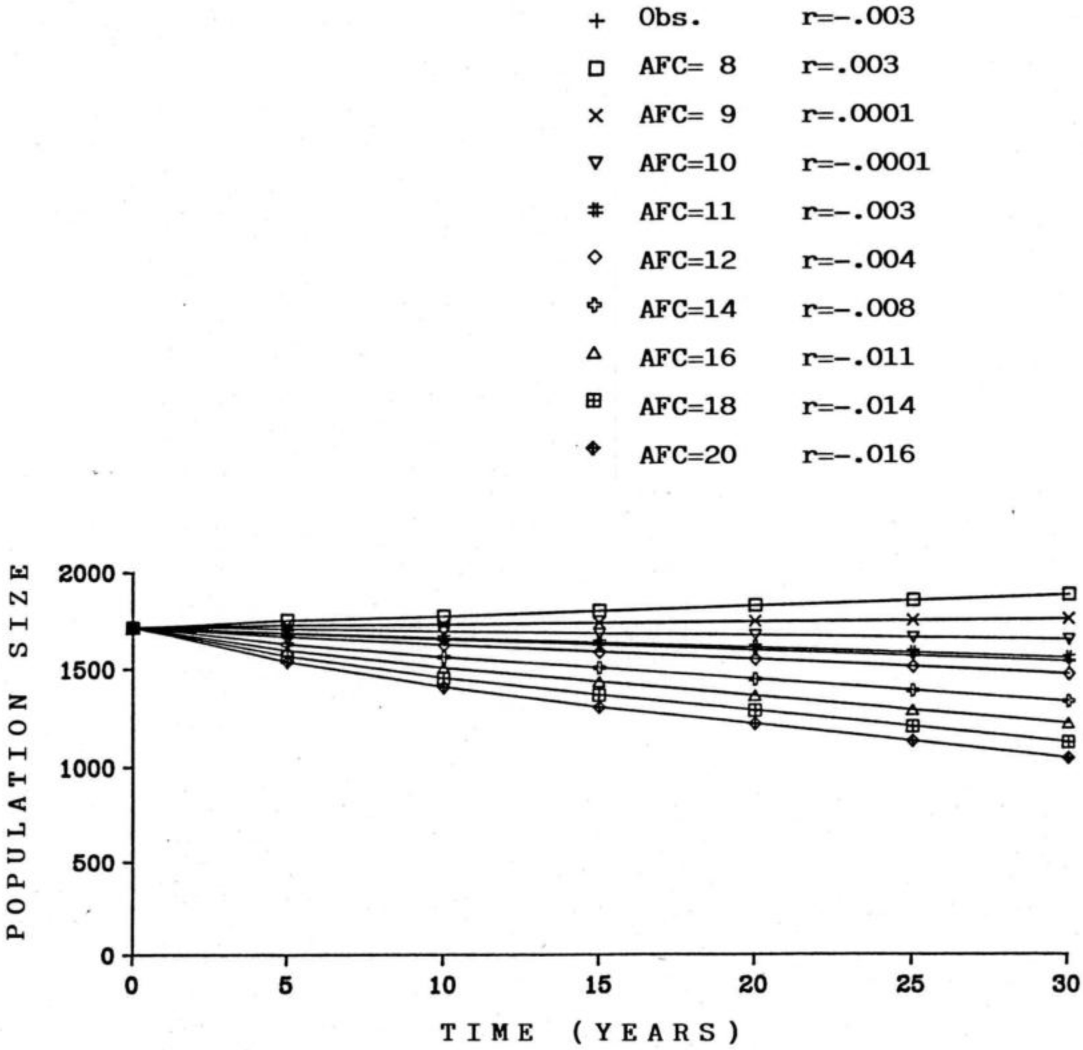


Figure 6.13 Simulated trends of a model elephant population by changes in the age at first conception (AFC).

older females. The final homeostat is the onset of senescence, which is simulated at different ages in Fig. 6.14. These simulations are exaggerated, as senescence usually affects only some females older than about 40 years of age in other populations.

Both MCI and AFC have a pronounced effect on population trend, while the onset of senescence is far less significant as the number of individuals affected is smaller. Changes in any parameter however could have far more or less severe effects on a population with an unstable age structure. The three parameters will also only rarely change individually, as all three are believed to be affected by the same conditions, namely overcrowding stress and nutrition.

Fecundity is also intimately dependent on calf survival, as discussed previously. An increase in the MCI observed in a population cannot necessarily be attributed to delayed breeding through stress or sub-optimal nutrition, but can also occur through an improvement in calf survival. Very short MCI's and a high probability of survival of newborn are unlikely to occur simultaneously in a population. Figure 6.15 illustrates that a very short calving interval in combination with a low pre-natal survival will still result in a population decrease, and likewise in Fig. 6.16, with a low survival of calves in their first year. An estimate of the MCI is therefore meaningless as an indication of the trend in numbers unless calf survival is also measured.

Changes in survival and fecundity

Hanks & McIntosh (1973) evaluated the combined effect of changes in average fecundity and survival by using a life-table type model and hypothetical survival schedules. This work has served as the basis for recent research on elephant dynamics (Croze et al. 1981, Botkin et al. 1981). Hanks & McIntosh's (1973) approach was refined by using observed age frequencies, age-specific fecundity and perhaps more realistic estimates of survival, in a matrix model.

Figure 6.17 illustrates the rates of increase of a model elephant population with a near-stable age structure, at three survival schedules (Table 6.10: ++, 0, --) and weighted mean fecundity rates corresponding to mean calving intervals of 2.1-10 years and ages at first conception of 7-20 years. Variation in the onset of senescence was ignored and all individuals were allowed to breed until the final age class. Table 6.12 presents the same rates of increase illustrated in Fig. 6.17, but in matrix form. The maximum

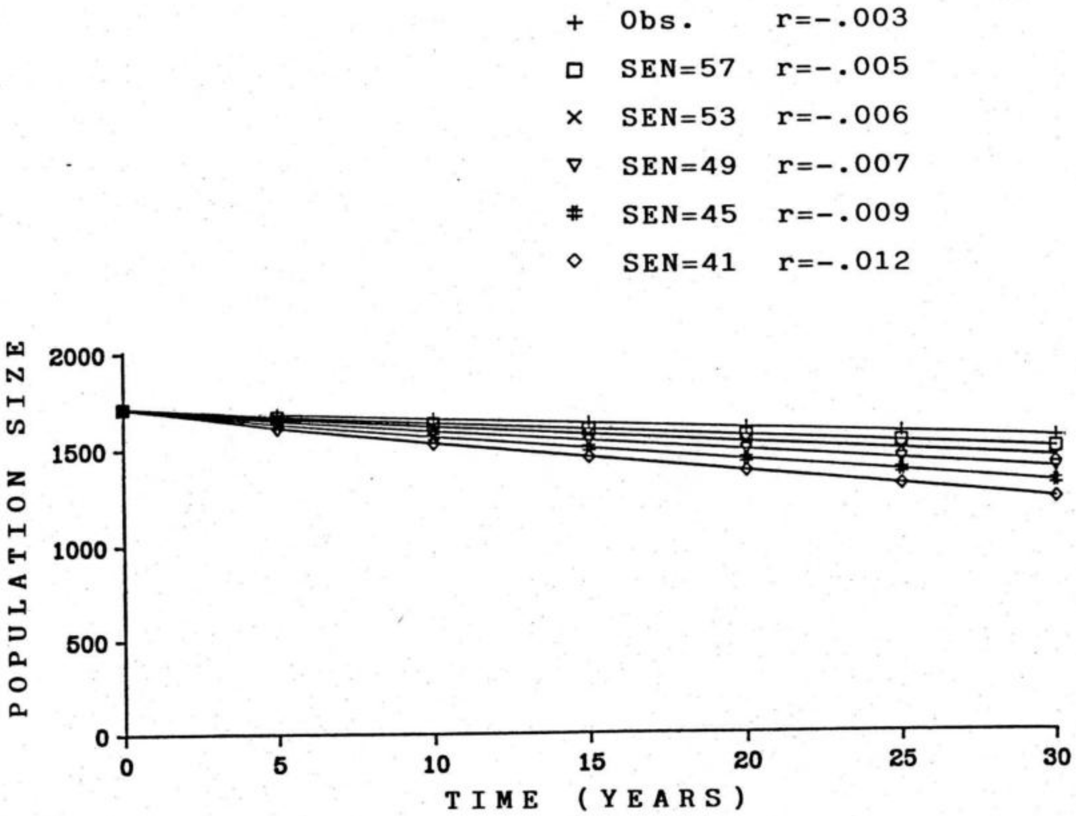


Figure 6.14 Simulated trends of a model elephant population by changes in the onset of senescence (SEN).

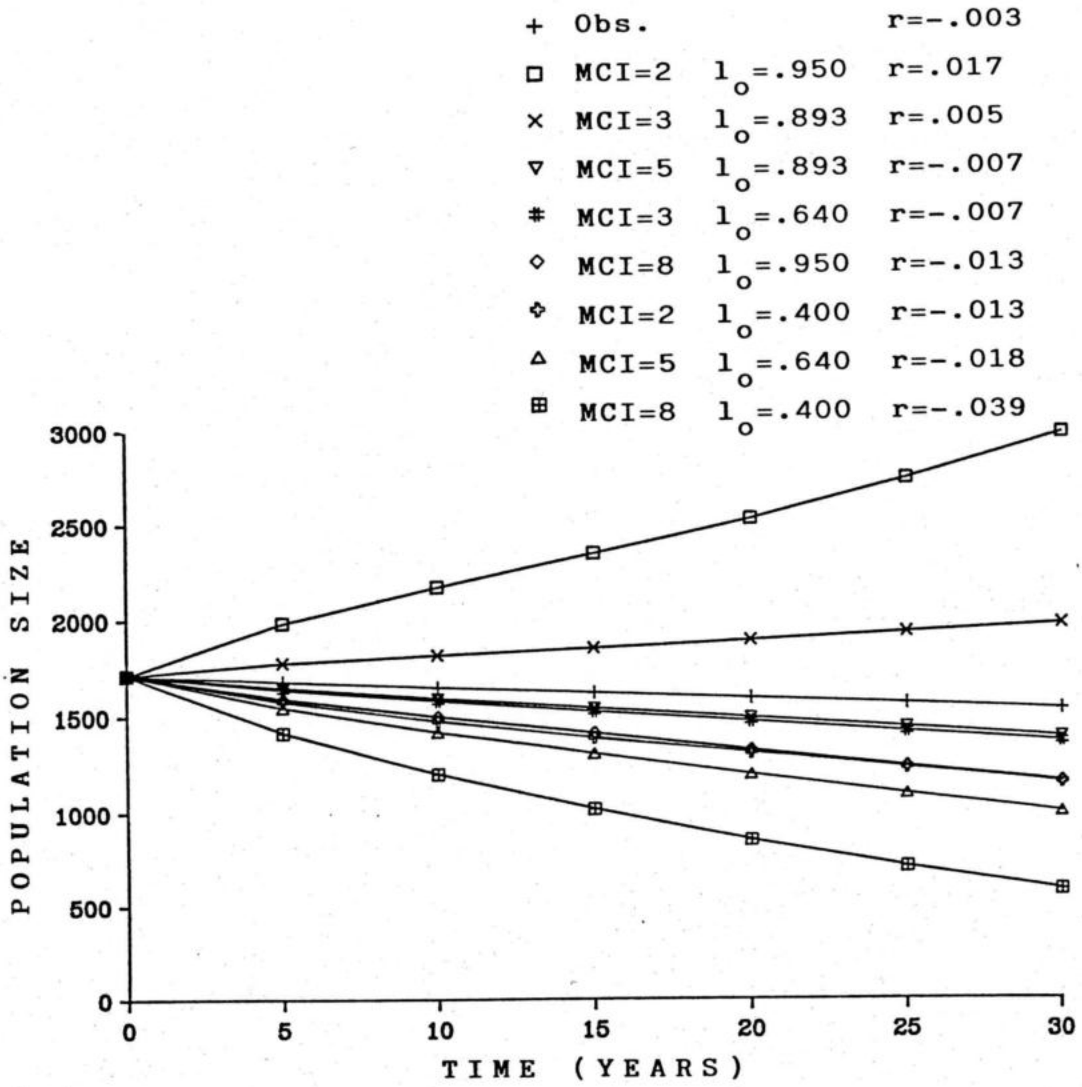


Figure 6.15 Simulated trends of a model elephant population by simultaneous changes in the mean calving interval (MCI) and the survival coefficient (l_o).

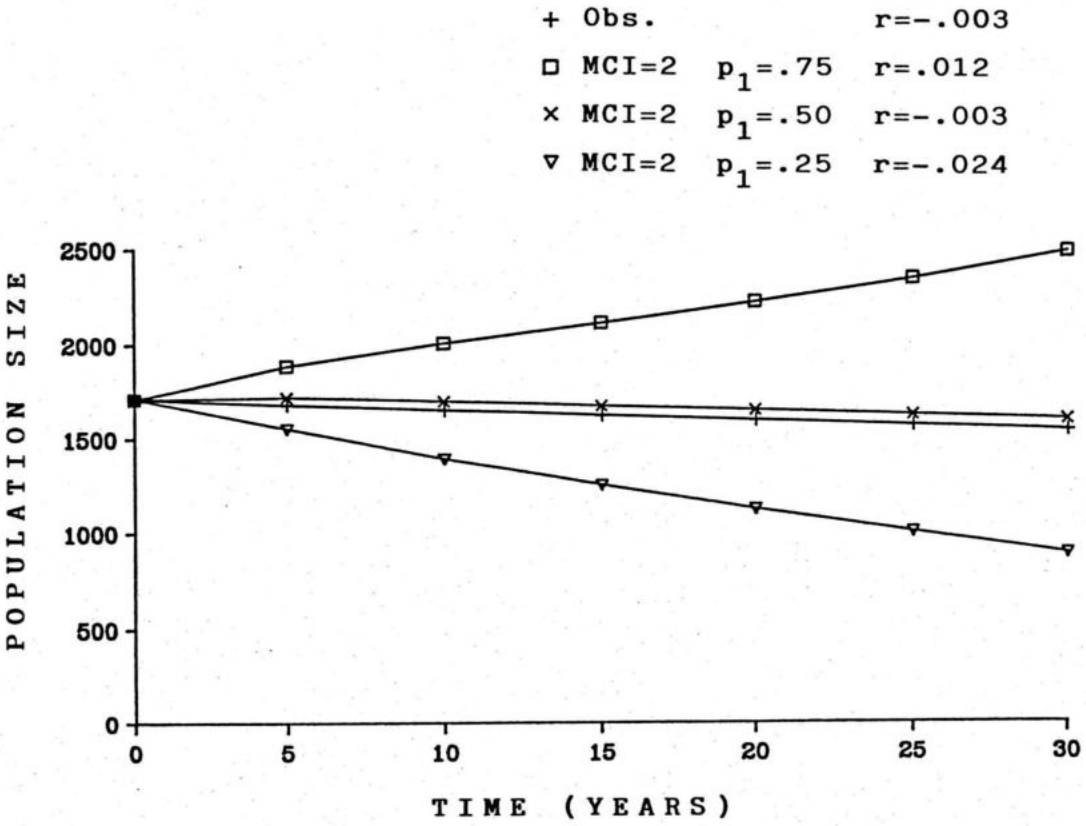


Figure 6.16 Simulated trends of a model elephant population by simultaneous changes in the mean calving interval (MCI) and yearling survival (p_1).

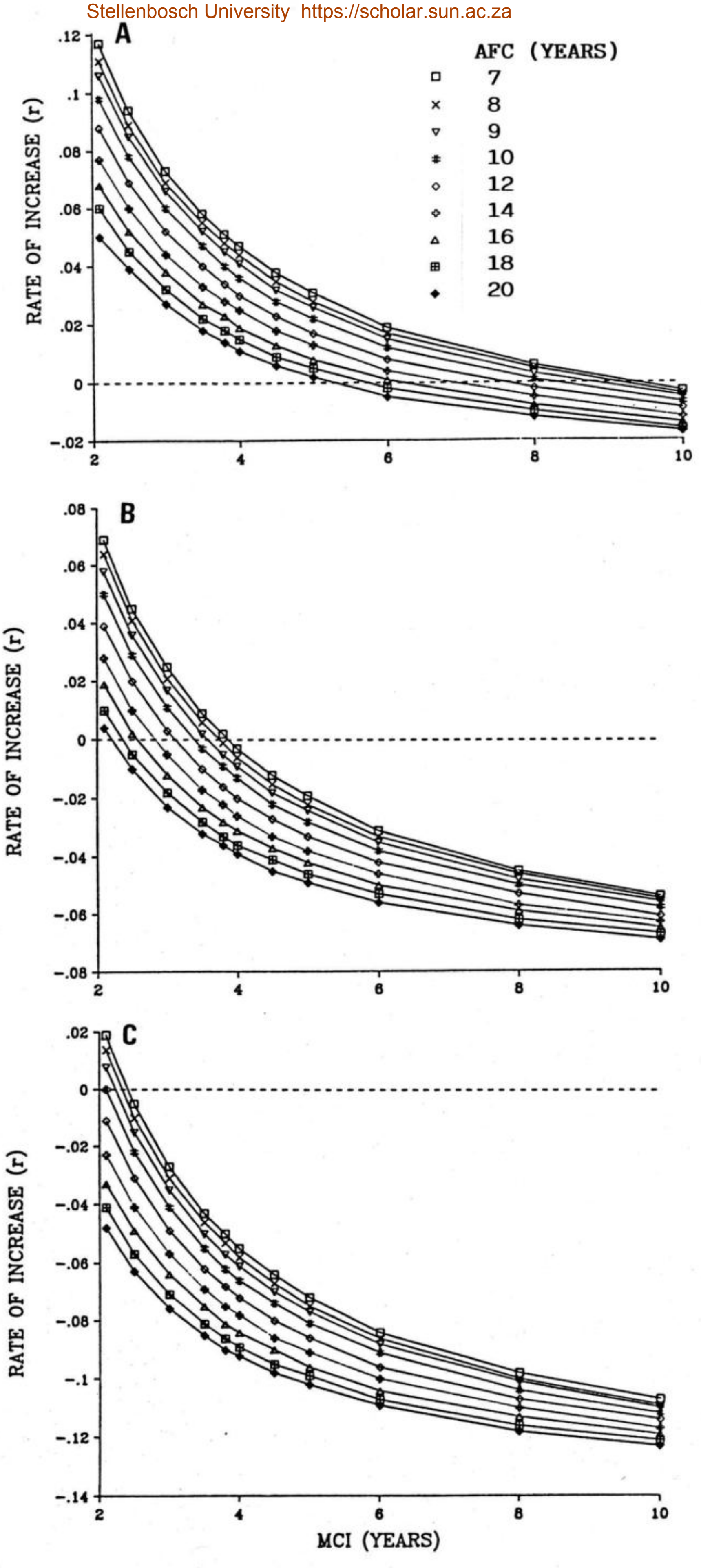


Figure 6.17 Simulated rates of increase of a model elephant population relative to the mean calving interval (MCI), age at first conception (AFC) and three schedules of survival rates (A: "High" survival rate - p_{3-56}=.97, B: "Medium" survival rate - p_{3-56}=.95, C: "Low" survival rate - p_{3-56}=.93).

Table 6.12 Simulated rates of increase of a model elephant population relative to the mean calving interval (MCI), age at first conception (AFC) and three schedules of survival rates. (Values in rectangles and parenthesis are discussed in text).

'High' survival rate (p_{3-56}=.97)

MCI (yrs)	AFC (years)									
	7	8	9	10	11	12	14	16	18	20
2.1	.117	.111	.106	.098	.093	.088	.077	.068	.060	.050
2.5	.094	.089	.085	.078	.073	.069	.060	.052	.045	.039
3	.073	**.069**	**.066**	**.060**	**.056**	**.052**	**.044**	**.038**	**.032**	**.027**
3.5	.058	**.055**	**.052**	**.047**	**.043**	**.040**	**.033**	**.027**	**.022**	**.018**
3.8	.051	**.048**	**.045**	**.040**	**.037**	**.034**	**.028**	**.023**	**.018**	**.014**
4	.047	**.044**	**.041**	**.036**	**.033**	**.030**	**.025**	**.019**	**.015**	**.011**
4.5	.038	**.035**	**.032**	**.028**	**.026**	**.023**	**.018**	**.013**	**.009**	**.006**
5	.031	**.028**	**.026**	**.022**	**.020**	**.017**	**.013**	**.008**	**.005**	**.002**
6	(.019)	**.017**	**.015**	**.012**	**.010**	**.008**	**.004**	**.001**	**-.002**	**-.005**
8	.006	**.005**	**.003**	**.001**	**-.001**	**-.002**	**-.005**	**-.008**	**-.010**	**-.012**
10	-.003	**-.004**	**-.005**	**-.007**	**-.008**	**-.009**	**-.012**	**-.014**	**-.016**	**-.017**

'Medium' survival rate (p_{3-56}=.95)

MCI (yrs)	AFC (years)									
	7	8	9	10	11	12	14	16	18	20
2.1	.069	.064	.058	.050	.045	.039	.028	.019	.010	.004
2.5	.045	.041	.036	.029	.025	.020	.010	.002	-.005	-.010
3	.025	**.021**	**.017**	**.011**	**.007**	**.003**	**-.005**	**-.012**	**-.018**	**-.023**
3.5	.009	**.006**	**.002**	**-.003**	**-.006**	**-.010**	**-.017**	**-.023**	**-.028**	**-.032**
3.8	.002	**-.001**	**-.005**	**-.009**	**-.013**	**-.016**	**-.022**	**-.028**	**-.033**	**-.036**
4	-.003	**-.006**	**-.009**	**-.013**	**-.016**	**-.020**	**-.026**	**-.031**	**-.036**	**-.039**
4.5	-.012	**-.015**	**-.018**	**-.022**	**-.024**	**-.027**	**-.033**	**-.037**	**-.041**	**-.045**
5	(-.019)	**-.022**	**-.024**	**-.028**	**-.031**	**-.033**	**-.038**	**-.042**	**-.046**	**-.049**
6	(-.031)	**(-.033)**	**-.035**	**-.038**	**-.040**	**-.042**	**-.046**	**-.050**	**-.053**	**-.056**
8	(-.045)	**-.046**	**-.048**	**-.050**	**-.052**	**-.053**	**-.057**	**-.059**	**-.062**	**-.064**
10	-.054	**-.055**	**-.056**	**-.058**	**-.059**	**-.061**	**-.063**	**-.065**	**-.067**	**-.069**

'Low' survival rate (p_{3-56}=.93)

MCI (yrs)	AFC (years)									
	7	8	9	10	11	12	14	16	18	20
2.1	.019	.014	.008	.000	.006	.011	.023	.033	.041	.048
2.5	.005	.010	.015	.022	.027	.031	.041	.049	-.057	-.063
3	.027	**.031**	**.035**	**.041**	**.045**	**.049**	**-.057**	**-.064**	**-.071**	**-.076**
3.5	.043	**-.046**	**-.050**	**-.055**	**-.059**	**-.062**	**-.069**	**-.075**	**-.081**	**-.085**
3.8	.050	**-.053**	**-.057**	**-.062**	**-.065**	**-.068**	**-.075**	**-.081**	**-.086**	**-.090**
4	-.055	**-.058**	**-.061**	**-.066**	**-.069**	**-.072**	**-.078**	**-.084**	**-.089**	**-.092**
4.5	-.064	**-.067**	**-.070**	**-.074**	**-.077**	**-.080**	**-.086**	**-.090**	**-.095**	**-.098**
5	-.072	**-.075**	**-.077**	**-.081**	**-.083**	**-.086**	**-.091**	**-.096**	**-.099**	**-.102**
6	(-.084)	**-.086**	**-.088**	**-.091**	**-.093**	**-.096**	**-.100**	**-.104**	**-.107**	**-.109**
8	-.098	**-.100**	**-.101**	**-.104**	**-.105**	**-.107**	**-.110**	**-.113**	**-.116**	**-.118**
10	-.107	**-.109**	**-.110**	**-.112**	**-.113**	**-.114**	**-.117**	**-.119**	**-.121**	**-.123**

rate of increase achieved by the model population was r=.117 but an MCI and AFC below three and eight years respectively are unlikely to be maintained in a real population for even a moderate period. If all values outside the rectangles in Table 6.12 are thus regarded as instantaneous growth rates likely to be achieved only after a major perturbation, the maximum rate of increase that can be expected to occur is r=.069. This value is practically the same as the maximum observed rate of increase recorded in Addo Elephant N.P. by Hall-Martin (1980). The maximum rate of increase achieved by the model population of Hanks & McIntosh (1973) was r=.047, compared to r=.052 in Table 6.12 at similar values for the MCI and AFC (3 and 12 years respectively).The main conclusion reached by Hanks & McIntosh (1973) that the survival rate is the most important determinant of the rate of increase of elephant populations, is supported by the simulations in Table 6.12 and Fig. 6.17. This is evident from the similarity between any two adjacent values in any of the three matrices in Table 6.12, compared to the difference between corresponding values in the three matrices, eg. the values in parenthesis in Table 6.12.

One would expect that simultaneous changes should occur in the survival and fecundity pattern, as conditions favouring an improvement in the one would likely have the same effect on the other. Changes in the same direction in both parameters might not, however, occur at the same rate. During increasingly adverse conditions, elephants are likely to first delay and eventually stop breeding before a reduction in adult survival is noticeable. It is not clear from other studies on elephants and the Etosha N.P. population if a direct inverse relationship between fecundity and survival should ever occur, for example the combination of high adult survival probabilities and poor fecundity, as in Fig. 6.18.

Periodic changes in survival and fecundity

Once the results of changes in either parameter are established, it is simple enough to simulate periodic changes in a single parameter, and concordant or disparate changes in both parameters. The origin and existence of periodicity remain hypothetical, particularly in Etosha N.P. where the clearest of periodicities in other areas, namely fluctuations in rainfall, seem to be more variable. In East Africa, rainfall patterns have currently very little relevance to changes in the elephant population compared to

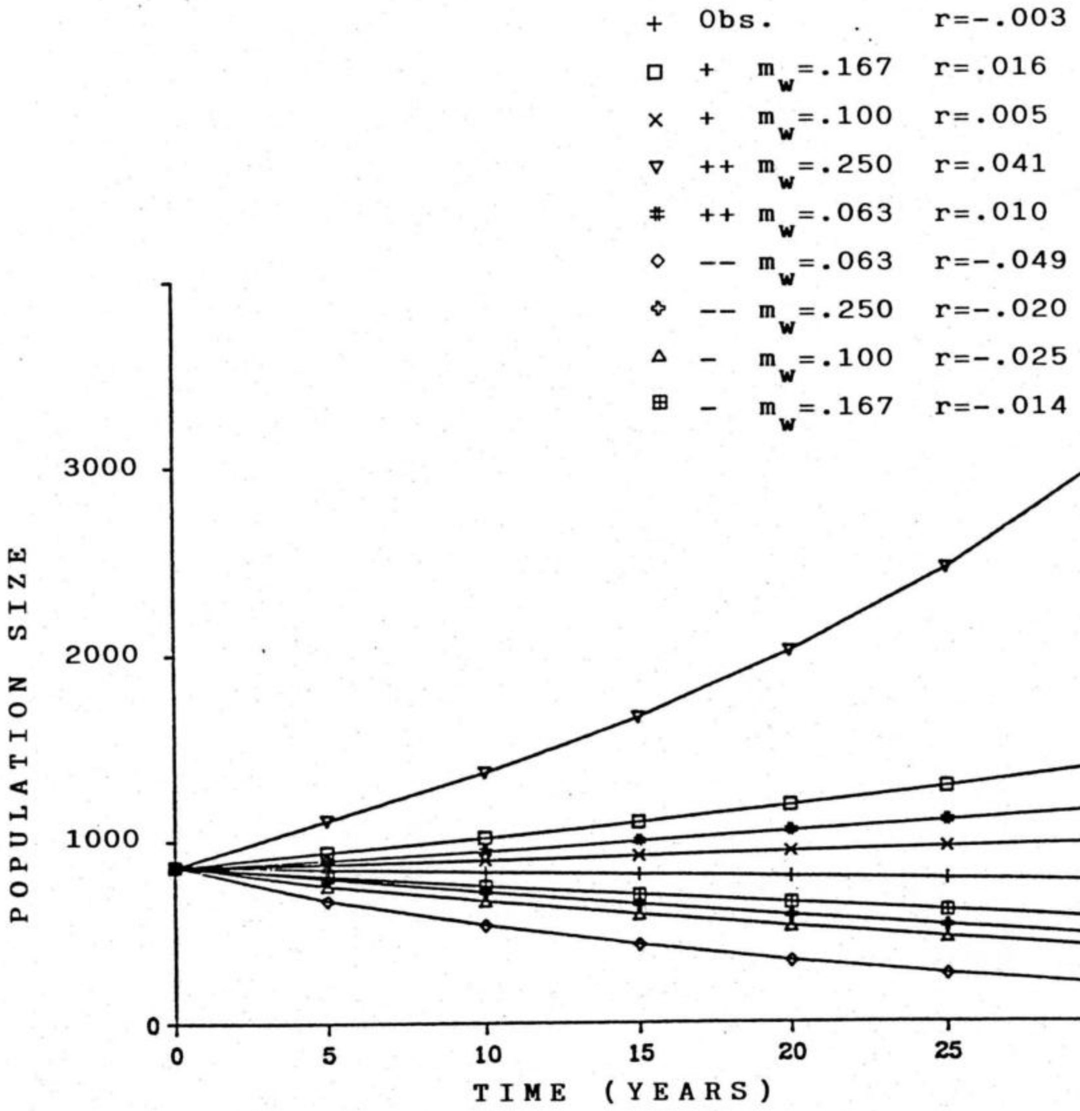


Figure 6.18 Simulated trends of a model elephant population due to synergistic and compensatory changes in fecundity (m_x) and survival (p_x).

socio-economic pressures which may be changing predictably or unpredictably (such as the price and demand for ivory in the rest of the world, inflation, political stability, corruption, access to automatic rifles) (Parker 1983, Martin 1986, Douglas-Hamilton 1987).

Although an inverse relationship between the number of elephants in Etosha N.P. and rainfall in the park can be predicted over the short-term, other events might finally determine the trend in elephant abundance. Such events might be human orientated, such as forced fencing of the northern boundary, poaching or harvesting, or natural, such as occasional severe frosts, fires, predation and disease.

A population trend can be modified by cyclic changes in survival or fecundity, or both. Analogous simulations were done by Croze et al. (1981) although their survival and fecundity schedules were unrealistic, and not referrable to a particular population. Their simulations were also based on unsexed age frequencies of elephants in Tsavo N.P. by Leuthold (1976) although the model treats all individuals as females. Their simulations are repeated in Fig. 6.19 using female age frequencies, where the survival of 1-4 year-olds and the onset of puberty are the only variables, are changed by the same factor and by using a sine function to generate a periodicity of about 12 years in an increasing (l_0=1) and decreasing (l_0=.82) population. This simulation confirms that changes in survival of juveniles potentially have a stronger effect on the population trend than changes in fecundity, in both an increasing or decreasing phase. Changes in first year survival alone are sufficient to generate a similar pattern, as in Fig. 6.20, although the amplitude of deviation is less, and increasingly so with a 1 and 2 year time lag between changes in survival and fecundity (Figs. 6.21 and 6.22).

Breeding synchrony

Where adverse conditions result in poor survival of calves, breeding females might become synchronized to such an extent that a peak in the age distribution of a population is produced. A repetition of this pattern might cause several such peaks interspersed by troughs in the age structure corresponding to years of poor calf survival or few births. This pattern can be created by periodic changes in calf survival only, as in Fig. 6.23 but are likely to cause temporal changes in fecundity as well. In this instance it would

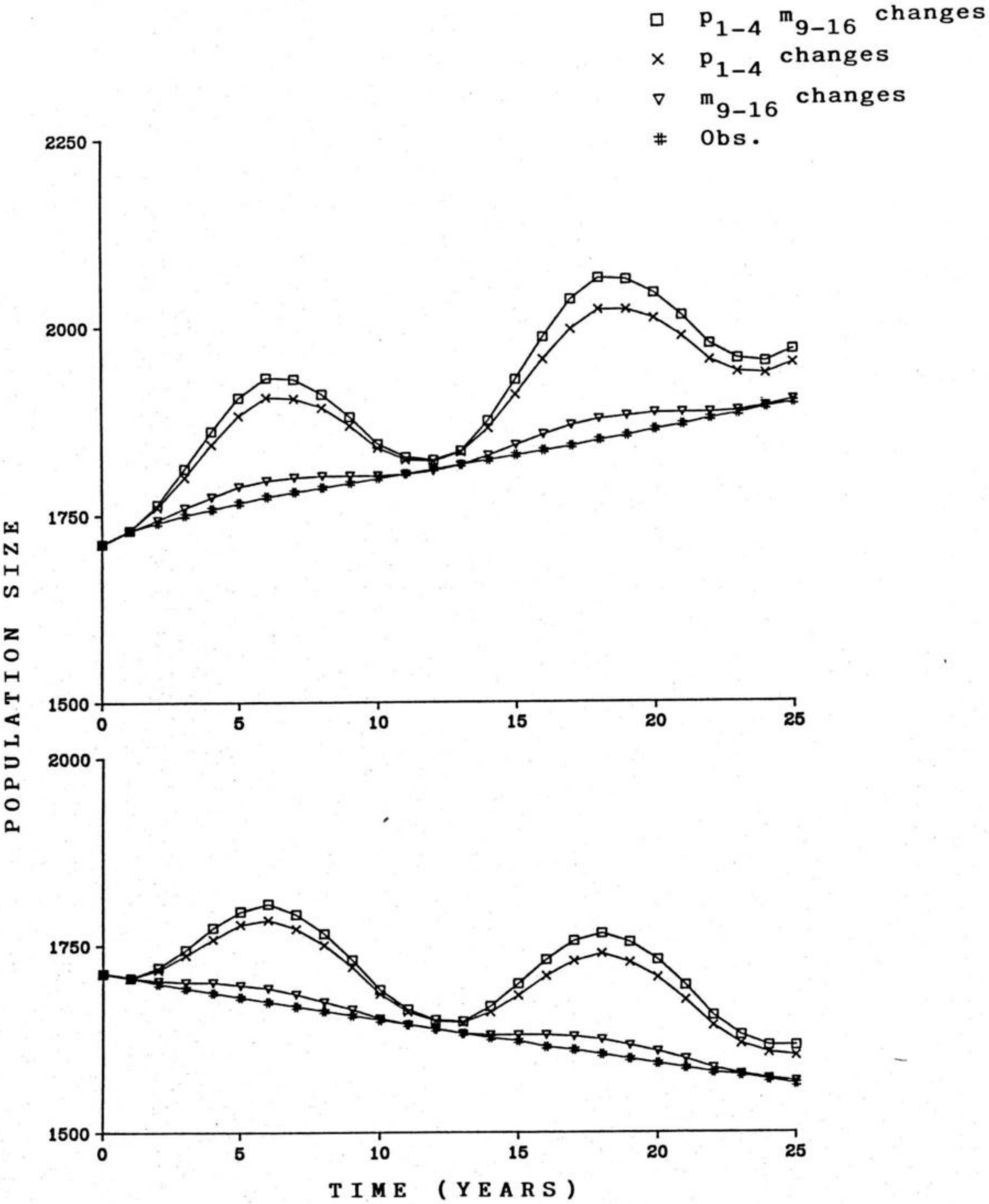


Figure 6.19 Simulated cycles in population increase of a model elephant population by proportional changes in the survival of 1-4 year-old elephants and the fecundity of 9-16 year-old individuals (thus AFC) only.

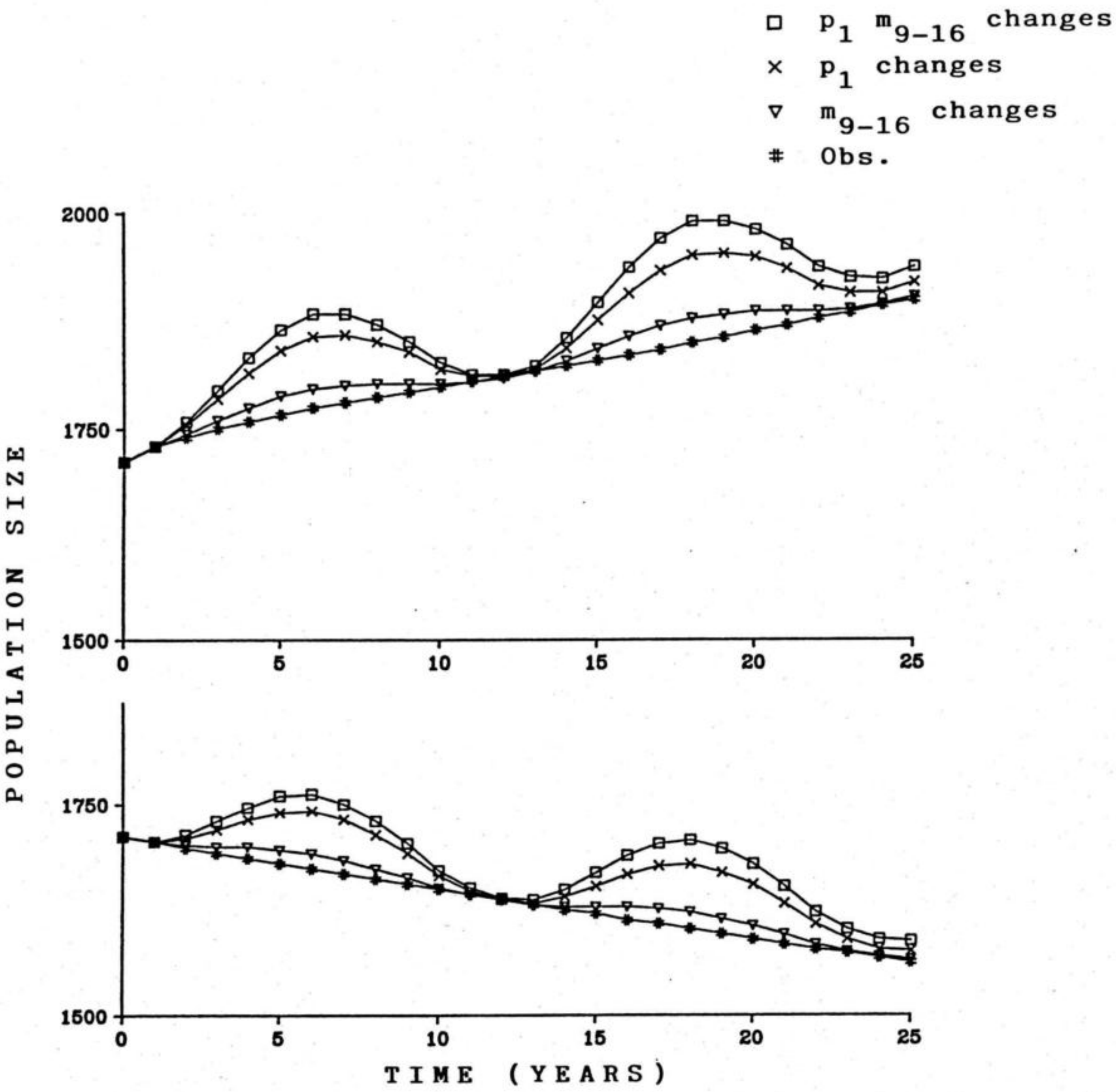


Figure 6.20 Simulated cycles in population increase of a model elephant population by proportional changes in the survival of yearlings and the age at first conception only.

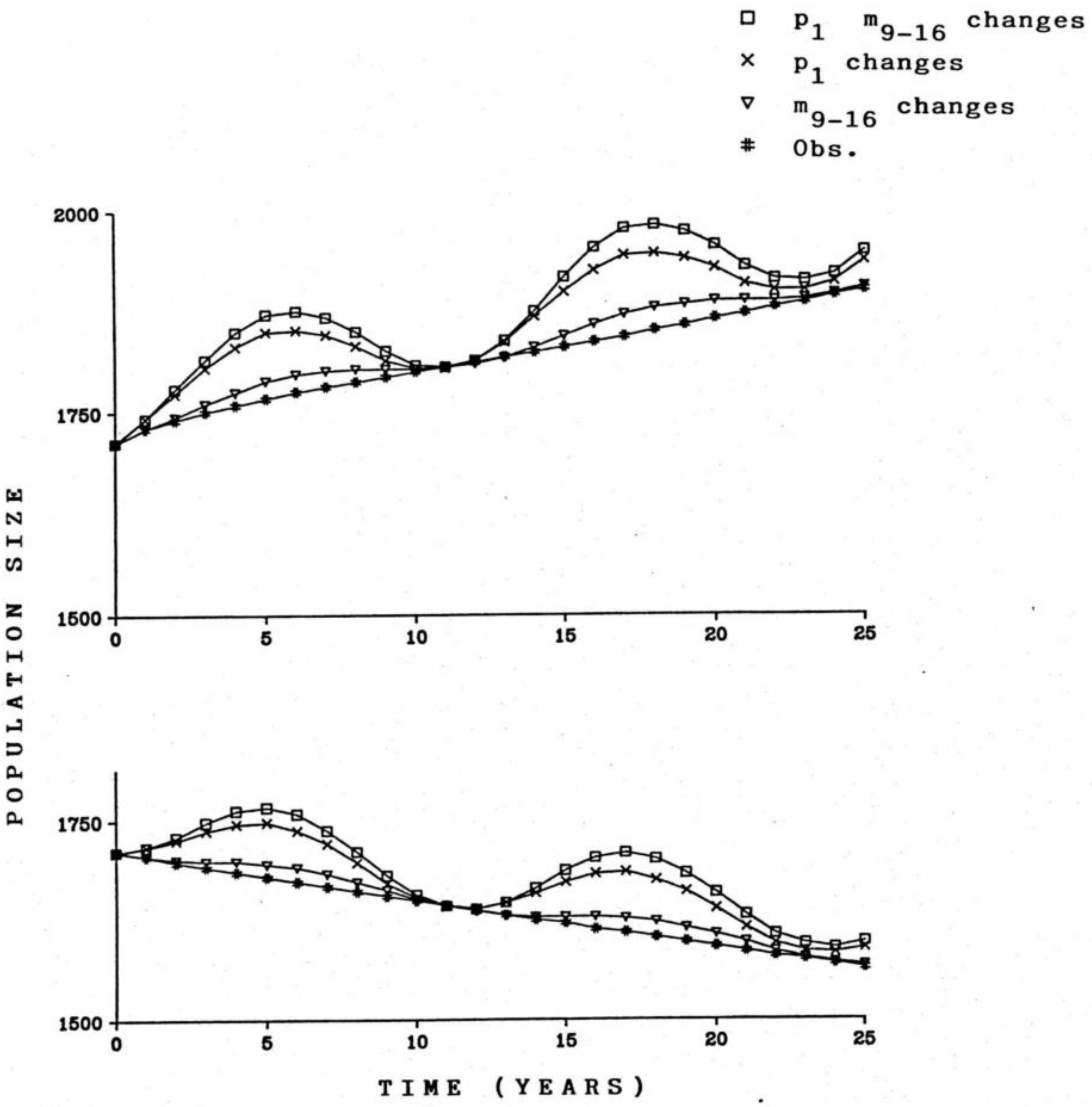


Figure 6.21 Simulated cycles in population increase of a model elephant population by proportional changes in the survival of yearlings and the age at first conception only, but with a one year time lag between changes in survival and fecundity.

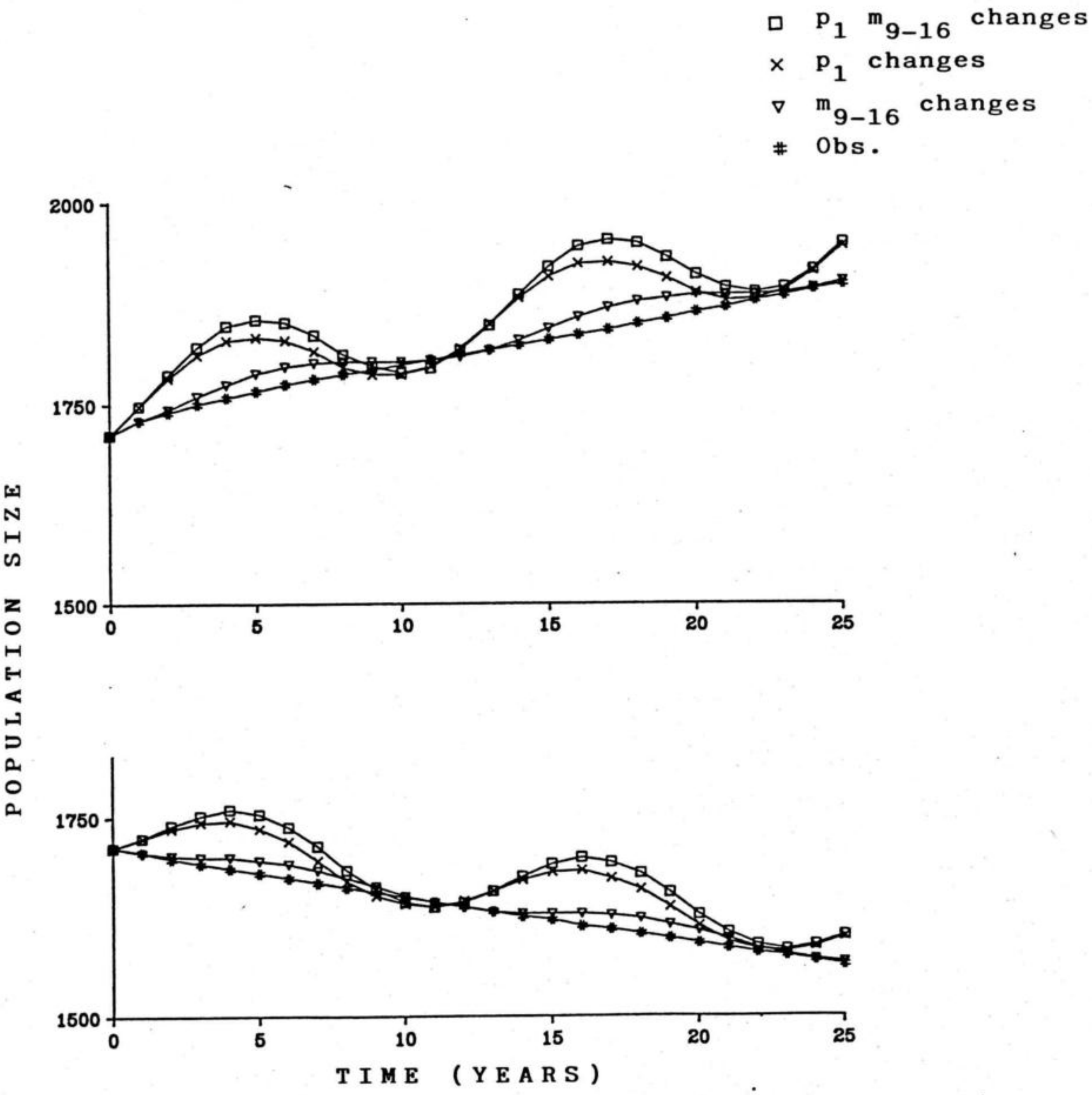


Figure 6.22 Simulated cycles in population increase of a model elephant population by proportional changes in the survival of yearlings and the age at first conception only, but with a two year time lag between changes in survival and fecundity.

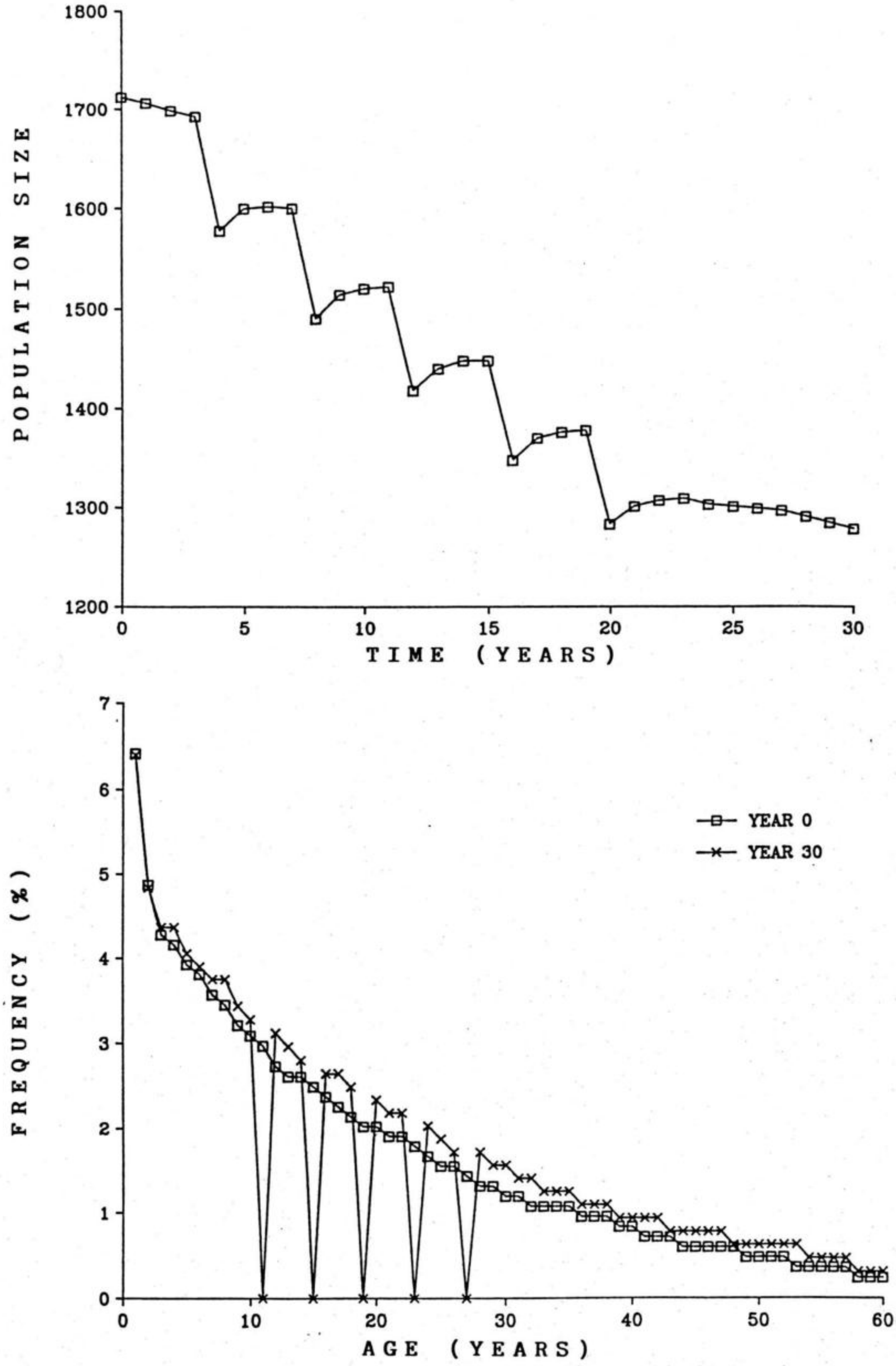


Figure 6.23 Simulated trends in population size and peaks in the age distribution resulting from periodic changes in yearling survival in a model elephant population.

maximum fecundity values to the model, as in Fig. 6.24, for the first year of conceptions after a period of high calf mortality. Only after two episodes of synchronized births are age structures significantly different (χ^2_{59}=79.4, p>.05; year 3 and 15) from the starting or ending age structure (Fig. 6.23). Compensatory fecundity as applied in Fig. 6.24, after two years of zero calf survival, is not sufficient to change the outcome of the modelled population trend, but maintains the population on the same original course. Age distributions, however, are significantly different after only one perturbation (χ^2_{59}=81.3, p>.05; year 3 and 6).

Drought and migration

The onset of a drought might be characterized by high juvenile mortality, lower survival of senior adults, followed by a reduction in fecundity and an overall reduction in survival. Figure 6.25 illustrates such a pattern in a decreasing population. In this simulation, age structures remained stable, which might imply that drought effects may be less disturbing to the population than I presumed.

One alternative strategy is to evade a drought, which is done by the regional population through movements. This might allow the population to escape intact or to delay drought responses when the drought is local rather than regional. Drastic changes in the population trend can be achieved by dispersal in the Etosha N.P. part of the population range. Other populations may also enter Etosha N.P. during a drought, as possibly occurred in the 1980-1983 drought, when elephants from Angola and possibly Zambia or Botswana could have entered the park. From Fig. 6.26 it is clear that as long as migrations are allowed to occur, hopefully ad infinitum, this feature will have the greatest effect on local trends in the abundance of elephants in Etosha N.P.

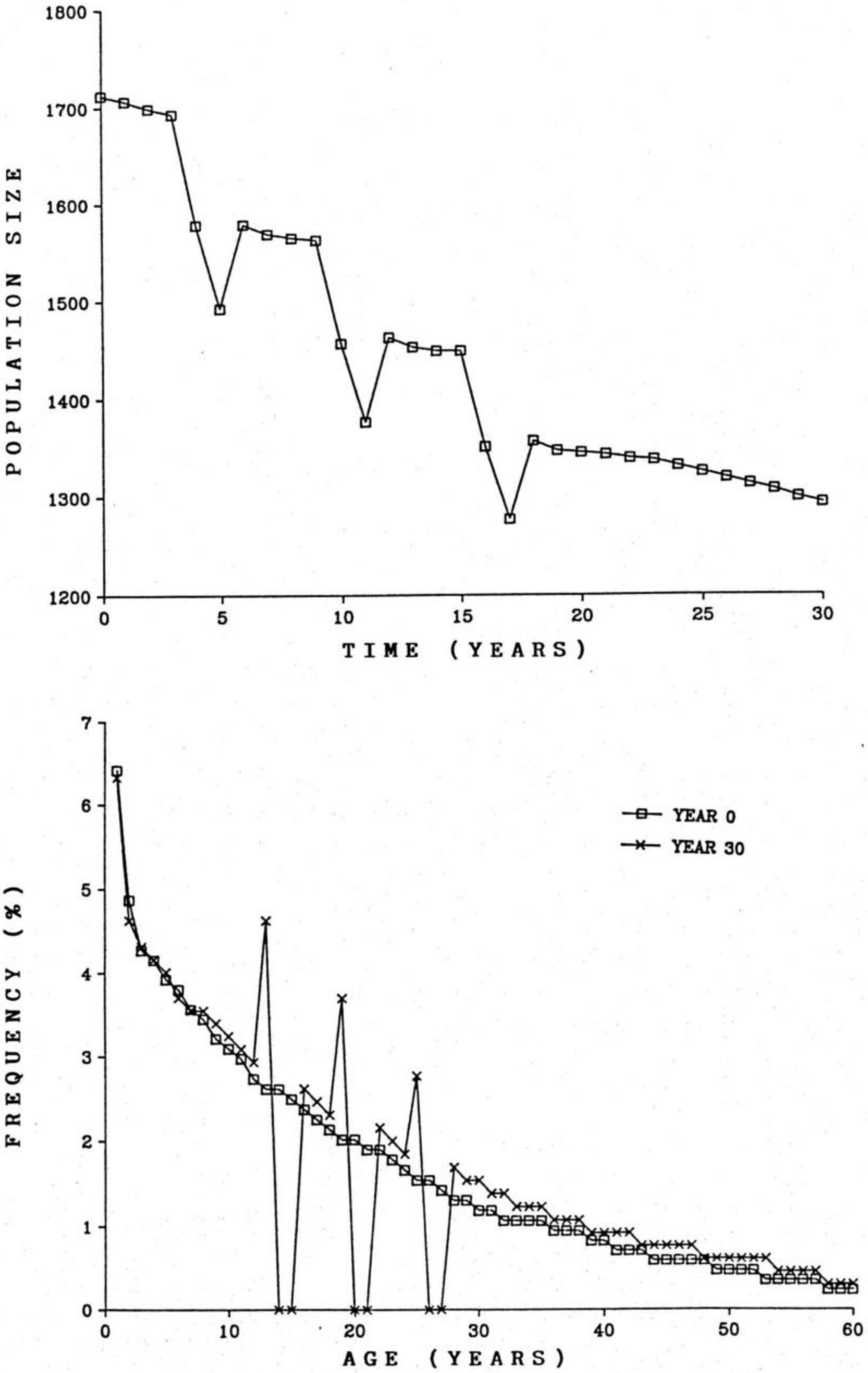


Figure 6.24 Simulated trends in population size and peaks in the age distribution resulting from periodic changes in yearling survival followed by compensatory changes in fecundity, in a model elephant population.

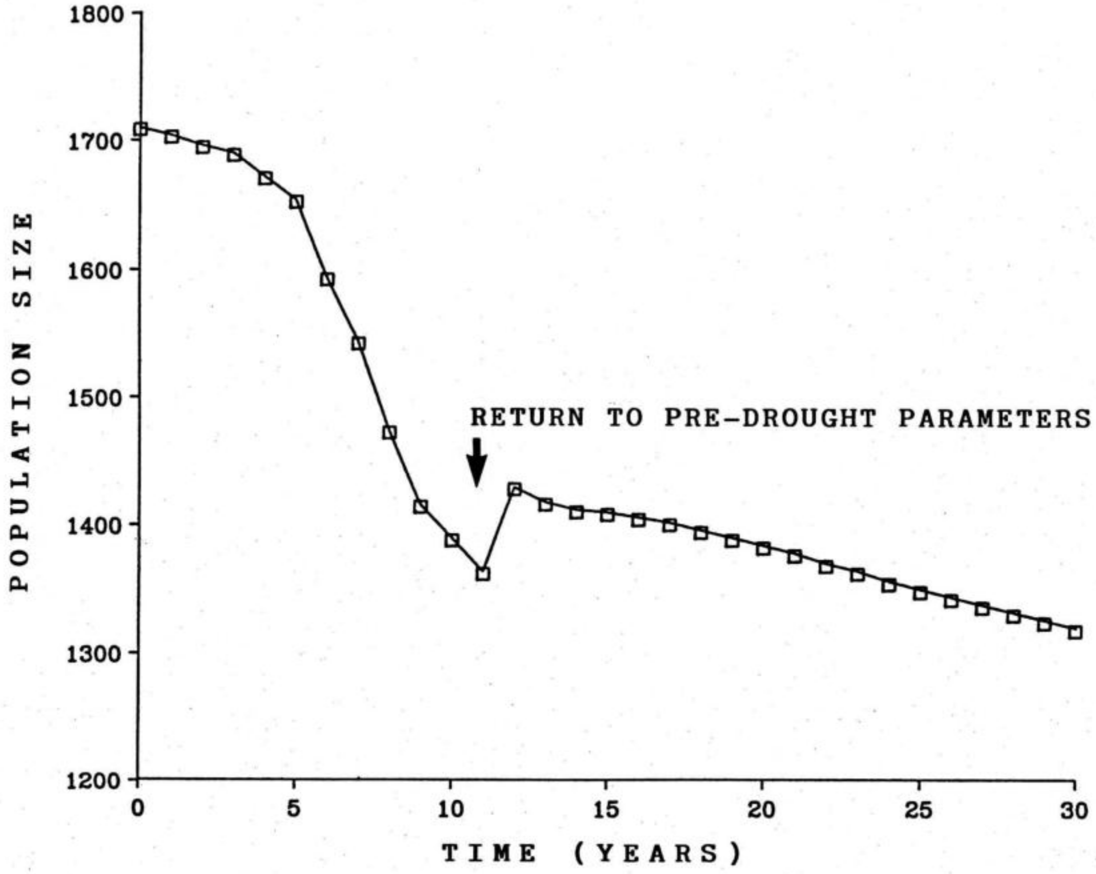


Figure 6.25 Simulated trend during a drought with sequential changes in juvenile survival, fecundity and adult survival for a model population.

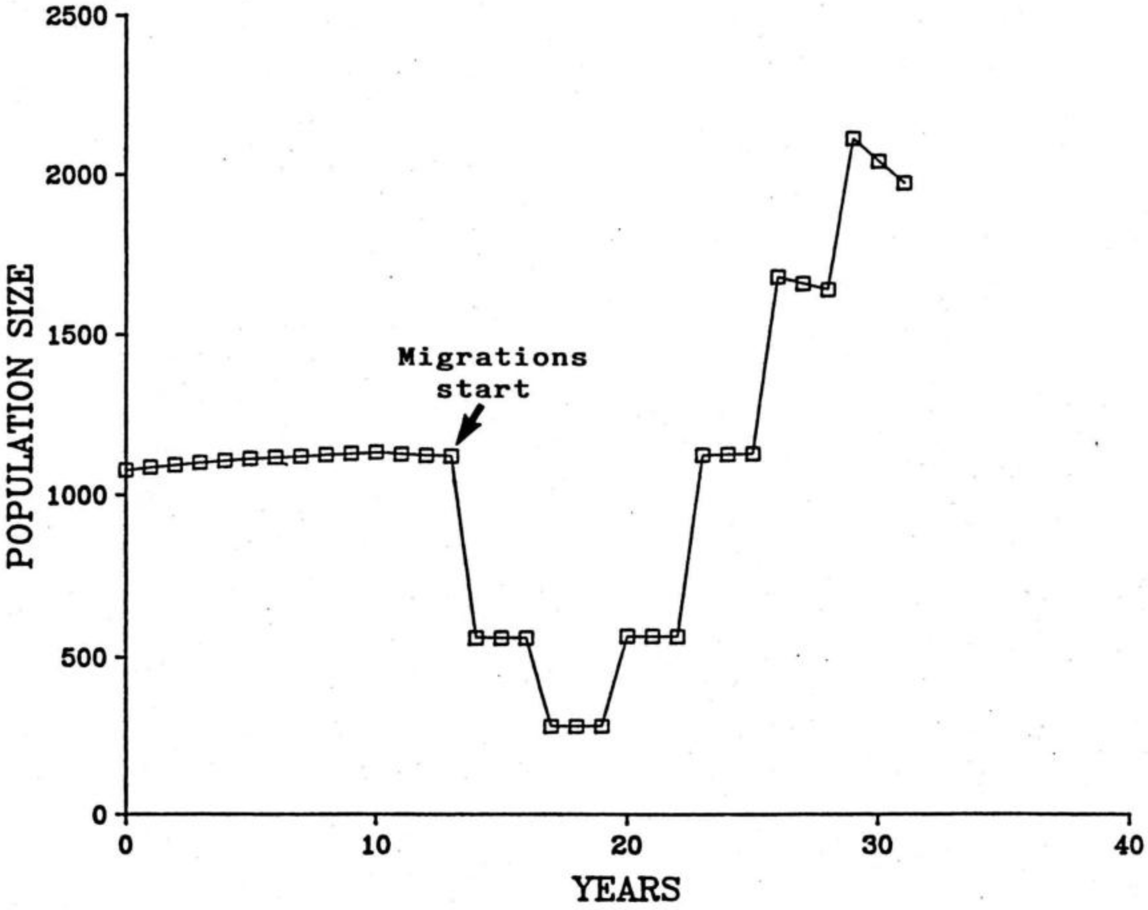


Figure 6.26 Simulated population trends by subjecting a model elephant population to representative gains and losses due to migration only.

CONCLUSIONS

The most important features of the elephant population in Etosha N.P. were that:

1. Recolonization of the park occurred in the early 1950's, after an absence of 70 years. The number of elephants in the park increased steadily until the late 1970's, followed by a period of rapid increase from 1900 to 2800 in four years (1979-1983). This phase of increase coincided with a severe regional drought. From 1983 to 1986, the number of elephants in the park declined from 2800 to about 1200 (a total of 570 elephants were culled), but increased again in 1987 to over 2000.

2. The age structure of the population changed little from before the drought to after it, or from the phase of increase to the period of decline in elephant abundance in Etosha N.P. Culling and epidemic anthrax removed near-representative segments from the population, which would not have affected the age structure (as determined by the resolution of present age estimation methods). The problematic peaks in age distributions of other populations were less noticeable in the Etosha N.P. elephants.

3. The age at first conception, incidence of reproductive senescence, and mean calving intervals were among the lowest recorded for all elephant populations studied. The Etosha N.P. elephants showed all the features of accelerated breeding from at least 1983 to 1985, and no evidence of density feedback on the rate of reproduction. Birth intervals were synchronized within herds, especially in 1985, and conceptions were synchronized with the wet season.

4. Mortality schedules in 1983 and 1985 were similar, and typical of mammalian mortality patterns. Age-specific mortality rates were higher than in other populations, possibly due to the incidence of anthrax in Etosha N.P. Anthrax affects all age classes, whereas other elephant populations are usually free of mortality factors operating in the middle age range, unless indiscriminate poaching occurs. Early calf mortality seems to be variable from year to year, and was approximately 40% and 20% respectively in 1983 and 1985 in Etosha N.P. Calf mortality might reduce calving intervals and account for conceptions outside the peak period. No mass-mortality of elephants occurred after 1982, apart from the two culls in Etosha N.P.

The series of population estimates obtained in Etosha N.P. seems to indicate that the population erupted from 1979 to 1983, and crashed from 1983 to 1986. An alternative explanation is that elephants moved into the park during the drought, and left again once conditions had improved. Support for the latter explanation is obtained from:

1. The observed rate of increase from 1979 to 1983 (r=.09) or 1982 to 1983 (r=.24) exceeded the maximum rate of increase found in other populations. Inaccurate population estimates could, however, be responsible for the high rate of increase.

2. Age structures determined from 1983 to 1987 or over the period of decline, did not change markedly from year to year. This only suggests that age-specific mortality rates remained relatively constant. The culling of 570 elephants would not have changed the age structure, but could also not account for the overall reduction in population size from 2800 in 1983 to 700 in 1985. If the age structures based on ground observations are used, accepting that they were systematically biased, population age structure appeared to have been relatively stable from at least 1977 to 1987. Rapid population increase through breeding would probably have altered the age structure, if it occurred.

3. The survival-fecundity rates of increase, as determined in 1983 and 1985 were both negative, while a positive r_s would have been expected to occur at the height of any eruption in 1983. Matrix modelling furthermore indicated that the elephant population would have declined in 1983 and 1985 by 0.5 to 1.0 per cent per year. The actual rate of decline was faster, eg. 44% from 1984 to 1985.

4. The decline in the number of elephants in Etosha N.P. from 1983 to 1986 could not have been caused by mortalities only, or the subsequent increase in 1987 would not have occurred. At least 1000 elephants died in Etosha N.P. from 1981 to 1987 (including 570 culled, 200 in the 1981-1982 anthrax epidemic), but at least 900 were born in the same period (based on the frequency occurrence of yearling calves in aerial surveys).

5. Seasonal variation in elephant abundance in Etosha N.P. determined by aerial censuses, could not be shown to be the result of inadequate census methods. A preliminary study on elephant movements showed that radio-collared elephants do leave the park, and some groups have only returned after two years. The best evidence for

large-scale movements of elephants in and out of the park is, however, the condition of the approximately 450 km fence on the northern and western boundary of the park. An estimated minimum of 1000 elephant breaks have to be repaired every year.

My interpretation of the available data is that there is no discrete elephant population in Etosha N.P. other than a seasonally and annually variable fraction of the regional elephant population whose distribution and size are unknown. Human population increases, the acquisition of fire-arms by local inhabitants, escalating civil-military disturbance, human settlement of increasing portions of elephant distribution range, and in some cases the exclusion of elephants from key dry-season water sources, have caused a regional shift in elephant distribution in north-western SWA/Namibia. Over three decades, more and more elephants entered Etosha N.P. in the dry season, and more of these remained in the park during the wet season, until nearly the entire regional population was present in the park in 1983. Etosha N.P. has probably become the most important dry season part of the distribution of an elephant population extending from the park to Ovambo, Kavango and the Kaokoveld.

Modelling population response in terms of fecundity and survival has shown that the regional elephant population, if the samples taken in Etosha N.P. are representative of this population, has declined since at least 1985 not only as the result of culling or epidemic anthrax, but because of the current rates of survival and fecundity operating in the population. The population probably has not experienced a prolonged phase of rapid increase for at least a decade, and appears to have been surprisingly stable in terms of the age structure. Small changes in the survival rate of yearling calves, can however cause sudden changes in the calculated rate of increase. Density dependent regulation of elephant population size by reproductive homeostasis could not be detected, and possible changes in reproductive parameters in response to improved environmental conditions might occur irrespective of elephant density. If the mortality rate of yearling calves is reduced in a post-drought situation, a population increase can be expected even if mean calving intervals increase.

The abundance of elephants in Etosha N.P. is expected to fluctuate as long as elephants are allowed to move in and out of the park in response to rainfall and human activities. The dry season distribution of elephants in northern SWA/Namibia can be expected to be reduced further if present trends in human land use continue. The ultimate limiting factor, as throughout the country, is water, particularly during the dry season. There are nevertheless large areas in Ovambo, Kavango and the Kaokoveld that are suitable for wet season dispersals by elephants. Options for future management of an "open" elephant population are discussed in Appendix 5.

SUMMARY

The rise and fall of the elephant population in Etosha N.P. superficially resembles a full colonization sequence, culminating in the over-shooting of the carrying capacity during the Trans-African drought of the eighties. The period of rapid population increase was defined by successive aerial censuses, and was the prime motivation for this study. Subsequent censuses revealed a population decline contrary to local predictions. Major changes in the vegetation due to an overpopulation of elephants did not occur, and no elephants died of starvation in the drought. It was therefore essential to validate the description of population trends using aerial censuses. Limited experimentation was possible, but census design incorporated a method of testing accuracy and precision of estimates. Random combinations of transect width and census altitude revealed that no significant trends in census bias were present within the range of these parameters used. Further confirmation was obtained from the distribution of numerical estimates of elephants at increasing distances away from the aircraft. No evidence could therefore be found to indicate that the population decline as observed is an artifact of estimation procedures.

There is no evidence that elephants in Etosha N.P. are isolated from elephants in parts of the Kaokoland, Ovambo and Kavango, and all belong to one regional population. The movements of elephants in and out of the park in response to rainfall, available surface water and disturbance by humans are regarded as the prime causes of seasonal and annual variation in elephant abundance in the Etosha N.P.

The series of six elephant censuses done in this study were also used to investigate alternative and less expensive census methods. Random transect samples of not less than 30% sampling intensity would yield acceptable levels of precision and accuracy in the estimate of population size.

The age structure of elephant populations, along with population size, are crucial parameters in demography. The traditional age estimation method of Laws (1966) has been criticized, in favour of the method of Sikes (1968). Variation in the number of molar laminae and inconsistencies regarding the foramen mentale as reference point in the mandible against which molar progression is measured, makes the latter method no less inaccurate. Molar remnants are lost from the mandibles of Etosha N.P. elephants earlier than in other populations, which complicates the use of Sikes' (1968) method further.

Age distributions derived from two culled samples in Etosha N.P. and using the age schedule of Laws (1966) and the modified version in Laws (1967a), differ from those of other populations by the absence of consistent irregularities. Such peaks and troughs in age frequency distributions were described as cycles of recruitment in response to rainfall, but were shown to coincide with age classes where final molar fragments are lost from the mandible. Considerable variation in the actual time of loss of molar remnants occur in the Etosha N.P. population, as shown by the absence of molars over the foramen mentale reference point and the condition of the alveolar socket. The actual loss of the final fragment is considered to be too variable to be a reliable measure of increasing age. Comparisons between posterior and anterior portions of the occlusal surface reveal that eruption is more regular than attrition, and age distributions derived from classification into age groups based on the appearance of the posterior molar are more even than those based on anterior molars. Laws' (1966) method is therefore upheld with minor modifications proposed by Jachmann (1988).

The age structure of elephants in Etosha N.P. was similar before and after the drought, as based on the classification of elephants into age groups in ground surveys since 1977. The relative stability of population age structure from at least 1983 to 1987 was confirmed by age distributions derived from two culled samples and aerial photogrammetrical surveys.

The Etosha N.P. elephants show seasonal reproduction as elsewhere in southern Africa, with 80% of births occurring from November to March, which includes the rainy season. The bulk of conceptions occur at the time of aggregation of breeding herds prior to dispersal into their wet season range. Foetal growth rates were described, but neither Perry's (1953) nor Craig's (1984) formulae could be proved correct or wrong. Significant differences in the apparent rate of foetal growth occurred between the 1983 and 1985 samples of foetuses, regardless of which formula is used. The leaner appearance of foetuses in 1983 indicate relative foetal starvation, probably as the result of the extreme drought.

Female fecundity in Etosha N.P. is higher than elsewhere, as shown by the comparatively early age at first conception (10-12 years), short calving intervals (3.8 years), absence of reproductive senescence, and the incidence of twins (4.7%). Estimates of the mean calving interval by using the rate of accumulation of placental scars are lower (2.1-2.5

years) than estimates based on the incidence of pregnancy and lactation in a sample of parous females. This discrepancy, as well as the incidence of non-lactating multiparous pregnant females indicate early calf mortality and compensatory breeding. Estimates of calving intervals without some measure of survival of those calves produced are confusing, as also shown by Moss (1983).

Calf mortality might synchronize the majority of breeding females to start in the same reproductive phase after a major perturbation such as a drought. Calves of the same age were recorded more frequently within individual herds in Etosha N.P., than if breeding was random between individual cows. This is regarded as due to the probability of access to receptive cows by bulls in musth, and suggests a synchronization effect by bulls on cows in the herd.

An analysis of all recorded mortalities of elephants showed that anthrax is the most important cause of death, followed by the shooting of boundary offenders on neighbouring farms. Anthrax in elephants is atypical, as it predominantly occurs during the dry season and is apparently independent of outbreaks among other susceptible species. One major epidemic accounted for about 200 elephants in 1981-1982. More males than females are killed by anthrax, particularly during non-epidemic outbreaks, presumably due to the longer time spent by males at contaminated water sources.

In spite of the drought, starvation has not been a cause of death except in very old individuals and very young calves. Predation by lions is the single most important cause of death in young calves, which are at least sometimes caught from within breeding herds.

As mostly adult males are shot on farms, and more males were recorded as dead from anthrax, the sex ratio in Etosha N.P. should show a strong bias towards females. Adult sex ratios, however, are difficult to determine, particularly in Etosha N.P. where variable fractions of the regional population might be present or absent at any given time.

Schedules of survival and fecundity were computed from age frequency distributions and reproductive parameters. There is no proof of a stable age distribution over the study period, and observed rates of increase as measured in Etosha N.P. have little bearing on rates of increase of the elephant population in north-western SWA/Namibia. Life tables were therefore discarded. Rates of increase of the number of elephants in Etosha N.P. are known, but exceed maximum rates of increase for elephant populations elsewhere in

Africa. I conclude that immigrations into the park were responsible for rapid growth in numbers, and emigration resulted in the observed decline. Current potential for increase based on survival and fecundity rates could not be calculated precisely, as a stable age distribution could not be proved, but appear to be negative.

Simulated population trends by use of a matrix model suggest that the regional population is in fact close to a stable age structure and currently decreasing at a rate of about 0.5% per year. Increasing the reproductive output of the female segment within the range of parameters known for elephant populations are insufficient to offset the mortality rate of elephants in Etosha N.P., probably the highest rate known for populations not subjected to severe poaching. Minor improvements in the probability of survival of yearlings are sufficient to maintain a stationary population. Overall improvements in the survival rate will produce a population increase.

The role of homeostatic reproduction mechanisms in population regulation, as described by Laws (1981) should be seen as interacting with survival rates, particularly yearling survival, as suggested by Hanks & McIntosh (1973) and Croze et al. (1981). Yearling survival is clearly a key determinant of population trend, and capable of modulating reproductive output by changing calving intervals through compensatory breeding. Periodic changes in calf survival could well account for irregularities in the age distribution described in other populations.

Elephant numbers in Etosha N.P. would remain variable as long as migrations in response to rainfall and surface water are possible. The population is presently not in an accellerated growth phase, and probably has not been for decades. The population has maintained itself through the worst period of perturbations, and the present trend of slow decline as the result of drought should be reversed if climatic conditions improve.

SAMEVATTING

Die waargenome styging en daling in bevolkingsgrootte van olifante in die Nasionale Etoshawildtuin stem ooglopend ooreen met 'n klassieke kolonisasie opeenvolging, wat 'n klimaks bereik het by oorskreiding van drakrag tydens die transafrikaanse droogte van die tagtigerjare. Die fase van vinnige bevolkingsgroei is omskryf deur opeenvolgende lugsensusse, en was die hoofoorweging vir hierdie studie. Latere sensusse het 'n bevolkingsdaling aangetoon wat teenstrydig was met plaaslike voorspellings. Dit was dus nodig om die grondige beskrywings van bevolkingstendense deur lugsensusse te bevestig. Beperkte eksperimentering was moontlik, maar sensusontwerp was geskik om akkuraatheid en presiesheid van bevolkingskattings te evalueer. Ewekansige kombinasies van transekwydtes en vlieghoogtes dui dat geen betekenisvolle tendense in oënskynlike olifantgetalle toegeskryf kan word aan variasie in hierdie parameters nie, binne perke van huidige gebruik. Verdere bevestiging hiervan is verkry uit die verspreiding van numeriese skattings van olifante op toenemende afstande weg van die vliegtuig. Geen inligting kon dus gevind word wat aandui dat die waargenome bevolkingstendens nie 'n weergawe van die ware verloop van sake is nie.

Daar is geen bewyse dat olifante in die Nasionale Etoshawildtuin geïsoleerd is van olifante in dele van die Kaokoveld, Owambo en Kavango nie, wat almal deel vorm van een streeksbevolking. Bewegings van olifante in en uit die Nasionale Etoshawildtuin word beskou as die hoofoorsaak van seisoenale en jaarlikse verskille in die aantal olifante teenwoordig in die wildtuin.

Die reeks van ses lugsensusse van olifante gedoen vir hierdie projek, is verder gebruik om alternatiewe en veral goedkoper lugsensusmetodes te evalueer. 'n Steekproeftelling van ewekansiggekiesde transekte teen minimum 30% bemonsteringsintensiteit kan aanvaarbare akkuraatheid en presiesheid in 'n bevolkingskatting verskaf.

Die ouderdomstruktuur van olifantbevolkings, sowel as bevolkingsgrootte, is kritieke parameters in demografiese analises. Die tradisionele ouderdomsbepalingsmetode van Laws (1966) is onlangs in twyfel getrek, ten gunste van die metode van Sikes (1968). Variasie in aantal laminae per molaartand, en onreëlmatigdhede in die posisie en aantal foramina mentale as verwysingspunt in die onderkaak waarteen die opeenvolging van molare gemeet word, bemoeilik gebruikmaking van laasgenoemde metode. Die laaste oorblyfsels van molare in olifante van Etosha word vroeër in die vervangingsproses verloor as elders, en dit

kompliseer Sikes (1968) se metode verder.

Verdelings van ouderdom gebasseer op twee uitdunningsmonsters in Etosha en volgens die ouderdomskedule van Laws (1966) en wysigings in Laws (1967 a), verskil van dié van ander bevolkings deurdat onreëlmatigdhede afwesig is. Reëlmatige bogemiddelde ouderdomsfrekwensies is verklaar as siklusse in rekrutering as gevolg van reenvalpatrone, maar kan ook te wyte wees aan variasie in die finale verlies van die laaste fragmente van molare, wat dan spesifieke ouderdomsklasse begunstig. Heelwat variasie in die verlies van molaarfragmente relatief tot die vervangingsproses kom wel voor in olifante vanuit Etosha. Molaartande is dikwels afwesig bo-oor die foramen mentale, en die voorkoms van die alveolus wissel. Die uiteindelike verlies van die laaste brokstuk van 'n molaar is dus te variërend om geskik te wees as 'n betroubare aanduiding van relatiewe ouderdom. Tanderupsie is hierteenoor 'n meer reëlmatige proses. Ouderdomsverdelings gebasseer op die posterior molaar se voorkoms is minder onreëlmatig as die teenoorgestelde. Laws (1966) se metode is dus tog bruikbaar, met sekere kleinere veranderinge soos voorgestel deur Jachmann (1988).

Die ouderdomstruktuur van olifante in die Nasionale Etoshawildtuin het min verskil voor en na die droogte, soos bepaal op grond van die indeling van olifante in ouderdomsklasse in grondopnames sedert 1977. Die relatiewe stabiliteit van die ouderdomstruktuur vanaf ten minste 1983 tot 1987 is bevestig deur die ouderdomsverdelings verkry uit twee uitdunningsmonsters en fotogrammetriese ouderdomsbepaling tydens lugopnames.

Die Etosha olifantbevolking teel seisoenaal, soos elders in suidelike Afrika, en 80% van geboortes geskied vanaf November tot Maart, wat die reënseisoen insluit. Meeste bevrugtings kom voor ten tyde van die samedromming van teeltroppe net voordat verstrooiing in die reënseisoen-konsentrasiegebiede plaasvind. Fetale groeitempo's is beskryf, maar die formules van Perry (1953) en Craig (1984) kon nie reg of verkeerd bewys word nie. Betekenisvolle verskille in oënskynlike fetale groeitempo's is gevind tussen die 1983 en 1985 versamelings van fetusse, onafhanklik van watter groeiformule toegepas is. Die maer voorkoms van fetusse versamel in 1983 dui op relatiewe ondervoeding, waarskynlik te wyte aan akute droogtetoestande.

Vroulike vrugbaarheid in Etosha is hoër as elders, soos te sien uit die relatiewe lae ouderdom by eerste bevrugting (10 - 12 jaar), kort kalfintervalle (3.8 jaar), die afwesigheid van voortplantingseniliteit, en die voorkoms van tweelinge (4,7%). Skattings van die gemiddelde kalfinterval op grond van die tempo van toename in plasentale littekens in koeie (2.1 - 2.5 jaar) is heelwat korter as skattings gebasseer op die voorkoms van dragtigheid en laktasie in volwasse koeie. Hierdie verskil, sowel as die voorkoms van nie-lakterende dragtige koeie, dui op vroeë mortaliteite onder kalwers en gepaardgaande kompensatoriese voortplanting. Skattings van die gemiddelde kalfinterval sonder 'n maatstaf van kalfoorlewing is bedrieglik, soos ook gevind deur Moss (1983).

Vrektes van kalwers mag die meerderheid van volwasse koeie na dieselfde fase van die voortplantingsiklus dwing, veral na afloop van 'n groot versteuring soos droogte, wat dus geboortes sinchroniseer. Kalwers van dieselfde ouderdom is meer dikwels waargeneem binne 'n individuele trop, anders as verwag indien voortplanting ewekansig tussen die koeie in 'n trop voorgekom het. Dit is moontlik te danke aan 'n stimulerende effek van bulle op koeie, waar dit in die Etosha bevolking by lae digtheid 'n bul in musth meer mag loon om by 'n trop te bly totdat koeie ontvanklik word, as om 'n reeds ontvanklike koei te soek.

Die mortaliteitsregister van olifante in Etosha dui dat miltsiekte (antraks) die hoofoorsaak van sterftes is, gevolg deur die vernietiging van olifante op aangrensende plase. Miltsiekte onder olifante is atipies, aangesien uitbrake hoofsaaklik in die droë seisoen voorkom, en oënskynlik onafhanklik is van uitbrake onder ander vatbare diersoorte. 'n Enkele uitbraak in 1981 - 1982 het ongeveer 200 olifante laat vrek. Meer bulle as koeie vrek van miltsiekte, veral tydens nie-epidemiese uitbrake, waarskynlik te wyte aan die feit dat bulle meer tyd as koeie by watergate spandeer, wat die kans vergroot om miltsiekte by 'n besmette bron op te doen.

Ten spyte van die droogte het hongersnood as oorsaak van dood slegs onder baie ou en baie jong diere voorgekom. Leeupredasie is die hoofoorsaak van sterftes in jong kalwers, en vangste kom ten minste af en toe voor binne olifanttroppe. Menslike versteuring mag veroorsaak dat kalwers geskei word van teeltroppe, wat later dan uitloop op predasie.

Hoofsaaklik bulle word geskiet op aangrensende plase en bulle toon ook 'n hoë insidensie van miltsiekte. Die geslagsverhouding in olifante van Etosha behoort dus 'n sterk voorkeur vir koeie te toon, maar volwasse geslagsverhoudings is moeilik bepaalbaar. Verskillende fraksies van die streeksbevolking, soos beïnvloed deur die migrasiepatroon, mag op enige tydstip in Etosha wees.

Skedules van oorlewing en vrugbaarheid is opgestel vanuit frekwensieverdelings van ouderdomme en voortplantingsparameters. Daar bestaan geen bewys van 'n stabiele ouderdomsverdeling oor die studietydperk nie, en waargenome groeitempo's in bevolkingsgrootte van olifante in Etosha is nie verteenwoordigend van die streeksbevolking in noordwestelike SWA/Namibië as geheel nie. Opgestelde lewenstabelle moet dus verwerp word. Groeitempo's van olifantgetalle binne Etosha is bekend maar oorskrei maksimum waardes beskryf vir olifantbevolkings elders in Afrika. Immigrasie van olifante na Etosha moes verantwoordelik gewees het vir die vinnige toename in getalle, en emigrasies moes bygedra het tot die waargenome daling sedert 1982. Huidige potensiaal vir groei aangedui deur die oorlewingstempo en vrugbaarheid van die bevolking, oënskynlik negatief, kan nie akkuraat bepaal word nie, omrede die aanname van 'n stabiele ouderdomsverdeling nie bevredig is nie.

Bevolkingsimulasies met behulp van 'n matriksmodel dui aan dat die Etosha bevolking inderdaad na aan 'n stabiele ouderdomstruktuur is en tans 'n geringe afname van 0,5% per jaar toon. Verhoging in die voortplantingstempo deur verhogings in alle parameters binne die waardes bekend in olifantbevolkings, is tans onvoldoende om die hoë mortaliteitstempo uit te kanselleer. Slegs bevolkings wat onder intense druk van onwettige jag verkeer sal na verwagting hoër sterftetempo's toon as die bevolking in Etosha. Klein verhogings in die oorlewingstempo van jaaroud kalwers is egter voldoende om statiese bevolkingsgroei te lewer. Algehele verhogings in die oorlewingstempo sal lei tot 'n bevolkingstoename.

Homeostatiese beheer van bevolkingsgroei deur voortplanting soos beskryf deur Laws (1981) is nou gekoppel aan oorlewingstempo's, veral van jong kalwers, soos voorgestel deur Hanks & McIntosh (1973) en Croze et al. (1981). Die oorlewingstempo in die eerste jaar is duidelik 'n sleutelfaktor in die bepaling van bevolkingstoename, en is in staat om kalfproduksie te reguleer. Die oorlewingstempo van jaaroud kalwers beïnvloed die kalfinterval deur kompensatoriese voorplanting. Periodieke wisseling in kalfoorlewing mag wel die oorsaak wees van reëlmatige afwykings in die ouderdomsverdeling soos gevind in ander bevolkings.

Olifantgetalle in Etosha sal na verwagting bly widssel solank dit fisies moontlik bly vir die bevolking in noordwestelike SWA/Namibië om te migreer na gelang van reënval en beskikbare oppervlakwater. Die bevolking is huidig nie in 'n fase van vinnige groei nie, en is waarskynlik reeds naby aan statiese groei vir 'n aantal dekades. Die bevolking kon homself handhaaf gedurende die ergste periode van versteurings, en die huidige tendens van geleidelike afname behoort omgeskakel te word na 'n toename sodra klimaatsomstandighede verbeter.

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APPENDIX 1

Abbreviations used in text for names of African conservation areas.

N.P. : National Park
A.N.P. : Amboseli National Park, Kenya
B.F. : Budongo Forest, Uganda
E.N.P. : Etosha National Park, SWA/Namibia
G.N.P. : Gonarezhou National Park, Zimbabwe
H.N.P. : Hwange National Park, Zimbabwe (formerly Wankie N.P.)
K.F.N.P.N & S. : Kabalega Falls National Park North & South, Uganda (formerly Murchison Falls N.P.)
K.N.P. : Kruger National Park, South Africa
K.N.P.M. : Kasungu National Park, Malawi
K.N.P.U. : Kidepo National Park, Uganda
L.M.N.P. : Lake Manyara National Park, Tanzania
L.V.N.P. : Luangwa Valley National Park, Zambia
M.P.N.P. : Mana Pools National Park, Zimbabwe
M.R.E. & C.: Mkomazi Reserve East & Central, Tanzania
R.N.P. : Rwenzori National Park, Uganda (formerly Queen Elizabeth N.P.)
T.N.P.E. & W. : Tsavo National Park East & West, Kenya

APPENDIX 2

Aerial sampling counts

The principles and use of sampling methods in aerial censuses have been described in detail by Jolly (1969), Caughley (1977a) and Norton-Griffiths (1978). Sample counts have supplanted total counts in most African conservation areas, and are the basis of several long-term monitoring programmes (Sinclair 1972, Eltringham & Din 1977, Pennycuick, Sale, Stanley Price & Jolly 1977, Barnes & Douglas-Hamilton 1982). The advantages offered by sampling instead of covering the total area, such as savings in cost, time and effort, as well as the incongruous fact that sample counts yield more accurate estimates, argue against the use of total counts.

Four basic and related sampling methods can be used in aerial censuses, namely quadrat sampling, block sampling, transect sampling and line-transect sampling. Quadrat and block samples are not considered here, as quadrats are difficult to locate in the almost featureless terrain of Etosha N.P. Blocks are defined by boundary features which strongly affect elephant distribution, such as roads and waterholes. Line-transects as a special form of belt-transects may be considered in future, but not enough data are available.

That leaves belt-transects, referred to as transects hereafter, which entails the selection of a sample from an infinite number of transects within the boundaries of the survey area. The sample is either drawn randomly or regularly, yielding what is known as random transect sample counts or systematic transect sample counts. Transects may be of unequal lengths, and can be weighted proportionally to counteract the irregular shape of Etosha N.P. and variable transect areas (Caughley 1977a, b).

A sampling system was investigated by using the series of elephant censuses in the study, without having the extra time or funds for experimentation. This was done by selecting a sample in various ways from a series of finite transects which had to be flown in any event. Two strata were defined, the eastern woodlands where transects were spaced 2 km apart from a randomly chosen starting point, and the western shrubland with transects at 4 km intervals. A maximum number of 186 transects was thereby established, essentially represented as a double row of north-south transects in two broad vegetation strata.

The validity of a sample estimate is assessed by determining the appropriate sampling intensity. Optimal sampling intensity yields the minimum variance of the estimate in terms of effort expended (time, cost) and is estimated by step-by-step increases of the sample size until additional sampling units do not increase the precision of the estimate.

Norton-Griffiths (1978) suggests the uses of Jolly's (1969) method 2 for unequal sized sampling units to calculate the population estimate (Y) and 95% confidence limits (CL) of Y (this means there is a 95% certainty that the true number of entities lies within the stated range), where:

N = the number of sample units in the population
n = the number of sample units in the sample
Z = area of the census zone
z = area of any one sample unit
Y = number of animals counted in that unit

R = ratio of animals counted to area searched = $\frac{Y}{z}$

and $Y = Z\ R$

and

$$\mathrm{Var}(Y) = \frac{N(N-n)}{n}\ s^2_y - 2Rs_{zy} + R^2 s_z^2$$

where

s_y^2 = the variance between elephants counted in all the units.

$$= \frac{1}{n-1}\ Y^2 - \frac{(\ Y)^2}{n}$$

s_z^2 = the variance between the area of all the sample units.

$$= \frac{1}{n-1}\ z^2 - \frac{(\ z)^2}{n}$$

s_{zy} = the covariance between the elephants counted and the area of each unit.

$$= \frac{1}{n-1}\ zy - \frac{(\ z)(\ y)}{n}$$

and population standard error

$$SE(Y) = \sqrt{VAR(Y)}$$

Precision of the estimate Y is therefore expressed as the 95% CL of Y as a percentage of Y and can be used to indicate optimal sampling intensity. An alternative indication of optimum sampling intensity is obtained by expressing the affinities between samples of transects drawn in the sample as the percentage similarity (PS) (Gauch 1982) where:

$$PS = \frac{200 \ \min A_j \ A_k}{A_j + A_k}$$

where

200 = denominator if samples are expressed as a percentage

A_j, A_k = abundance of elephants in samples j and k.

min = minimum abundance of elephants in either samples j or k (by implication, the number of elephants in common in samples j and k).

Percentage similarity is primarily a measure of homogeneity between sampling units and is therefore a useful indication of intra-sampling variation.

A computer program was written (P.M. Lindeque, unpubl.) where series of transect samples were chosen at increasing sampling intensities. The method of selection of transects depended on the type of sampling system. A population estimate (Y) and the 95% confidence limits of the estimate were calculated for each sample and expressed as a percentage of the estimate. A next sample at the same sampling intensity was chosen, and Y and CL calculated. The two samples chosen were compared to calculate the percentage similarity (PS) between samples. This procedure was repeated 20 times at each sampling intensity. For example, at a sample size of 30, 40 estimates of Y, 40 estimates of CL and 20 estimates of PS were calculated.

Systematic sampling at increasing sampling intensity however, implies the sampling of transects at decreasing intervals. The smallest interval indicates the highest sampling intensity. The spacing of intervals is measured by increasing the number of fixed transects. As there is a fixed number of transects in the area, for each sampling interval there is only a fixed number of different possible samples. For example, an interval of two transects means that one sample consists of every second transect in the series (all odd numbered transects), thus there will only be one other possible different sample (all even numbers). The number of estimates of Y, 95% CL and PS is therefore equivalent to that particular sampling interval which is being investigated.

The mean (± SE) of Y (n=40), CL (n=40) and PS (n=20) of random transect samples (weighted and unweighted) and systematic transect samples for the entire unstratified survey area in May and August in Etosha N.P., are illustrated in Figs. A2.1-A2.3. Curves are evaluated by eye, as the calculation of asymptotic values is not warranted (Norton-Griffiths 1978).

A comparison of Figs. A2.1, A2.2 and A2.3 reveals that:

1. Asymptotic values of CL and PS in systematic sampling are not reached significantly below 100% sampling intensity.
2. Weighted random transect sampling shows a greater variation in Y relative to the actual number counted, thus a less accurate estimate of Y than in unweighted random transect sampling.
3. Random transect sampling (Figs. A2.2 A & B) in both May and August 1985, shows a reasonably clear levelling off in precision with increasing sampling intensity. More than 60 transects in both May and August will be superfluous and will not improve the precision of accuracy of the estimate. The estimate Y oscillates around the actual number counted, but remains within 10% of that number.
4. If any choice has to be made between sample systems, random transect sampling is clearly the preferred method, if on no other grounds than simply the uncomplicated picture that emerges from the simulation. The minimum recommended sampling intensity will be 60. A sample of 60 transects randomly chosen (a third of the total) should be approximately 90% accurate and 80% precise.

Separate samples in the woodland and shrubland strata did not improve the accuracy or precision of the estimate for each stratum. Further stratification based on other criteria appears to be superfluous, in view of the adequacy of estimates from the unstratified area.

Random sampling of unweighted transects provided surprisingly high degrees of accuracy and precision in both May and August 1985. Sampling intensities of between 30-40% appear

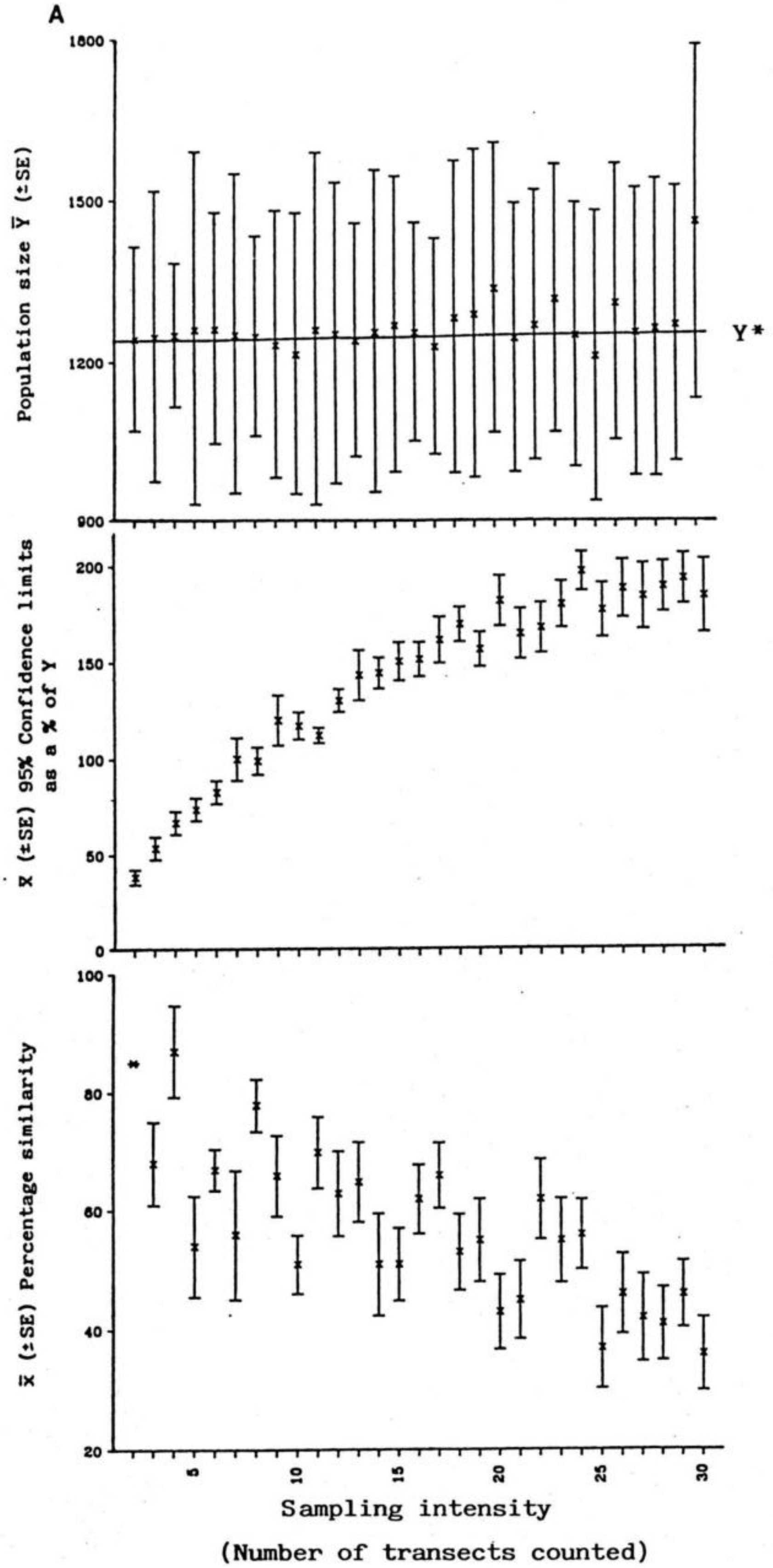


Figure A2.1 Systematic transect samples of the total unstratified census area in Etosha National Park in May 1985 (A) and August 1985 (B). (Y* = Observed number of elephants).

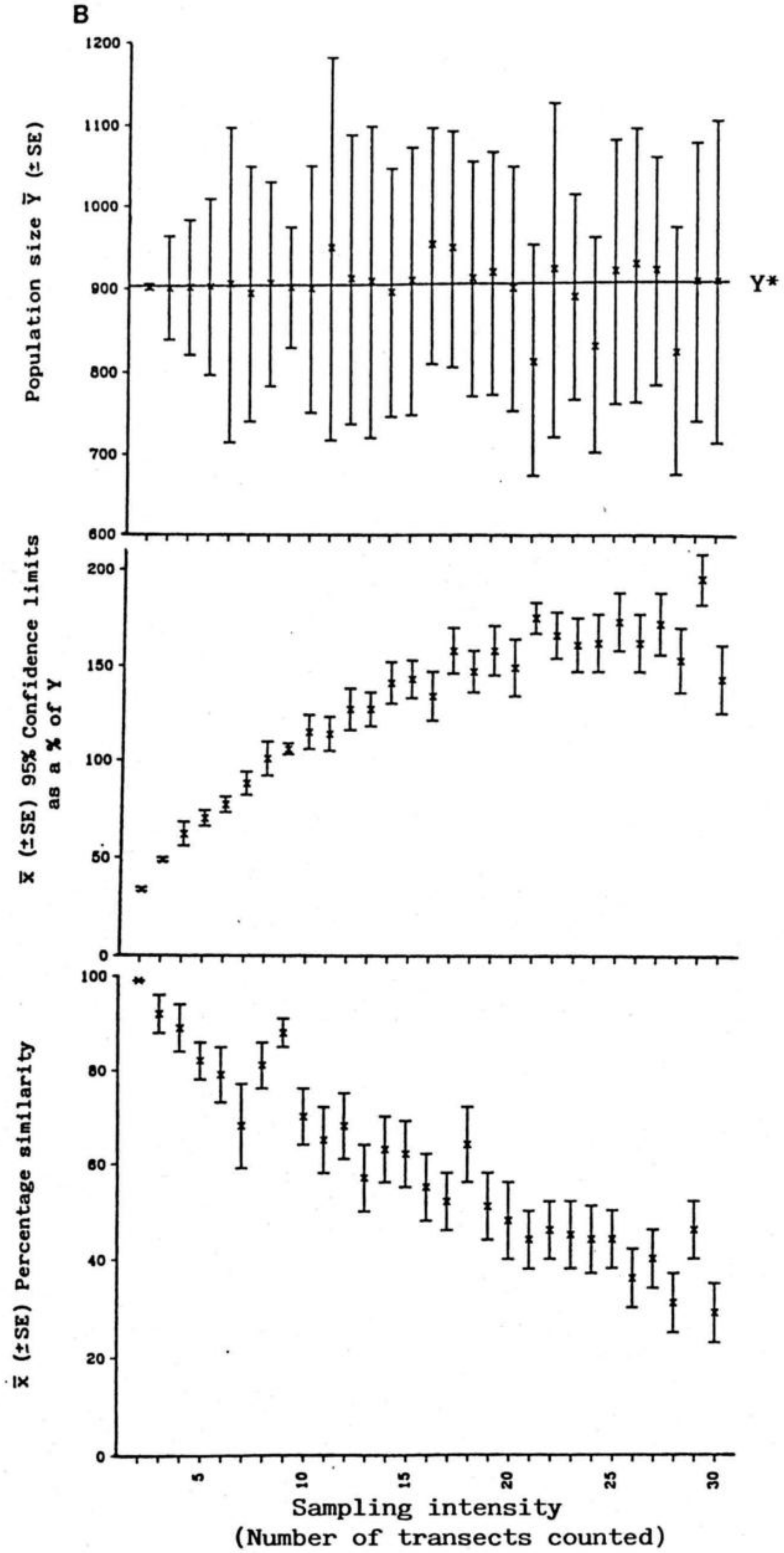


Figure A2.1 continued.

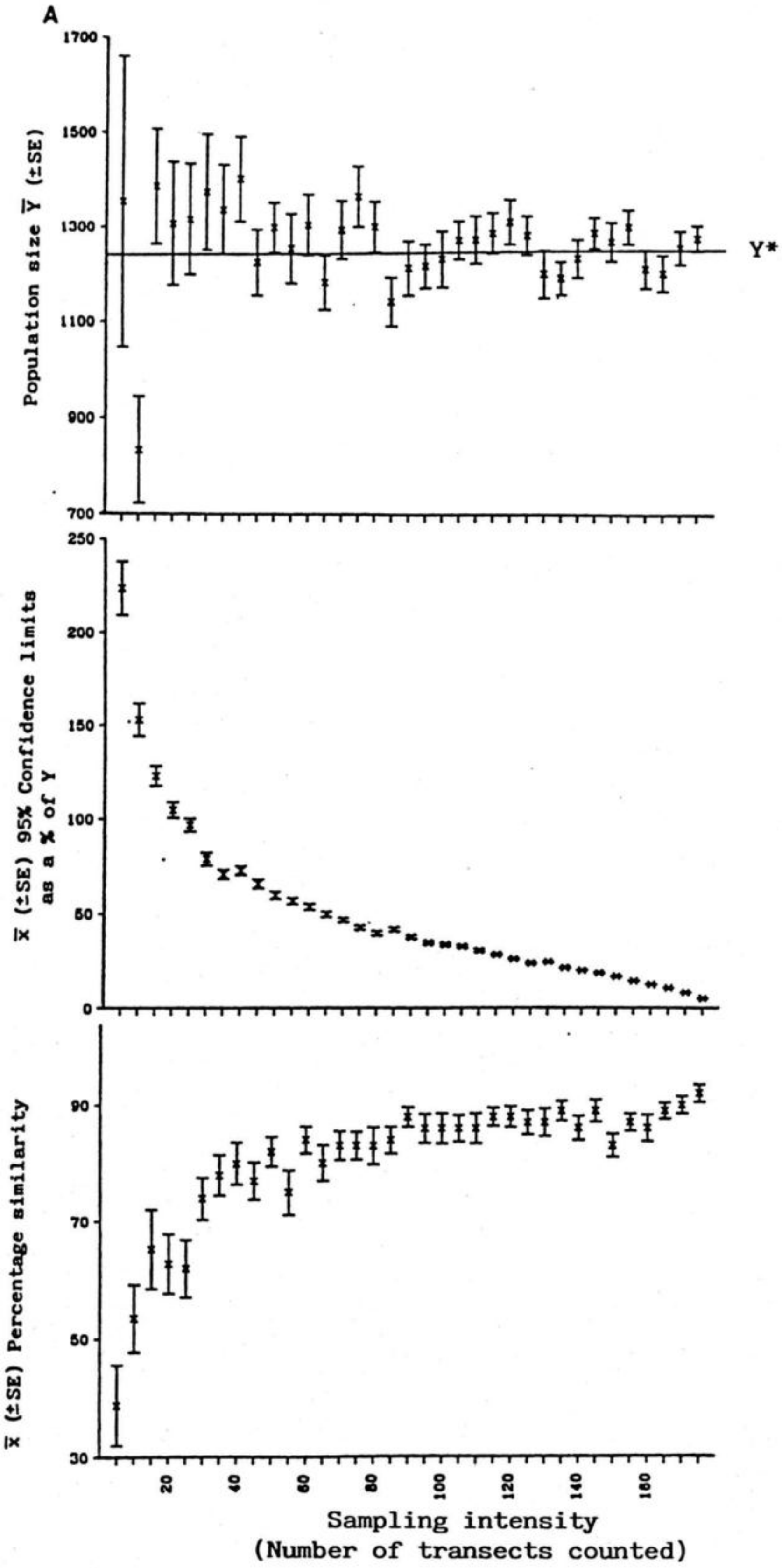


Figure A2.2 Random transect samples of the total unstratified census area in Etosha National Park in May 1985 (A) and August 1985 (B). (Y* = Observed number of elephants).

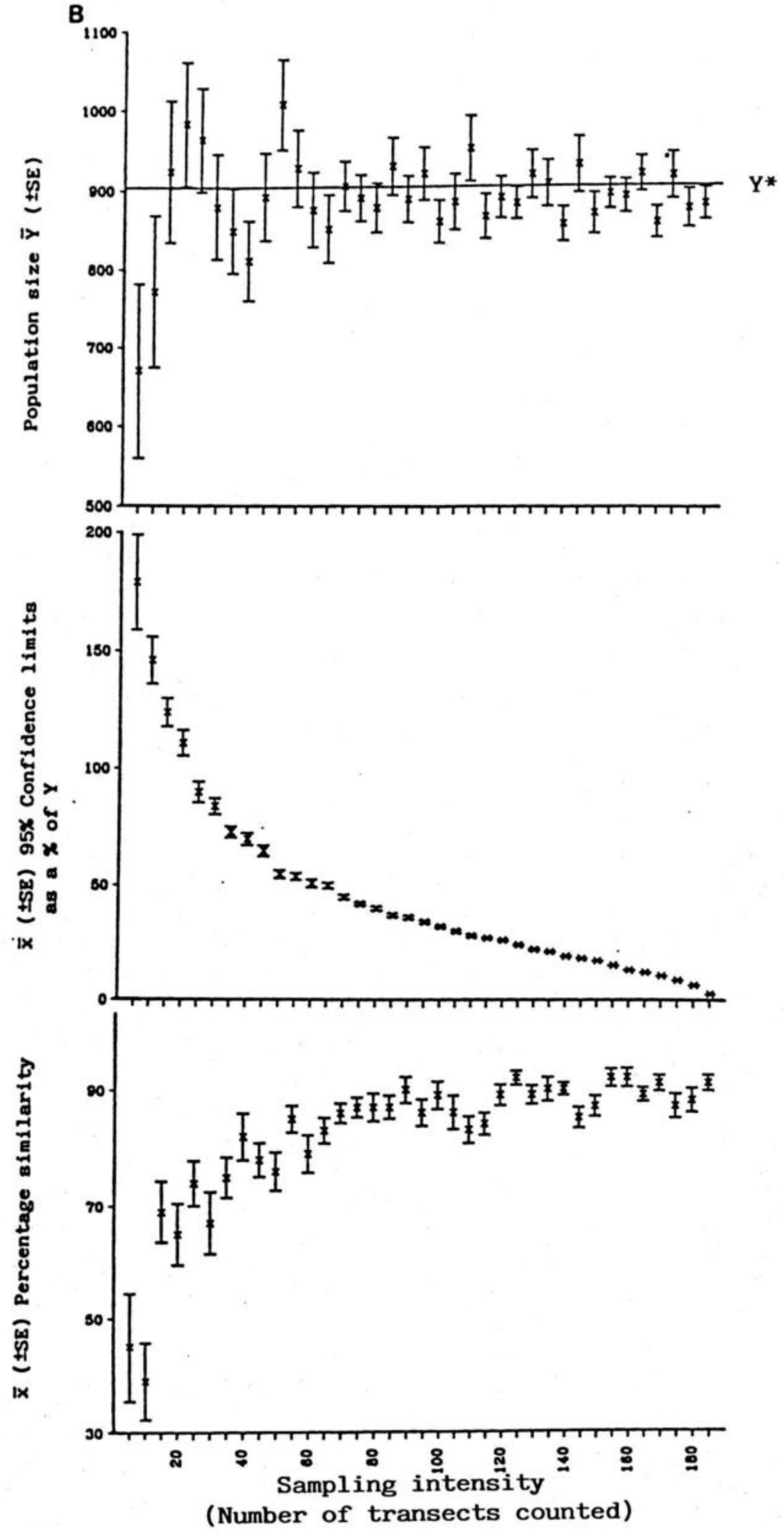
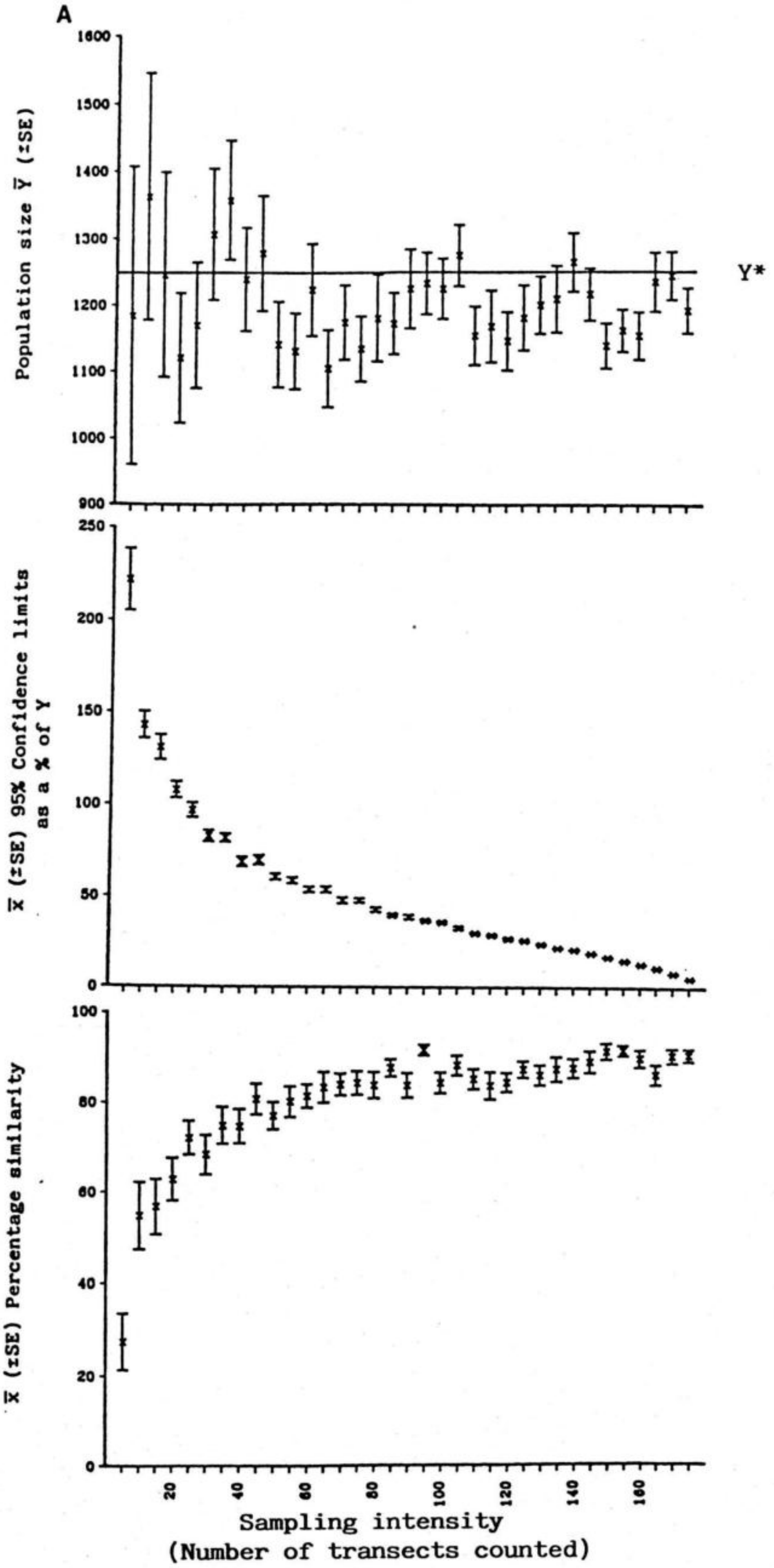


Figure A2.2 continued.



gure A2.3 Weighted random transect samples of the total unstratified census area in Etosha National Park in May 1985 (A) and August 1985 (B). (Y* = Observed number of elephants).

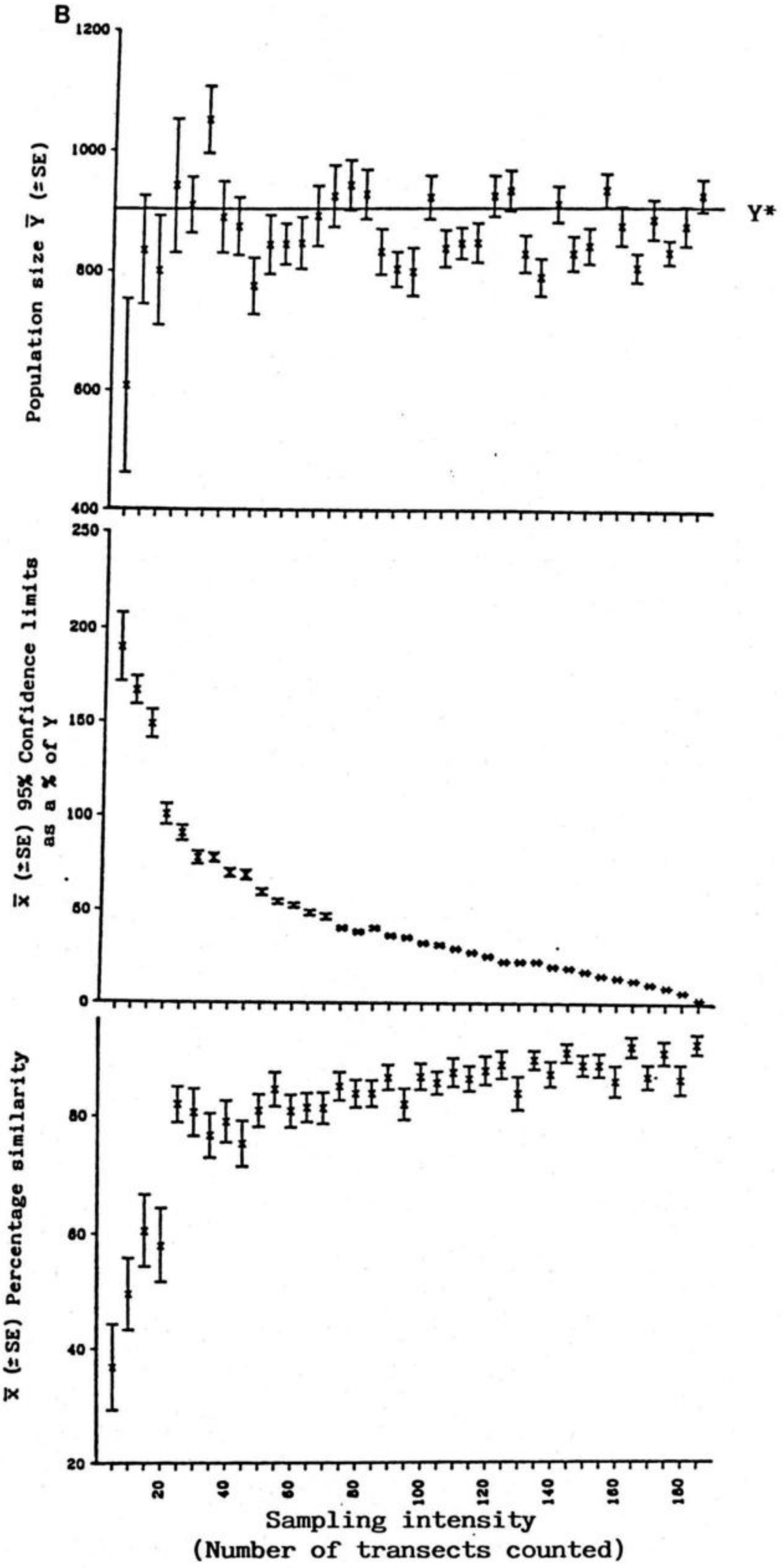


Figure A2.3 continued.

to be adequate, and the simulation in Fig. A2.2 may perhaps be used as the basis for future sample censuses of elephants in Etosha N.P. There is no need in future to draw a random sample from the finite series of transects used in this study. Once the decision is taken to change the census strategy from total coverage to a sample count, randomness should be strictly adhered to. A semi-random sample as in Caughley & Goddard (1972) defeats the object. Systematic samples should similarly be taken from a random starting point.

Systematic samples may nevertheless still be considered, provided that some attempt is made to ascertain whether periodicities in elephant distribution or ground features such as dunes or waterholes coincide with the sampling system. Systematic sampling is ideal for general ecological monitoring where a large number of parameters other than population estimates are recorded, as in Sinclair (1972) and Western & Grimsdell (1979).

The objectives of an aerial census should therefore indicate which system is more appropriate. Sample censuses in Etosha N.P. will nevertheless require some adjustment in the evaluation of population estimates by people. A total count of 2081 (and not 2082) sounds so much better than a sample count of 2000 ± 100. An estimate of population size, resulting from the one random transect sample done in December 1985 when the aircraft was only available for a limited period, was indeed received with more scepticism than usual by fellow staff members.

Minimum suitable sampling intensities for counting the other main target species in Etosha N.P. by using a random transect sample, have been determined (Lindeque & Lindeque 1987). These range from about 25-30% in the concentration areas (counted by helicopter) and 38-50% in the remainder (counted by fixed-wing aircraft). Only eland (Taurotragus oryx), red hartebeest (Alcelaphus buselaphus caama) and black rhinoceros cannot be counted from the air at these sampling intensities. All three species are considered rare in Etosha N.P., numbering from 250-600 in 1987.

Unweighted random transect samples provide a viable alternative to a total census, at least for estimating the number of elephants and the more common large herbivores in Etosha N.P., and will enable the continuation of the long-term monitoring programme if sufficient funds for more intensive censuses should not be available in future.

APPENDIX 3

Matrix model of an elephant population.

(Written in Basic for an IBM PC)

```
10 REM **********************
20 REM *      MODEL60       *
30 REM *                    *
40 REM *     WRITTEN BY     *
50 REM *                    *
60 REM *   P.M. LINDEQUE    *
70 REM **********************
80 REM ELEPHANT POPULATION MODEL USING 60 AGES
90 CLS
100 INPUT "NUMBER OF YEARS FOR WHICH MODEL MUST RUN?";NY
110 DIM P(60):REM AGECLASS FREQUENCIES
120 DIM R(4,60):REM Px, MxLo, STARTING Fx, Mx
130 DIM T(2,NY):REM YEARLY TOTAL, R FROM PREVIOUS YEAR
140 DIM Y(NY,60):REM YEARLY AGECLASS FREQUENCIES
150 FOR I=1 TO 60
160 PRINT "INPUT NUMBER OF FEMALES IN AGE ";I;
170 INPUT "   ";R(3,I)
180 NEXT I
190 CLS
200 FOR I=1 TO 60
210 PRINT "INPUT Px VALUE (SURVIVAL) FOR AGE ";I;
220 INPUT "   ";R(1,I)
230 NEXT I
240 CLS
250 FOR I=1 TO 60
260 PRINT "INPUT Mx VALUE (FECUNDITY) FOR AGE ";I;
270 INPUT "   ";R(4,I)
280 NEXT I
290 GOSUB 810
300 CLS:PRINT "RUNNING PROGRAM"
310 FOR I=1 TO 60
320 LET P(I)=R(3,I)
330 LET R(2,I)=R(4,I)*LO
340 NEXT I
350 REM ADD STARTING FREQUENCY TO SET
360 FOR I=1 TO 60
370 LET Y(0,I)=P(I)
380 NEXT I
390 FOR J=1 TO NY
400 REM CALCULATE FREQUENCIES FOR NEXT YEAR
410 FOR I=2 TO 60
420 LET Y(J,I)=P(I-1)*R(1,I-1)
430 NEXT I
440 REM CALCULATE No BORN INTO AGECLASS 0
450 LET Y(J,1)=0
460 FOR I=2 TO 60
470 LET Y(J,1)=Y(J,1)+Y(J,I)*R(2,I)
480 NEXT I
490 FOR I=1 TO 60
```

```
500 LET P(I)=Y(J,I)
510 NEXT I
520 NEXT J
530 REM PRINTING RESULTS
540 LPRINT DATE$:LPRINT
550 LPRINT "ELEPHANT MODEL - PROJECTION FOR ";NY;" YEARS"
560 LPRINT
570 LPRINT "WHERE : "
580 LPRINT:LPRINT "Lo = ";LO
590 LPRINT
600 LPRINT "CLASS";TAB(15);"SURVIVAL";TAB(30);"  Mx";TAB(40)
;"Lo X Mx";TAB(50);"INITIAL POPULATION"
610 FOR I=1 TO 60 STEP 10
620 LPRINT I;TAB(15);R(1,I);TAB(30);R(4,I);TAB(40);INT((R(2,
I)*1000)+.5)/1000;TAB(50);R(3,I)
630 NEXT I
640 LPRINT:LPRINT:LPRINT
650 REM CALCULATE YEARLY TOTALS
660 FOR J=0 TO NY
670 LET T(1,J)=0
680 FOR I=1 TO 60
690 LET T(1,J)=T(1,J)+Y(J,I)
700 NEXT I
710 NEXT J
720 LPRINT:LPRINT:LPRINT "YR";TAB(15);"TOTAL";TAB(25);"r (FR
OM PREVIOUS YR)"
730 REM CALCULATE OBSERVED RATE OF INCREASE
740 FOR I=1 TO NY
750 LET T(2,I)=LOG(T(1,I))-LOG(T(1,I-1))
760 NEXT I
770 FOR I=0 TO NY
780 LPRINT I;TAB(15);INT(T(1,I)+.5);TAB(25);INT((T(2,I)*1000
!)+.5)/1000!
790 NEXT I
800 GOTO 290
810 REM ALLOW FOR CHANGES
820 CLS
830 INPUT " INPUT Lo ";LO
840 CLS
850 PRINT "CLASS";TAB(10);" Fx ";TAB(20);" Px ";TAB(30);" Mx
"
860 PRINT
870 FOR I=1 TO 60
880 PRINT I;TAB(10);R(3,I);TAB(20);R(1,I);TAB(30);R(4,I)
890 NEXT I
900 PRINT:INPUT "DO YOU WANT TO MAKE CHANGES";Y$
910 IF Y$="Y" OR Y$="y" THEN GOTO 930
920 RETURN
930 PRINT:PRINT "1     TO CHANGE Px"
940 PRINT "3     TO CHANGE Fx"
950 PRINT "4     TO CHANGE Mx"
960 INPUT "ENTER YOUR CHOICE ";A
970 INPUT "DO YOU WANT TO CHANGE THE ENTIRE RANGE";Y$
980 IF Y$="Y" OR Y$="y" THEN GOTO 1060
990 CLS
1000 INPUT "NUMBER OF AGES TO BE CHANGED";N
1010 FOR I=1 TO N
1020 INPUT "CLASS ";CL
```

```
1030 INPUT "NEW VALUE ";R(A,CL)
1040 NEXT I
1050 GOTO 840
1060 CLS
1070 FOR I=1 TO 60
1080 IF A=4 AND I=21 THEN INPUT "WILL THE REST ALL BE THE SA
ME?";Y$:IF Y$="Y" OR Y$="y" THEN GOTO 1130 ELSE GOTO 1090
1090 PRINT I;
1100 INPUT "NEW VALUE ";R(A,I)
1110 NEXT I
1120 GOTO 840
1130 INPUT "VALUE ";V
1140 FOR I=21 TO 60
1150 LET R(A,I)=V
1160 NEXT I
1170 GOTO 840
```

APPENDIX 4

Variable periodicity matrix model.

(Written in Basic for an IBM PC)

```
10 REM **********************
20 REM *     MODCYCLE       *
30 REM *                    *
40 REM *  WRITTEN BY        *
50 REM *                    *
60 REM *   P. LINDEQUE      *
70 REM **********************
80 REM ELEPHANT POPULATION MODEL USING 60 AGES AND ALLOWING
FOR CYCLICAL CHANGES
90 CLS
100 INPUT "NUMBER OF YEARS FOR WHICH MODEL MUST RUN?";NY
110 DIM P(60):REM AGECLASS FREQUENCIES
120 DIM R(4,60):REM Px, MxLo, STARTING Fx, Mx
130 DIM T(2,NY):REM YEARLY TOTAL, R FROM PREVIOUS YEAR
140 DIM Y(NY+2,60):REM YEARLY AGECLASS FREQUENCIES
150 DIM O(3,61):DIM E(2,60):REM FOR CONTINGENCY TABLES
160 FOR I=1 TO 60
170 PRINT "INPUT NUMBER OF FEMALES IN AGE ";I;
180 INPUT "  ";R(3,I)
190 NEXT I
200 CLS
210 FOR I=1 TO 60
220 PRINT "INPUT Px VALUE (SURVIVAL) FOR AGE ";I;
230 INPUT "  ";R(1,I)
```

```
240 NEXT I
250 CLS
260 FOR I=1 TO 60
270 PRINT "INPUT Mx VALUE (FECUNDITY) FOR AGE ";I;
280 INPUT "  ";R(4,I)
290 NEXT I
300 GOSUB 1050
310 CLS:PRINT "RUNNING PROGRAM"
320 FOR I=1 TO 60
330 LET P(I)=R(3,I)
340 NEXT I
350 REM ADD STARTING FREQUENCY TO SET
360 FOR I=1 TO 60
370 LET Y(0,I)=P(I)
380 NEXT I
390 LPRINT DATE$,"ELEPHANT CYCLE MODEL"
400 FOR K=1 TO NY
410 FOR I=1 TO 60
420 LET R(2,I)=R(4,I)*LO
430 LET P(I)=R(3,I)
440 NEXT I
450 INPUT "HOW MANY YEARS IN THIS CYCLE ";CY
460 IF K+CY-1>NY THEN PRINT "THAT EXCEEDS THE TOTAL NUMBER "
;NY;" ASKED FOR - TRY AGAIN" :GOTO 450
470 FOR J=K TO K+CY-1
480 REM CALCULATE FREQUENCIES FOR NEXT YEAR
490 FOR I=2 TO 60
500 LET Y(J,I)=P(I-1)*R(1,I-1)
510 NEXT I
520 REM CALCULATE No BORN INTO AGECLASS 0
530 LET Y(J,1)=0
540 FOR I=2 TO 60
550 LET Y(J,1)=Y(J,1)+Y(J,I)*R(2,I)
560 NEXT I
570 FOR I=1 TO 60
580 LET P(I)=Y(J,I)
590 NEXT I
600 NEXT J
610 LPRINT "PROJECTION FOR ";CY;" YEARS     "
620 LPRINT
630 LPRINT "WHERE : "
640 LPRINT:LPRINT "Lo = ";LO
650 LPRINT
660 LPRINT "CLASS";TAB(15);"SURVIVAL";TAB(30);"  Mx";TAB(40)
;"Lo X Mx";TAB(50);"INITIAL POPULATION"
670 FOR I=1 TO 60 STEP 10
680 LPRINT I;TAB(15);R(1,I);TAB(30);R(4,I);TAB(40);INT((R(2,
I)*1000)+.5)/1000;TAB(50);R(3,I)
690 NEXT I
700 LPRINT:LPRINT:LPRINT
710 FOR J=K-1 TO K+CY-1
720 LET T(1,J)=0
730 FOR I=1 TO 60
740 LET T(1,J)=T(1,J)+Y(J,I)
750 NEXT I
760 NEXT J
770 LPRINT:LPRINT:LPRINT "YR";TAB(15);"TOTAL";TAB(25);"r (FR
OM PREVIOUS YR)"
```

```
780 FOR I=K TO K+CY-1
790 LET T(2,I)=LOG(T(1,I))-LOG(T(1,I-1))
800 NEXT I
810 FOR I=K-1 TO K+CY-1
820 LPRINT I;TAB(15);INT(T(1,I)+.5);TAB(25);INT((T(2,I)*1000
!)+.5)/1000!
830 NEXT I
840 LPRINT
850 INPUT "DO YOU WANT A FREQUENCY PRINTOUT ";Y$
860 IF Y$="Y" OR Y$="y" THEN GOTO 870 ELSE GOTO 940
870 INPUT "WHICH YEAR ";J
880 LPRINT "YEAR = ";J;"      ";
890 FOR I=1 TO 60
900 LPRINT INT(Y(J,I)+.5);
910 NEXT I
920 LPRINT:LPRINT
930 GOTO 850
940 LET K=K+CY-1
950 FOR I=1 TO 60
960 LET R(3,I)=P(I)
970 IF K=NY THEN GOTO 1000
980 NEXT I
990 GOSUB 1050
1000 NEXT K
1010 CLS
1020 GOSUB 1480
1030 LOCATE 10,20:PRINT "NEW RUN"
1040 GOTO 160
1050 REM ALLOW FOR CHANGES
1060 INPUT "Lo ";LO
1070 CLS
1080 PRINT "CLASS";TAB(10);" Fx ";TAB(20);" Px ";TAB(30);" M
x"
1090 PRINT
1100 FOR I=1 TO 60
1110 PRINT I;TAB(10);R(3,I);TAB(20);R(1,I);TAB(30);R(4,I)
1120 NEXT I
1130 PRINT:INPUT "DO YOU WANT TO MAKE CHANGES";Y$
1140 IF Y$="Y" OR Y$="y" THEN GOTO 1160
1150 RETURN
1160 PRINT:PRINT "1     TO CHANGE Px"
1170 PRINT "3     TO CHANGE Fx"
1180 PRINT "4     TO CHANGE Mx"
1190 INPUT "ENTER YOUR CHOICE ";A
1200 INPUT "DO YOU WANT TO CHANGE THE ENTIRE RANGE";Y$
1210 IF Y$="Y" OR Y$="y" THEN GOTO 1290
1220 CLS
1230 INPUT "NUMBER OF AGES TO BE CHANGED";N
1240 FOR I=1 TO N
1250 INPUT "CLASS ";CL
1260 INPUT "NEW VALUE ";R(A,CL)
1270 NEXT I
1280 GOTO 1070
1290 CLS
1300 INPUT "DO YOU WANT A PROPORTIONAL CHANGE ";Y$
1310 IF Y$="Y" OR Y$="y" THEN GOTO 1320 ELSE GOTO 1370
1320 INPUT "PROPORTION ";PROP
1330 FOR I=1 TO 60
```

```
1340 LET R(A,I)=PROP*R(A,I)
1350 NEXT I
1360 GOTO 1070
1370 FOR I=1 TO 60
1380 IF A=4 AND I=21 THEN INPUT "WILL THE REST ALL BE THE SA
ME?";Y$:IF Y$="Y" OR Y$="y" THEN GOTO 1430 ELSE GOTO 1390
1390 PRINT I;
1400 INPUT "NEW VALUE ";R(A,I)
1410 NEXT I
1420 GOTO 1070
1430 INPUT "VALUE ";V
1440 FOR I=21 TO 60
1450 LET R(A,I)=V
1460 NEXT I
1470 GOTO 1070
1480 REM COMPARE TWO SERIES OF AGE DISTRIBUTIONS USING CONTI
NGENCY TABLES
1490 CLS
1500 INPUT "DO YOU WANT TO TEST FOR DIFFERENCES ";Y$
1510 IF Y$="Y" OR Y$="y" THEN GOTO 1520 ELSE GOTO 1830
1520 INPUT "TWO YEARS TO BE TESTED (A,B) ";X,Z
1530 FOR I=1 TO 60
1540 LET O(1,I)=Y(X,I)
1550 LET O(2,I)=Y(Z,I)
1560 NEXT I
1570 LET O(1,61)=0:O(2,61)=0
1580 FOR I=1 TO 2
1590 FOR J=1 TO 60
1600 LET O(I,61)=O(I,61)+O(I,J)
1610 NEXT J
1620 NEXT I
1630 FOR I=1 TO 61
1640 LET O(3,I)=O(1,I)+O(2,I)
1650 NEXT I
1660 REM CALCULATE EXPECTED TABLE
1670 FOR J=1 TO 2
1680 FOR I=1 TO 60
1690 LET E(J,I)=(O(J,61)*O(3,I))/O(3,61)
1700 NEXT I
1710 NEXT J
1720 REM CHI-SQUARED CALCULATION
1730 CHI=0
1740 FOR J=1 TO 2
1750 FOR I=1 TO 60
1760 IF E(J,I)=0 THEN GOTO 1780
1770 CHI=CHI+((O(J,I)-E(J,I))^2)/E(J,I)
1780 NEXT I
1790 NEXT J
1800 PRINT:PRINT
1810 LPRINT "CHI-SQUARED VALUE BETWEEN YEARS ";X;" AND ";Z;"
 IS ";CHI
1820 GOTO 1500
1830 CLS:RETURN
```

APPENDIX 5

Management implications.

The Masterplan for Etosha National Park contains the following objectives:

- the maintenance, and in special cases the increase, of biotic diversity of the local biota, and
- the sustained utilization of its resources for the benefit of humanity (sic),

and a series of operational goals which are the measure of attainment of the two objectives. The primary goal is the maintenance of plant and animal diversity within permissable limits, beyond which interventive management is applied. The prime consideration for interventive management of the elephant population is whether changes in plant species diversity beyond permissable limits are directly caused by elephants. Plant species diversity is measured as the number of species and the abundance of each species along environmental gradients. The key issue is clearly the definition of permissable limits of change, which presents a considerable challenge to future research.

Harvesting (cropping) of the population for economic purposes is currently not intended, although strictly speaking allowed in terms of the second objective. Culling the elephant population depends on the qualifier over-abundance, which has not been defined in Etosha N.P. Until vegetation trends are better quantified in Etosha N.P., and the effects of elephants are clearly separated from changes induced by fire, frost, drought, other species and injudicious management actions, it is impossible to advise pre-emptive culling of the population. Elephant abundance in the park is unstable and it is impossible to predict how the pattern of migration and recent shifts in distribution will change in future. The population has furthermore responded to the Trans-African drought by showing a modest decline in the potential rate of increase, expressed as a decrease at present. Calf and adult mortality rates are higher than elsewhere, and the population is already breeding at near-maximum rates. If environmental conditions improve after the present drought, the survival rates should improve, and the population will probably increase.

Short-term changes in the number of elephants counted in Etosha N.P. are caused by movement of elephants in and out of the park. Further influxes of elephants could occur if the drought continues or worsens, but the duration of elephant concentrations in the park will be terminated by the first rains. When the population in Etosha N.P. peaked at nearly 3000 in 1983, serious effects on the vegetation as a consequence of elephant density were negligible compared to subsequent frost, fire and fungus mortalities of trees later in the drought. Conditions favouring the recovery of woodlands will also favour the dispersal of elephants out of the park. The population of elephants has not caused irreversible changes on a regional scale thus far, and I recommend a course allowing for population fluctuations until irreversible changes are imminent. Skill and manpower are available in the park to intervene rapidly if necessary.

Short-term problems.

Vegetation around waterholes

It is impossible for elephants not to have a visible effect on the vegetation, particularly around waterholes which are also the foci of human attention. The destruction of picturesque trees is inevitable and any action to preserve them would be purely for aesthetic reasons. Reducing the number of elephants by culling will only delay the inevitable, as trees do not reach adult height around waterholes owing to continuous browsing by other species.

The most serious problems in this regard is in the location of artificial waterholes, and the modifications of natural springs. Sensitive tree communities near present or future sites will inevitably disappear, unless further management is applied. The closure of boreholes "Reficiens" and "Gruenewald" reduced the rate of change in community structure of Acacia reficiens, Moringa ovalifolia and Colophospermum mopane respectively. At several other sites, individuals or colonies of Acacia species and Albizia anthelmintica are, or have been, under severe threat due to artificial provisioning of water nearby, such as at Adamax, Leeubron, Gemsbokvlakte and two leaking artesian boreholes between Okaukuejo and Homob.

Controlling elephant numbers in these areas is unlikely to succeed, but closing of those boreholes will remove the cause. Where waterholes cannot be closed for other reasons, alternative measures might be considered. Much of the resistance against closing water points come from those involved with tourism. I personally see a bleak future for the

Etosha National Park if tourism objectives dominate management objectives, and if the original features and attributes of the park are ignored.

Recent vegetation changes in the drought stricken and fungus riddled Acacia communities in the sandveld north of Namutoni were beyond human control, but subsequent damage by elephants could have been avoided by manipulation of artificial waterholes in this area. This could not be done for fear of forcing elephants east instead of south, and thus into a military training area. If the fence in that area had been effective, such management could be effective as virtually no other water-dependent species occur in this formerly waterless section of the park. Recent studies have shown that elephants avoid burnt areas (Bell & Jachmann 1984, Lewis 1987, McShane 1987), and this aspect has local management potential, particularly regarding isolated stands of locally rare trees.

Long-term problems.

Two possible scenarios regarding the long-term status of elephants in north-western SWA/Namibia and Etosha N.P. can be considered.

1. Forced confinement of the bulk of the regional population inside Etosha N.P. by the erection of elephant-proof fences on the northern boundary in particular. This option might be chosen in order to prevent large-scale poaching of black rhinoceros inside the park, or to finally demarcate the boundaries of Etosha N.P. by a very visible and durable fence to discourage further territorial claims against the park. The park would thus be sealed-off as far as large mammals are concerned, and ripe for serious manipulatory management, and a fair reflection of the isolationist conservation attitude prevalent in other parts of southern Africa up to the early 1980's. The conservation status of elephants hardly features in this scenario, yet they will be the most seriously affected. An elephant-proof fence around the park is not necessarily the cure against the poaching of black rhinoceros. Poachers in Etosha N.P. have recently crossed an electrified fence designed to be elephant-proof, in pursuit of ostrich and gemsbok, and will probably go to far greater extremes in order to hunt black rhinoceros.

2. By maintaining the status quo, seasonal movements of elephants in and out of the park will occur, and Etosha N.P. will continue to act as a vital drought refuge for elephants. The present system of "rotational" feeding will continue, largely in response to the seasonal deterioration of water quality inside the park and the

distribution of rainfall, which would prevent persistent browsing pressure on the woodlands by a sedentary population. Anthrax in the park will continue to impose high mortality rates, and the elephant population is unlikely to enter a prolonged phase of increase. Severe drought and anthrax outbreaks will act as the equivalent of age-specific harvesting (calf mortalities) or culling (anthrax outbreaks). In this scenario, the black rhinoceros population would have to be safeguarded by the translocation of individuals from vulnerable areas to places of safety, preferably outside the park. This would have the additional benefit of creating additional populations. If the future presence of elephants outside Etosha N.P. is in question due to poaching or other human activities, the elephant population should respond by moving to and limiting dispersals out of the park, as occurred elsewhere in Africa.

Restriction of migrations.

The present system of seasonal migration in and out of the park as determined by rainfall, is desireable as a form of rotational utilization of vegetation. Threats of erecting an elephant-proof fence on the entire northern boundary will have a severe effect on particularly that part of the population not contained within Etosha N.P. Dry season water sources outside the park are very limited and the consequences of such a fence might be disastrous. Having the bulk of the population in the park and then fencing it off, if this is possible, and then culling elephants inside because there are too many, is not a logical or even honourable option.

Further development of artificial waterholes in Etosha N.P. will also affect trends in vegetation change and elephant distribution. Permanent water in the wet season dispersal regions in the park will lead to sedentary elephants in those regions. The prime reason why the bulk of woodlands in the park have not been affected by elephants is because elephants only occupy the woodlands during the wet season when they predominantly feed on grass.

Human threats.

The absence of a buffer zone around Etosha N.P. brings the wildlife-human interface into sharp conflict at the park boundary. No development of private game reserves and a lucrative tourist industry on the borders of Etosha N.P. has occurred, as around, for example the Kruger National Park. Private landowners have little sympathy with elephants and have at present little inclination to exploit their favourable geographical position in terms of wildlife utilization. Communal landowners in Kaokoland and Ovambo are settling closer and closer to the park boundaries, presumably as more people are armed and wild animals do not pose the same threat as before. Several claims have been made against the park for deproclamation, and a minor battle of wills is currently being fought by farmers and rangers to push cattle in and out of the park.

The common intolerance towards wild animals and park affairs by both the private and communal land owners is a source of great concern, and an indictment against park staff and Directorate alike for allowing this situation to deteriorate to the present level. The real threat to elephants and conservation itself will most certainly come from the perceptions and aspirations of the Ovambo majority in this country, who are separated from the park by a single fence, and from conservation by a huge chasm.

As long as people on our borders receive no benefit from the park or elephants, conflicts are likely to increase. The situation in Kaokoland and Ovambo is particularly acute, as these people are likely to have decisive political control in the future. The fact that Etosha N.P. earns a substantial portion (exact figures are restricted) of the GNP from tourism means little if those on the frontline see virtually no benefit from these earnings. National benefit from parks and wildlife should certainly also be more vigourously expounded to local inhabitants, but a more direct solution to channel income from the park to the area around it should be sought. There is, for example, no initiative or incentive to enter the curio trade, virtually absent outside Etosha N.P., and products sold in tourist camps are virtually exclusively factory-produced. Yet Etosha N.P. is blessed with a large foreign tourist component traditionally receptive to rural articles.

Direct benefit from the park and game can be derived from various forms of hunting, by access to meat and products and fees for skills and services. Elephants culled in 1983 and 1985 were mostly processed as tinned corned meat, but little of the output reached local consumers, despite the very low price. This is one clear instance where a golden opportunity to win local goodwill by access to very cheap protein was lost. A tin of elephant meat might be a curiosity in urban communities, or a cheap ration for industry, but is possibly more valuable to a person with an income of less than R500 per annum (in 1987).

Opportunities for trophy hunting of elephants are decreasing throughout Africa, as populations outside parks dwindle from poaching. Elephants from SWA/Namibia have traditionally not yielded record ivory trophies, but are reknowned for another feature, namely size. The tallest elephants occur in this country (and southern Angola), and shoulder heights are listed separately in Rowland Ward records (Smith 1984). Elephants presently shot on boundary farms by park officials should qualify for trophy hunting, for obvious economic reasons. Hunting opportunities for elephant are sufficiently limited to still make the occasional bull from Etosha N.P. a lucrative proposition to a hunting agent.

This concept could be extended to the northern boundary, where harvesting could be initiated in a buffer zone, proposed as long ago as 1964 (Bigalke 1964). As long as our neighbours derive some income from elephants, they will tolerate them on their land, which is infinitely more desirable than restricting elephants to the Etosha N.P. by a fence. Farming practices in southern Ovambo are also ideally suited to accomodating a seasonal population of elephants. The idea is not as far-fetched as it seems, similar schemes are already operational in Zimbabwe, contemplated for Damaraland, and are in fact reminiscent of earlier days throughout subtropical Africa. Political stability of Ovambo is, however, the first requirement for this plan.