Impact of severe drought on the age structure of a population of African savannah elephants

Kevin M Dunham

PO Box CH385, Chisipite, Harare, Zimbabwe
email: kmdunham@protonmail.com

Abstract

Hundreds of elephants died during a severe drought in Gonarezhou National Park (Gonarezhou) in south-east Zimbabwe during 1992. The following year, entire female herds comprising 670 female and juvenile elephants were captured and translocated elsewhere. Sex-specific von Bertalanffy growth functions for shoulder height against age for elephants culled in Gonarezhou a decade earlier allowed 667 elephants captured during 1993 to be aged based on shoulder height. The captured elephants provided a representative sample of the age and sex structure of the population one year after the drought. Immediately after the drought, the age structure was determined by deducting one year from each elephant's age at capture and compared with that of elephant herds culled in Gonarezhou during 1972–1987. Adult females formed a high proportion (45%) of the individuals in female herds immediately after the 1992 drought, implying that there was high mortality of non-adults during the drought. There were relatively few surviving individuals in the 0–4-year age class, suggesting that mortality was greatest amongst the youngest individuals. When non-adults of all ages were considered, there were fewer males than females amongst the drought survivors, suggesting that the males experienced greater mortality than the females. Significant mortality of weaned elephant calves during droughts is uncommon and the high mortality of non-adults in Gonarezhou during 1992 highlights the particular severity of the drought.

Résumé

Des centaines d'éléphants sont morts lors d'une grave sécheresse qui a touché en 1992 le parc national de Gonarezhou, au sud-est du Zimbabwe. L'année suivante, des hardes entières comprenant 670 femelles et juvéniles ont été capturées et transférées en d'autres lieux. La fonction de croissance de von Bertalanffy spécifique au sexe (permettant de calculer l'âge des éléphants selon la hauteur de leurs épaules) a rendu possible de déterminer l'âge de 667 de ces individus capturés, par rapport aux données de hauteur d'épaules obtenues sur des éléphants abattus une décennie plus tôt à Gonarezhou. Les individus transférés ont fourni un échantillon représentatif de la répartition des âges et des sexes dans la population un an après l'épisode de sécheresse. La détermination des âges directement après la sécheresse a été effectuée en déduisant une année à l'âge de chaque éléphant lors de sa capture, et en le comparant à celui des hardes abattues à Gonarezhou entre 1972 et 1987. Les femelles adultes représentaient une large proportion des individus (45 %) dans les hardes de femelles immédiatement après la sécheresse de 1992, laissant entendre un taux élevé de mortalité chez les juvéniles pendant cet épisode. Relativement peu de survivants ont été comptés dans la classe d'âge de 0 à 5 ans, ce qui indique une plus grande mortalité des individus les plus jeunes. L'étude des juvéniles de tous âges a révélé qu'un nombre inférieur de mâles se trouvaient parmi les survivants de la sécheresse, ce qui tend à signifier que les mâles ont subi une plus grande mortalité que les femelles. Lors d'une sécheresse, il n'est pas rare de voir mourir une partie importante des éléphanteaux sevrés, et le taux élevé de mortalité chez les juvéniles de Gonarezhou en 1993 témoigne de la sévérité de la sécheresse de 1992.

Introduction

The frequency, duration and intensity of droughts have increased in southern Africa since the late nineteenth century (Chiang et al. 2021) and vulnerability to drought is predicted to increase across Africa (Ahmadalipour et al. 2019). Drought-induced mortality can have major impacts on the numbers of African savannah elephant *Loxodonta africana*, with juveniles and older adults often disproportionately affected (Corfield 1973; Dunham 1988; Dudley et al. 2001; Lee et al. 2022). Commonly, elephants that die during droughts are in poor condition and die close to water, implying that these animals die from dehydration, rather than starvation, or conditions associated with malnutrition.

Drought-related mortality can impact the age-sex structure of a population, with periods of high juvenile mortality causing a pronounced depression in the age profile (Lee et al. 2022). Even during relatively dry years, but not necessarily drought, elephant calf mortality may be elevated. Environmental factors also influence elephant conception rates. A further consequence of these impacts on mortality and conception may be the appearance of population pulses, with brief, exceptional rates of population increase if females become synchronized in their conceptions and births (Lee et al. 2011).

During 1992, there was a severe drought in south-eastern Zimbabwe and hundreds of elephants died in Gonarezhou National Park (henceforth Gonarezhou) (Leggett 1994). A year after the drought Wildlife Management Services (WMS) captured entire female herds in the park and these animals were translocated elsewhere (Coetsee 1996). Female herds are elephant herds that contain adult females and immatures, both females and males. These herds may be accompanied by adult males, which are assumed to be temporary visitors. The relatedness of the adult females and immatures in a female herd is unknown, but it is assumed that the herd is a family unit sensu Moss et al. (2011). The capture of numerous elephants in entire female herds during 1993 provided a representative sample of the population of females and immature males, from which the immediate post-drought sex and age structure of the female herds could be estimated. This study uses these estimates to demonstrate the severe impact of the 1992 drought on the population structure, as the first step in a study of the long-term consequences of the drought on the dynamics of the Gonarezhou elephant population.

Methodology

Study area

Gonarezhou NP lies <600 m above sea level and covers ~5,000 km^2 in the south-east lowveld of Zimbabwe, along the border with Mozambique. The region experiences a hot wet season during November–March, a cool dry season during April–July, and a hot dry season during August–October. Mean maximum temperatures exceed 30°C during all months except June and July. The area is noted for low, but very variable, annual rainfall, which declines slightly towards the south. Based on Climate Hazards Group InfraRed Precipitation with Station (CHIRPS) records (Funk et al. 2015), annual rainfall over the entire park averages 486 mm (July–June rainfall year, n = 42 years; coefficient of variation 29%). The 1992 drought followed a year when annual rainfall was 157 mm (32% of the mean) (Fig. 1). The period between the 1983 and 1986 elephant culls (see below) included two successive years of low rainfall during 1982/83 and 1983/84, when rainfall was 60% and 79% of the long-term mean, respectively. Dry season precipitation in the form of drizzle (*guti*) is common and averaged 21 mm during June–September (1981–2023), but with a significant decline since 1980.

The CHIRPS records do not fully capture the impact of the 1992 drought. During March 1992, a lowveld resident (T. Balance, quoted by Tayler 1992) wrote: "Zimbabwe has experienced the worst drought in living memory. In the south-east lowveld, the season's rainfall, which should have started in November, has ranged from 20 mm to 100 mm. This, in conjunction with high temperatures and endless cloudless days, has meant that there has been no summer growth. In addition, there is very limited browse, and in some areas, the trees have not flushed at all. There is therefore a total lack of food." The rain gauge on Malilangwe Wildlife Reserve, which adjoins the northern boundary of Gonarezhou, recorded 72 mm during the 1991/92 rainfall year, which contrasts with the annual mean of 563 mm (n = 73 years; coefficient of variation 34%) (B. Clegg pers. comm. 23 May 2024).

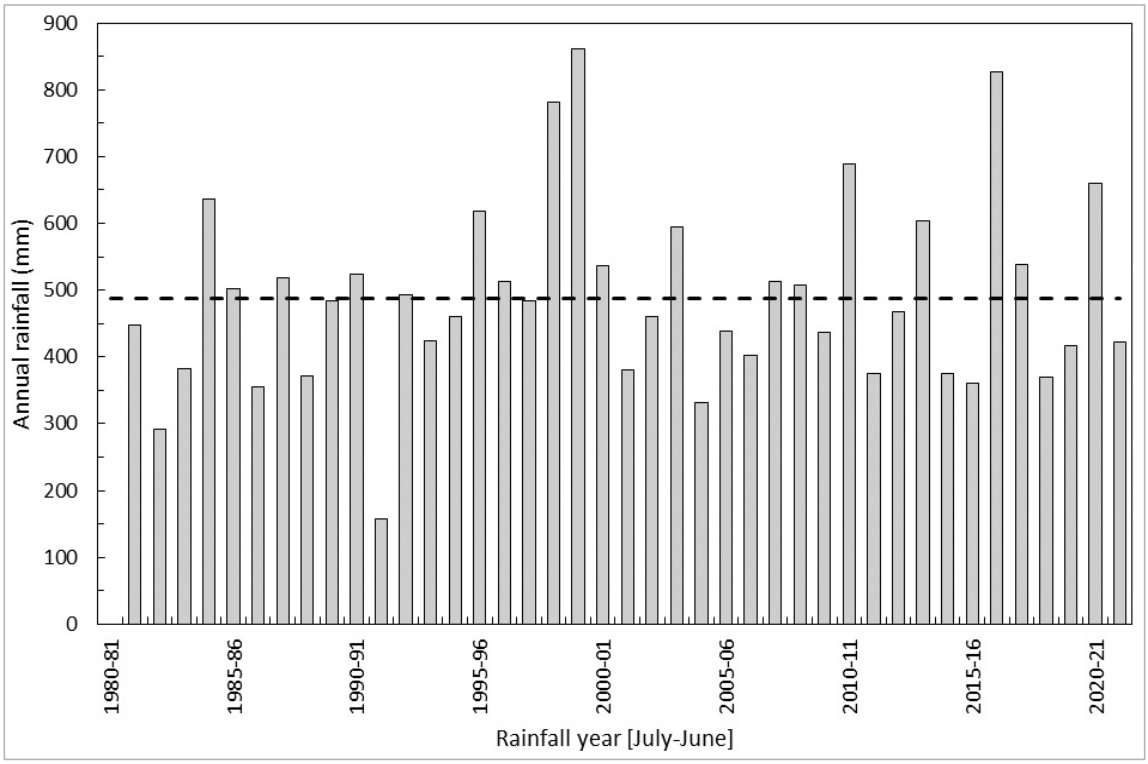


Figure 1. Temporal trend in annual rainfall (July–June) over Gonarezhou NP since 1981. The dashed line indicates the mean annual rainfall. Source: Climate Hazards Group Infrared Precipitation with Stations (CHIRPS) daily rainfall data downloaded from https://climateserv.servirglobal.net/

The Save, Runde and Mwenezi Rivers dominate Gonarezhou. The Runde and Save Rivers are perennial and dry-season flow in the Mwenezi River is controlled by the release of water from the Manyuchi Dam, ~130 km to the northwest. Other rivers flow only seasonally. The vegetation has been significantly impacted by elephants, drought and fire (Cunliffe et al. 2012; O'Connor et al. 2024). The major vegetation types are *Colophospermum mopane* shrubland or woodland on heavier soils; *Guibourtia conjugata* dominated woodland on sands; mixed woodland on granophyre; and riverine woodland (Farrell 1968; Cunliffe et al. 2012). As well as elephants, the Park supports hippopotami, buffalos, zebras and a range of antelope species and large predators (Dunham 2012; Groom et al. 2014).

During the 1970s, >2500 elephants were culled in Gonarezhou in response to concerns about the impact of elephants on the vegetation and another >4,000 were culled in total during 1983, 1986 and 1987 in response to continuing concerns (Booth 1989). Aerial sample surveys during the 1980s gave population estimates as shown in Table 1.

During culls, entire breeding female herds were sampled and so it is likely that these herds were representative of the population as a whole, excluding adult males, and therefore also that their removal had no significant effect on the age-sex structure of the remaining breeding population.

Culls were usually conducted during the middle of the dry season, before the onset of any drought-related mortality, as this normally occurs during the late dry season. Thus, for example, the age structure of the elephant population culled in 1983 cull might have been impacted by rainfall during the 1981/82 climate year (and/or preceding years), but was unlikely to have been affected by rainfall during the 1982/83 climate year, which ended shortly before the cull.

A year before the 1992 drought, the number of elephants in Gonarezhou and the corresponding 95% confidence interval (CI) were estimated using a transect sample survey as 6,306 ± 39% (Jones 1991). A sample survey a year after the drought used a

non-stratified design and produced an even less precise population estimate, namely 5,223 ± 55% (Bowler 1995).

During 1992, the fences bordering sections of the park boundary were not electrified and hence were ineffective at preventing the movement of elephants in or out of the park. However, there is no evidence that significant numbers of elephants moved in or out of the park as a consequence of the drought. An unrecorded number of elephants were culled by management staff during 1992; Tayler (1992) gives the number as ~350. A further 257 elephants were captured and removed from the park during late 1992 (Dobb 1993; Mockrin 2000). Of these, based on age estimates from shoulder heights (see Table 2, Fig 2 below), nine were aged 1.5–3.5 years, 194 were aged 3.5–7.5 years, 54 were described as 'adults' (taller than 185 cm and thus >7.5 years old). Many of these animals were expected to die as a consequence of the drought if they were not removed from Gonarezhou (Dobb 1993). The sex ratio of the animals captured is not known, as detailed records of the individuals captured during 1992 were seized from Wildlife Management Services, which undertook the captures, by the Department of National Parks and Wild Life Management. These were never returned and now appear effectively lost (Mockrin 2000).

Leggett (1994) searched near the Park's major rivers 12–18 months after the drought and collected jawbones and skulls from 251 drought victims, but, as he acknowledged, other jawbones may have disappeared during the interval between the drought and the collections. He determined the estimated age at death from 216 of the jawbones.

Table 1. Estimated elephant population and confidence intervals in Gonarezhou, 1980–1989. Sources: Coulson (1980, 1981); Sharp (1982, 1983, 1984, 1986, 1987); Gibson (1989)

Year	Estimated number of elephants	95% Confidence interval (%)
1980	4,704	30
1981	6,103	35
1982	7,315	34
1983	3,986	25
1984	3,937	36
1986	4,450	44
1987	3,802	42
1989	5,286	27

Age and sex composition of elephant female herds before and after 1992 drought

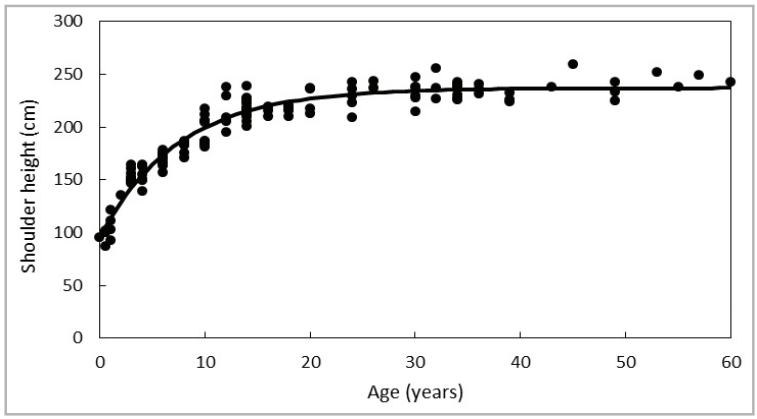
During August–October 1993, WMS captured 670 elephants in Gonarezhou (Coetsee 1996). Complete female herds of elephants were captured and translocated elsewhere. Sex and shoulder height were recorded for 667 of these elephants. Shoulder height was recorded whilst an elephant was immobilized, lying on its side.

Elephants were culled in Gonarezhou in 1983 (G.P. Sharp, unpublished data in the files of Gonarezhou NP). Data from that cull were used to determine, for each sex, a von Bertalanffy growth function for shoulder height against age for females aged up to 60 years and males aged up to 24 years. After this cull, the jawbone of each animal was examined and the individual was allocated to an age class based on molar eruption and wear (Laws 1966). For the current study, an actual age was allocated to each culled animal following Jachmann (1988). The Laws (1966) technique provides a robust mechanism for age determination and Jachmann's revision corrects for some deviations at younger ages (Lee et al. 2012), and the revision was used during this study because it included a high proportion of animals in these younger ages. The von Bertalanffy growth functions were fitted by minimizing the sum of the squared deviations for the data points, using the *Solver* tool in MS Excel. The equations for these sex-specific growth functions were used to estimate the age of each non-adult elephant captured during 1993 from its recorded shoulder height. The age of each captured elephant immediately after the 1992 drought was estimated by deducting one year from its age when caught during 1993.

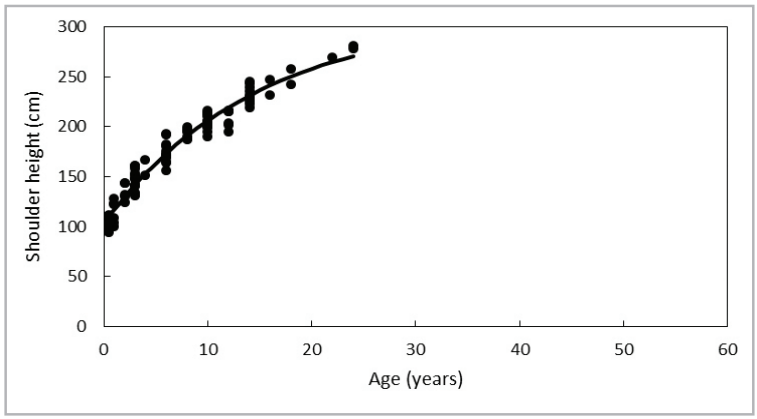
The age and sex composition of Gonarezhou elephant female herds immediately after the 1992 drought was compared with the compositions determined from the culls in Gonarezhou during 1972 (Sherry 1975), 1983, 1986 and 1987. Age determinations from 1972 were based on the criteria of Laws (1966) incorporating Jachmann's (1988) adjustments. For the 1983–87 culls, the age of each elephant was estimated from its shoulder height using the sex-specific von Bertalanffy

Table 2. The parameters of the von Bertalanffy growth functions relating shoulder height to age for elephants in Gonarezhou, using data from the 1983 cull. Following Hanks (1972), the von Bertalanffy growth function can be written as $h_t = H_\infty (1 - e^{-K[t - t_0]})$, where h_t is shoulder height (cm) at age t, K is the growth coefficient, t_0 is the theoretical age when height is zero, and H_∞ is the asymptotic shoulder height. The asymptotic shoulder height calculated for females is similar to the figure calculated for females culled in Gonarezhou during 1971–72 (241 cm; Sherry 1978).

Growth parameter	Asymptotic shoulder height (cm) (H_∞)	Growth coefficient (K)	Theoretical age when height is zero (t_0)	Sample size
Shoulder height females (0.5–60 years)	237	0.133	–3.877	125
Shoulder height males (0.5–24 years)	311	0.068	–5.916	91



(a) Females



(b) Males

Figure 2. Growth of shoulder height against estimated age for: (a) female elephants aged 0.5–60 years and (b) males aged 0.5–24 years, based on data from elephants culled in Gonarezhou during 1983. Age estimated from the lower molars using the Jachmann (1988) revision of the Laws (1966) criteria. The bold lines are the von Bertalanffy growth functions (See Table 2).

growth functions. During 1983–87, some young elephants within cull herds were captured for live sale. Only females were captured during 1983 and the age of each was estimated from its shoulder height. For 1986 and 1987, the number of captured elephants is known, but the shoulder height and sex of each was not recorded (although it is likely that, as during 1983, most were female aged 1–3 years). The dataset for the 1987 cull is incomplete and animals were included in this analysis only when the available data are for complete herds.

Results

Growth of Gonarezhou elephants

The von Bertalanffy growth function for the shoulder height of culled elephants in Gonarezhou (Table 2, Fig. 2) implied that the shoulder height of a female elephant averaged 218 cm at 15 years. Most females were mature by this age (Sherry 1975) and so females captured during 1993 that had a shoulder height ≥218 cm are defined as adults, with an estimated age of ≥15 years. Male elephants grew faster than females and the shoulder height of a male averaged 236 cm at 15 years and 271 cm at 24 years.

Age and sex composition of elephant female herds immediately after the 1992 drought

i. Proportion of immature elephants in female herds

Based on the age and sex structure of the elephants captured during 1993 (Table 3), it was estimated that a year earlier, immediately after the 1992 drought, there were, on average, 1.23 immature elephants aged 0–14 years in the female herds for each adult female. This compared with 2.00–2.96 immatures per adult female during the earlier years (Table 4). The ratio differed significantly between years, based on a chi-square test of the numbers of immatures and adult females during each year ($\chi2 = 57$, df = 4, n = 2,546, $p < 0.001$) and the 1992 ratio was also significantly different from the smallest of the earlier ratios, that for 1987 ($\chi2 = 5.7$, df = 1, n = 725, $p = 0.02$). The ratios also differed among years before the 1992 drought, based on a chi-square test of numbers during the years 1972, 1983, 1986 and 1987 ($\chi2 = 8.9$, df = 3, n = 1,947, $p = 0.03$).

ii. Ages of immature elephants

After the 1992 drought, there were 0.22 juveniles aged 0–4 years per adult female, compared with 0.75–1.49 per adult female during earlier years (Fig. 3). The ratio differed significantly between years ($\chi2 = 127$, df = 4, n = 1,457, $p < 0.001$) and the 1992 ratio was significantly different from the smallest of the earlier ratios, that for 1986 ($\chi2 = 58$, df = 1, n = 949, $p < 0.001$).

After the 1992 drought, there were 0.30 females in the 5–9 year age class per adult female, compared with 0.41–0.45 per adult female during earlier years (Fig. 3), but the ratio did not differ significantly between years ($\chi2 = 5$, df = 4, n = 1,166, $p = 0.29$). For males in this age-class, the ratio differed significantly between all years ($\chi2 = 17.5$, df = 4, n = 1,159, $p < 0.002$), but did not differ significantly between 1972, 1983, 1986 and 1987 ($\chi2 = 3.5$, df = 3, n = 825, $p = 0.32$).

For immature elephants in the 10–14 year age-class, the number per adult female did not differ between years for females ($\chi2 = 6$, df = 4, n = 1,078, $p = 0.2$), males ($\chi2 = 5$, df = 4, n = 1,066, $p = 0.29$), or both sexes combined ($\chi2 = 5$, df = 4, n = 1,299, $p = 0.27$).

iii. Sex ratio of non-adults

Immediately after the 1992 drought, the numbers of females and males aged <2 years (aged 1–3 years at the time of the captures a year after the drought) were identical (Table 3). But in each year class (except one) covering the ages 3–13 years, the number of females exceeded the number of males. Considering all elephants aged 3–13 years, the ratio of females to males (150:111) was significantly different from 1:1 (binomial test, $p < 0.02$).

The ratio of females to males aged 3–13 years in 1972 (131:111) and 1983 (54:61) did not differ significantly from 1:1 (1972: $p = 0.27$; 1983: $p = 0.6$). For 1986 and 1987, the sex ratio of immatures could not be determined, because the sex of captured animals is not known.

Table 3. Shoulder heights and numbers of elephants in female herds captured in Gonarezhou during August–October 1993 (Coetsee 1996). The age of each elephant was estimated from sex-specific, von Bertalanffy growth functions derived from data for elephants culled in Gonarezhou during 1983. The individuals in the 0–0.99 year age class were born during the year after the 1992 drought. The age of all other individuals at the end of the drought was estimated by subtracting 1 year from their age at capture.

Females			Males		
Age class (years)	**Shoulder height (cm)**	**Number in class**	**Age class (years)**	**Shoulder height (cm)**	**Number in class**
0–0.99	<114	23	0–0.99	<117	30
1–1.99	114–129	6	1–1.99	117–130	6
2–2.99	130–142	3	2–2.99	131–142	3
3–3.99	143–154	13	3–3.99	143–153	2
4–4.99	155–164	7	4–4.99	154–163	6
5–5.99	165–173	8	5–5.99	164–173	5
6–6.99	174–181	22	6–6.99	174–182	10
7–7.99	182–188	15	7–7.99	183–191	21
8–8.99	189–194	17	8–8.99	192–199	10
9–9.99	195–200	9	9–9.99	200–206	8
10–10.99	201–204	18	10–10.99	207–213	16
11–11.99	205–208	13	11–11.99	214–219	11
12–12.99	209–212	11	12–12.99	220–225	9
13–13.99	213–214	17	13–13.99	226–231	13
14–14.99	215–217	7	14–14.99	232–236	7
15–15.99	218–219	19	15–15.99	237–241	12
≥16	≥220	269	16–16.99	242–246	6
			≥17	≥247	15
Total		**477**			**190**

*Elsewhere in this paper, the ages of elephants are described simply by the number of full years; for example, animals described as 4 years old are in the 4–4.99 year age class.

Table 4. The numbers of females and immature males in entire female herds of elephants in Gonarezhou. Adult females are estimated to be 15 years of age or older and immatures 0–14 years of age. Data for 1972–1987 is from culls and data for 1992 from the 1993 captures. The sex and height of young elephants captured during the 1986 and 1987 culls was not recorded. The table gives the minimum and maximum possible numbers, but it is likely that most, if not all, were female.

Year	Immature female			Immature male			Adult female	Total
	0 to 4 yr	5 to 9 yr	10 to 14 yr	0 to 4 yr	5 to 9 yr	10 to 14 yr		
1972	97	52	45	86	49	28	123	480
1983	35	24	22	35	30	20	56	222
1986	(79–166)	145	89	(100–187)	159	105	355	1119
1987	(16–24)	19	10	(10–18)	11	10	42	126
1992	37	81	67	22	65	58	269	599

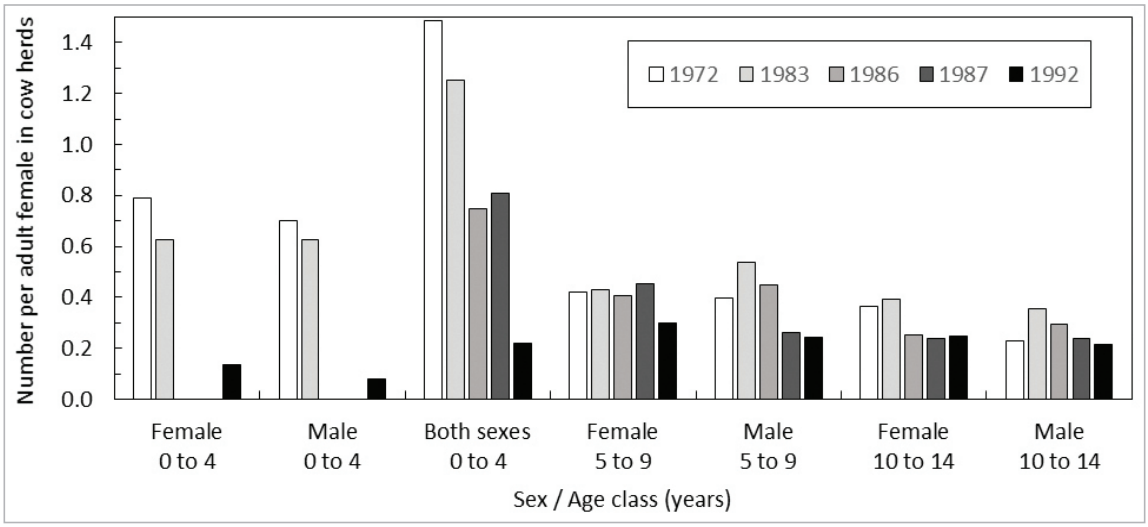


Figure 3. Ratio of the numbers of immature elephants, by sex and age class, to the number of adult females in female herds in Gonarezhou immediately after the 1992 drought and during culls in earlier years. The sex of some young elephants captured during the 1986 and 1987 culls was not recorded, but it is likely that most, if not all, were female.

Discussion

The small number of calves aged 0–4 years per adult female immediately after the 1992 Gonarezhou drought compared to earlier years (Fig. 3) suggests that there was major drought-related mortality amongst juvenile elephants in this age class. Determining if the impact of this mortality varied between males and females aged 0–4 years is complicated by the incomplete sex records for the 1986 and 1987 culls. Numbers of females and males aged 5–9 years per adult female were smaller during 1992 than during earlier years, but the difference between years was not statistically significant for females. The difference between years for males was significant only when 1992 was included in the comparison. This implies that there were significantly fewer males aged 5–9 years per adult female in 1992 than during earlier years, which was likely a consequence of greater mortality amongst these males than amongst similarly aged females during the 1992 drought. The female bias amongst the 1992 drought survivors aged 3–13 years (Table 3) also suggests that there was greater drought-related mortality amongst non-adult males than amongst non-adult females. The number of elephants in the 10–14 year age class per adult female did not vary significantly between years for males or females (Fig. 3). This suggests that mortality amongst animals in this age class during the 1992 drought was similar for males and females, and that the drought-related mortality experienced by elephants in this age class was similar to that experienced by adult females.

These observations are consistent with those of Leggett (1994) who recovered jawbones of drought victims up to ~50 years. A high proportion (49%, n = 216) were from elephants aged <12 years. That non-adults suffered greater mortality during the Gonarezhou drought and that, amongst younger non-adults, males probably suffered greater mortality than females, is also consistent with the pattern of drought mortality observed amongst elephants elsewhere (Foley et al. 2008; Lee et al. 2022).

In common with the Gonarezhou results, studies elsewhere find high drought mortality among immature elephants. In Amboseli, Kenya, extreme, prolonged droughts during the 1970s and 1980s resulted in exceptionally high calf mortality of between 40 and 60% during the first two years of life, while average non-drought calf mortality was ~12% (Lee et al. 2011, 2022). In Tarangire, Tanzania, drought mortality during 1993 among animals aged <8 years was 20%, with the majority of these deaths occurring amongst dependent calves (Foley et al. 2008). Elephants aged <8 years were also highly vulnerable to drought in Mana Pools, Zimbabwe, during 1983 and Hwange, Zimbabwe, during 2019 (Dunham 1988; Ndlovu et al. 2023) and in Tsavo NP, Kenya during 1970 and 1971,

when high juvenile mortality occurred amongst youngsters in the 2–4 and 5–10-year age classes (Corfield 1973).

When males aged 15 years or older within breeding herds were ignored, the percentage of adult females in Gonarezhou herds varied from 25% during 1972 and 1983, to 32–33% during 1986 and 1987, and 45% in 1992. These differences may reflect high non-adult mortality during droughts, with the first increase in the proportion of adult females coinciding with low rainfall during 1982/83 and 1983/84, and the second increase overlapping the 1992 drought. However, the relatively high proportion of adult females in herds during 1986 and 1987 could also reflect a low birth rate two years after the droughts (two years being the gestation period), or a combination of high juvenile mortality during droughts and a low birth rate two years afterwards. Although the 1993 captures provide good data on the age and sex structure of the female herds after the 1992 drought, there is no information available about the structure immediately before it. Hence, any attempt to use the post-drought age structure to quantify the impact of the drought on the Gonarezhou elephant population would be speculative and is avoided here.

The demographic consequences of the high mortality amongst the non-adults and its impact on the age and sex structure of the female herds will be examined in a forthcoming paper. This will demonstrate how the high rate of increase in the number of elephants in female herds observed after the drought (7.3% per annum during 1995–2009; Dunham 2012) is consistent with the high proportion of mature females in the female herds immediately following the drought. It will also argue that the absence of any observed increase in the number of males in bull groups over that same period is consistent with the low recruitment of males from female herds to bull groups for ~15 years after the drought, until the cohort of males born during 1993, the year after the drought, left their natal female herds.

Acknowledgements

All the data used during this study were collected by other people. The foundations of the study are the records of the elephants captured during 1993 by the late Clem Coetsee and I am grateful to Em Coetsee for making her husband's data available to me. The study also draws on unpublished data collected by Gary Sharp and his colleagues during the 1980s. Hugo and Elsabe van der Westhuizen of the Frankfurt Zoological Society have helped me over many years. I thank them for their patience.

References

Booth VR. 1989. The number of elephants killed in Zimbabwe: 1960–1988. In: Martin RB, Craig GC, Booth VR (Eds). *Elephant Management in Zimbabwe*. Department of National Parks and Wild Life Management, Harare, pp. 41–45.

Bowler M. 1995. The aerial census of elephant and other large mammals in north-west Matabeleland, Zambezi Valley and Gonarezhou National Park, Zimbabwe: August–October 1993. Department of National Parks and Wild Life Management, Harare.

Coetsee C. 1996. Elephant translocations. *Pachyderm* 22: 81–82.

Corfield TF. 1973. Elephant mortality in Tsavo National Park, Kenya. *East African Wildlife Journal* 11: 339–368.

Cunliffe R, Muller T, Mapaura A. 2012. Vegetation survey of Gonarezhou National Park, Zimbabwe. Frankfurt Zoological Society, Gonarezhou Conservation Project, Chiredzi.

Dobb L. 1993. A world first—the translocation of adult African elephants in Zimbabwe. *Zimbabwe Wildlife* 71: 14–15.

Dudley JP, Craig GC, Gibson DStC, Haynes G, Klimowicz J. 2001. Drought mortality of bush elephants in Hwange National Park, Zimbabwe. *African Journal of Ecology* 39: 187–194.

Dunham KM. 1988. Demographic changes in the Zambezi Valley elephants (*Loxodonta africana*). *Journal of Zoology* 215: 382–388.

Dunham KM. 2012. Trends in populations of elephant and other large herbivores in Gonarezhou National Park, Zimbabwe, as revealed by sample aerial surveys. *African Journal of Ecology* 50: 476–488.

Farrell JAK. 1968. Preliminary notes on the vegetation of the lower Sabi-Lundi basin, Rhodesia. *Kirkia* 6: 223–248.

Foley C, Pettorelli N, Foley L. 2008. Severe drought and calf survival in elephants. *Biology Letters* 4: 541–544.

Funk C, Peterson P, Landsfeld M, Pedreros D,

Verdin J, Shukla S, Husak G, Rowland J, Harrison L, Hoell A, Michaelsen J. 2015. The climate hazards infrared precipitation with stations—a new environmental record for monitoring extremes. *Scientific Data* 2: 150066.

Gibson DStC. 1989. Aerial census of larger mammals in the National Parks Estate of Zimbabwe. Department of National Parks and Wild Life Management, Harare.

Groom RJ, Funston, PJ, Mandisodza R. 2014. Surveys of lions *Panthera leo* in protected areas in Zimbabwe yield disturbing results: what is driving the population collapse? *Oryx* 48: 385–393.

Hanks J. 1972. Growth of the African elephant (*Loxodonta africana*). *East African Wildlife Journal* 10: 251–272.

Jachmann H. 1988. Estimating age in African elephants: a revision of Laws' molar evaluation technique. *African Journal of Ecology* 26: 51–56.

Jones MA. 1991. Aerial census of elephant and other large mammals in Gonarezhou National Park and adjacent areas: September 1991. Department of National Parks and Wild Life Management, Harare.

Laws RM. 1966. Age criteria for the African elephant *Loxodonta africana*. *East African Wildlife Journal* 4: 1–37.

Lee PC, Lindsay WK, Moss CJ. 2011. Ecological patterns of variability in demographic rates. In: Moss CJ, Croze H, Lee PC (Eds). *The Amboseli elephants: a long-term perspective on a long-lived mammal*. University of Chicago Press, Chicago, pp. 74–88.

Lee PC, Moss CJ, Njiraini N, Poole JH, Sayialel K, Fishlock VL. 2022. Cohort consequences of drought and family disruption for male and female African elephants. *Behavioral Ecology* 33: 408–418.

Lee PC, Sayialel S, Lindsay WK, Moss CJ. 2012. African elephant age determination from teeth: validation from known individuals. *African Journal of Ecology* 50: 9–20.

Leggett K. 1994. Implications of the drought on elephants on Gonarezhou National Park – a preliminary report. Report on the Raleigh International Expeditions 93K and 948 to Gonarezhou National Park, September 1993 to May 1994. Unpublished report.

Mockrin MH. 2000. The restocking of Save Valley Conservancy with African elephants: an assessment of the translocation exercises and a model to predict population growth. Unpublished report.

Moss CJ, Croze H, Lee PC. 2011. The Amboseli elephants: introduction. In: Moss CJ, Croze H, Lee PC (Eds). *The Amboseli elephants: a long-term perspective on a long-lived mammal*. University of Chicago Press, Chicago, pp. 1–7.

Ndlovu M, Madiri TH, Madhlamoto D, Tadyanehondo KM, Vambe A, Mungoni E. 2023. Age-sex structure of drought-driven African elephant (*Loxodonta africana*) mortality in Hwange National Park, Zimbabwe. *Scientific African* 19: e01459.

O'Connor TG, Pallett NCM, Clegg BW, Shimbani J. 2024. Local extirpation of woody species in *Colophospermum mopane* woodland under chronic utilisation by elephants. *African Journal of Ecology* 62: e13296.

Sharp GJ. 1982. 1982 aerial survey of the Gonarezhou elephant population. Unpublished report, Department of National Parks and Wild Life Management, Chiredzi.

Sharp GJ. 1983. 1983 aerial survey of the Gonarezhou elephant population. Unpublished report, Department of National Parks and Wild Life Management, Chiredzi.

Sharp GJ. 1984. 1984 (dry season) aerial survey of the Gonarezhou elephant population. Unpublished report, Department of National Parks and Wild Life Management, Chiredzi.

Sharp GJ. 1986. 1986 aerial survey—Gonarezhou National Park. Unpublished report, Department of National Parks and Wild Life Management, Chiredzi.

Sharp GJ. 1987. 1987 (early season) aerial survey—Gonarezhou National Park. Unpublished report, Department of National Parks and Wild Life Management, Chiredzi.

Sherry BY. 1975. Reproduction of elephant in Gonarezhou, south-eastern Rhodesia. *Arnoldia* 7 (29): 1–13.

Sherry BY. 1978. Growth of elephants in the Gonarezhou National Park, south-eastern Rhodesia. *South African Journal of Wildlife Research* 8: 48–58.

Tayler D. 1992. November to November—the Lowveld drought. *Hartebeest (Journal of the Lowveld Natural History Society)* 24: 6–11.