Impact of severe drought-related mortality on the subsequent dynamics of a population of African savannah elephants

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Abstract

Drought-induced mortality can significantly impact the numbers of African savannah elephants (*Loxodonta africana*) in a population, with juveniles and older adults often disproportionately represented among the elephants that die. During the severe drought in south-eastern Zimbabwe in 1992, hundreds of elephants perished, especially young elephants under eight years of age. Notably, more male juveniles than females succumbed to the drought. The impacts on the age and sex structure of an elephant population may persist for many years following such a drought period. This manuscript utilises data from frequent aerial surveys and a simple population model based on age and sex, including the unusual age and sex structure of the female herds recorded a year after the drought, to examine these impacts over a 30-year period in a population of several thousand elephants in southern Africa. Immediately after the drought, the number of elephants in female herds increased rapidly, but there was no corresponding increase in the number of elephants in bull groups. Male recruitment—when young male elephants transfer from their natal female herds to bull groups—decreased to low levels during the ~16 years following the drought. Only when males born after the drought transferred to bull groups did the predicted and observed numbers of bulls increase. Model-predicted trends in the numbers of elephants in female herds and bull groups were a credible fit with survey estimates. The number of elephants in Gonarezhou National Park increased threefold after 1993. Since 2013, the population has numbered ~11,000. This levelling off coincided with the movement of some elephants into areas bordering the Park.

Résumé

La mortalité due à la sécheresse peut avoir de lourdes répercussions sur le nombre d'éléphants de savane d'Afrique (*Loxodonta africana*), notamment chez les individus juvéniles et les adultes plus âgés, souvent surreprésentés dans le nombre de morts recensées. Lors de la sécheresse qui a frappé le sud-est du Zimbabwe en 1992 et qui a vu périr des centaines d'éléphants, un taux de mortalité particulièrement élevé a été relevé parmi les individus de moins de huit ans. Dans cette classe d'âge, les mâles ont été plus touchés que les femelles. À la suite d'une période de sécheresse, les incidences sur les structures d'âges et de sexes d'une population d'éléphants peuvent s'observer durant de nombreuses années. Cet article s'appuie sur les résultats de recensements aériens réguliers et sur un modèle démographique simple basé sur l'âge et le sexe – y compris les structures d'âge et de sexe inhabituelles relevées chez les hardes de femelles un an après l'épisode de sécheresse – afin d'étudier ces impacts sur trente ans dans une population de plusieurs milliers d'éléphants en Afrique australe. Immédiatement après la sécheresse, le nombre d'éléphants dans les hardes de femelles a rapidement augmenté, mais aucune hausse dans les groupes de mâles n'a été constatée. Pendant les seize années qui ont suivi la sécheresse, le taux de recrutement d'éléphants mâles (lorsque de jeunes individus quittent leur harde de femelles d'origine pour rejoindre des groupes de mâles) a décliné jusqu'à atteindre des niveaux faibles. Ce n'est que lorsque des mâles nés après la sécheresse ont intégré des groupes de mâles que les prévisions et les chiffres observés ont augmenté. Les tendances prévues par le modèle quant au nombre d'éléphants dans les hardes de femelles et les groupes de mâles correspondaient de manière crédible aux chiffres des estimations. Le nombre d'éléphants dans le parc national de Gonarezhou a été multiplié par trois après 1993. Depuis 2013, la population compte environ 11 000 individus. Cette stabilisation a coïncidé avec la migration de certains éléphants vers des zones adjacentes au parc de Gonarezhou.

Introduction

Drought-induced mortality can have major impacts on the numbers of African savannah elephant (*Loxodonta africana*), with juveniles and older adults often disproportionately represented among the elephants that die (Corfield 1973; Dudley et al. 2001; Lee et al. 2022). Hundreds of elephants died during the 1992 drought in south-eastern Zimbabwe, with particularly high mortality among youngsters <8 years of age (Leggett 1994), but there is no reliable estimate of the number that died. During 1993, the year after the drought, Coetsee (1996) captured >600 elephants in entire female herds in Gonarezhou National Park (Gonarezhou going forward). The age of each captured immature elephant was estimated from its recorded shoulder height using sex-specific growth curves constructed from shoulder height and age data collected during earlier culls in Gonarezhou (Dunham 2024).

The 667 elephants in 55 female herds captured during 1993 were removed from a population estimated to have included 3,000–4,000 elephants in female herds (see Fig. 7a). Hence, the captured elephants formed a sample of 17–22% of elephants in female herds. Because entire herds were caught, the captured elephants provided a representative sample of the population of females and immature males during 1993, from which the sex and age structure of the female herds could be estimated (Dunham 2024). The captured herds contained a high proportion of adult females and a low proportion of immatures.

Aerial surveys of the elephant population in Gonarezhou during 1995–2009 revealed that the estimated number of elephants in female herds increased by 7.3% per annum (Dunham 2012). The numbers of buffalo (*Syncerus caffer*), eland (*Taurotragus oryx*), kudu (*Tragelaphus strepsiceros*), waterbuck (*Kobus ellipsiprymnus*), wildebeest (*Connochaetes taurinus*) and zebra (*Equus quagga burchellii*) also increased rapidly during this post-drought period. But for elephants in bull groups, the trend was different: their number was approximately constant from 1995 to 2009, but increased rapidly after 2009 (see Fig. 3).

While drought-induced mortality is immediately noticeable, it can have long-term population impacts that are less obvious. This study aimed to reveal if and how the different population trajectories of elephants in bull groups and those in female herds can be explained by the unusual age structure of the elephants that survived the drought. A simple, sex-age structured model of an elephant population was constructed to mimic the population of Gonarezhou. The model population started a year after the drought mortality and immediately after the 1993 captures, with an age structure similar to that recorded. Other model parameters were based on information from Gonarezhou or from the literature. The model population mimicked the period 1993–2022, each year increasing the population by births and reducing it by natural mortality, the recorded offtakes, and emigration. The 1993 age structure was the only parameter in the model that was unusual for an elephant population. Therefore, if the modelled population numbers are a reasonable fit to the survey estimates, this would suggest that the unusual population trends observed after the drought were likely a consequence of that age structure.

The advantage of a simple model, such as used here, is that, if the modelled population trends are a reasonable fit to the survey estimates, then it is likely that the parameters included in detail in the model and which vary annually (e.g. the sex and age structure of immatures in the model) play a major role in producing the trends. Conversely, parameters that are simply averaged for the entire run of the model (e.g. the fecundity schedule) likely play little or no role in producing the trends.

The absence of an increase in the number of elephants in bull groups prior to 2009 could perhaps be attributed to a factor such as emigration or unrecorded poaching (the latter especially so, given that the number increased rapidly after 2009, following the commencement of technical support to Park management by Frankfurt Zoological Society

(FZS)). However, any attempt to explain the observed trend in the number of elephants in bull groups after 1993 needs to commence with the unusual age structure of the female herds recorded during 1993—because these herds provided the males that were recruited to the bull groups. If emigration or poaching were significant factors in determining the observed trend, then a model incorporating these factors—and the unusual age structure—would better fit the survey estimates than a model that included just the unusual age structure. Hence, the model described above, starting with the unusual age structure, was also run assuming that some adult males were poached annually prior to 2008. The model was run several times, each time assuming that the number of poached bulls was constant between years, but varying between model runs.

After 2014, the estimated number of elephants in the female herds in Gonarezhou stopped increasing and appeared to stabilise (Fig. 3). It was not intended that the model presented here would mimic this levelling off, which is likely not related to the 1992 drought.

Methods

Study area

The study area is described briefly here, and in more detail by Dunham (2024). Gonarezhou NP lies <600 m above sea level and covers ~5,000 km^2 in south-eastern Zimbabwe, bordering Mozambique to the east (Fig. 1). 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, and is noted for low and variable annual rainfall. Annual rainfall over the Park averages 486 mm (July–June rainfall year, n = 42 years; coefficient of variation 29%, CHIRPS records (Funk et al. 2015)). The 1992 drought followed a season of very low rainfall (annual rainfall during the 1991–1992 climate year was 157 mm, 32% of the mean). The CHIRPS records do not fully capture the impact of the 1992 drought, described by a lowveld resident as "the worst drought in living memory" (see Dunham (2024) for more details).

The Save, Runde and Mwenezi rivers dominate the area, although all rise well outside the Park. The Runde and Save are perennial, and dry season flow in the Mwenezi is controlled by water release through Manyuchi Dam, ~130 km upstream. Other rivers flow only seasonally. Elephants, drought and fire have significantly impacted the vegetation. The main vegetation types are: *Colophospermum mopane* shrubland or woodland in heavier soils; *Guibourtia conjugata* and *Combretum* dominated woodlands in sands; mixed woodland in granophyre; and riverine woodland (Cunliffe et al. 2012).

Since 2011–2012, electric fences have limited elephant movement to the north and north-west of Gonarezhou (Mandinyenya 2021) and, during 2016, the fence line was extended southwards. The Naivasha area (a wilderness area within the adjacent communal land) was included within this fenced area. Elephants are free to move from Gonarezhou to the Mahenye communal area (which includes subsistence agriculture and livestock, as well as uncultivated land), Naivasha, the Malipati Safari Area (henceforth Malipati) (a protected area) and Mozambique. Within Mozambique, adjacent to the international border, are *fazendas de bravio* (privately-owned areas intended for both wildlife conservation and hunting) totalling ~1,400 km^2. Malilangwe Wildlife Reserve (WR) lies on the northern border of Gonarezhou and since its boundary fence was completed during 2011, net movements of elephants in or out of Malilangwe WR have been limited to <5 bulls per year (B. Clegg, pers. comm., 3 January 2023).

Small numbers of elephants (<50) are also shot annually in communal areas in Zimbabwe immediately adjacent to the Park, either for problem animal control (PAC), or by trophy hunters. Prior to 2018, trophy hunting also occurred in Malipati. Some illegal hunting of wildlife occurs in the Park. A year after the 1992 drought, Coetsee (1996) captured complete female herds in Gonarezhou and translocated them elsewhere. These herds comprised 477 females of all ages, 169 males of 15 years of age or younger, and 21 males of 16 years of age or older (Dunham 2024). It is assumed here that the age and sex structure of the immatures in those herds, and the ratio of immatures to adult females, were representative of the Gonarezhou female herds during 1993.

Male and female elephants fitted with satellite collars stayed mainly within the Gonarezhou boundaries during 2009–2012 (Westhuizen 2012). The use of areas outside the Park, was mainly to the east, on the Mozambique side of the unfenced international border in the *fazendas de bravio*. Elephants

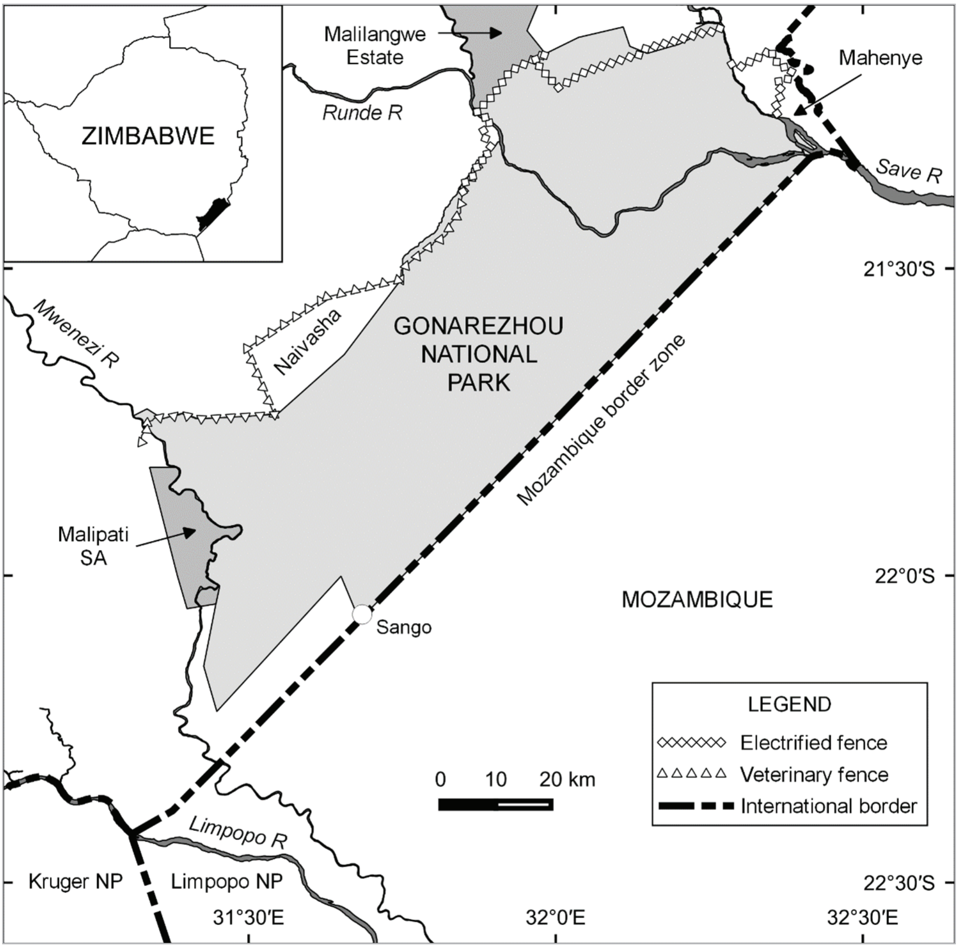

Figure 1. Gonarezhou, Kruger NP (South Africa) and Limpopo NP in Mozambique, together with the communal land between Gonarezhou and Kruger NPs, form the Great Limpopo Transfrontier Park. The insert shows the location of Gonarezhou on the south-eastern border of Zimbabwe.

occasionally move between Gonarezhou and Kruger National Park (NP), but there is no evidence that this movement is permanent and hence would constitute emigration (Sherry 1978; Henley 2013; Mandinyenya et al. 2024).

Sample surveys of the Gonarezhou elephant population

The first rigorous census of Gonarezhou elephants was carried out during 1980 and since then, similar sample aerial surveys have been undertaken regularly during the dry season. The survey methods followed those recommended for large African herbivores (Norton-Griffiths 1978). Surveys since 1995 have provided separate estimates of the number of elephants in bull groups and the number of elephants in female herds. Bull groups contained subadult and adult males, with solitary males treated as a bull group of size one. Elephants in female herds included adult females, immature elephants of both sexes and probably a few adult bulls. Elephant carcasses were also counted during the surveys. Estimating mortality from survey carcass data would be complex (Huso 2011), but the carcass ratio—the percentage of elephants seen that are dead—can provide a useful index of elephant mortality during the years preceding a survey (Douglas-Hamilton and Hillman 1981; Douglas-Hamilton and Burrill 1991). During surveys, Malipati was treated as part of Gonarezhou until 2007, but separately since 2009. Surveys since then have included the Mahenye and Naivasha areas.

Surveys during 2009, 2014 and 2022 included an area ~15 km wide of Mozambique adjacent to the international border and stretching from the Save River towards the Sango border post. This area was also surveyed in 2018 (Craig and Gibson 2018). Since 2014, the number of dead elephants in this Mozambique border zone has exceeded the number of live ones: the carcass ratio (Douglas-Hamilton and Burrill 1991) was 87–100% during 2014, 2018 and 2022.

Estimating how many elephants moved into this zone and died there depends on the duration of the period after the death of an elephant, that its carcass remains visible to a survey observer. Two trend lines were calculated for the estimated number of elephants (alive or dead) in the Mozambique border zone. A lower trend line assumed that all carcasses seen during surveys remained visible to observers during subsequent surveys; and an upper trend line assumed that all carcasses had disappeared (from the view of survey observers) by the time of the next survey, four or five years later.

When a plot of survey estimates against time suggested that it was appropriate, an exponential rate of population change per annum (r hat) was calculated, with 95% confidence limits (CL), using a weighted regression of natural logarithms of the survey estimates against time, with the variance of this rate of change based on the sampling variances of the survey estimates (Gasaway et al. 1986). For the variable estimates of the number of adult males in Malipati or Mahenye, an annual linear rate of population change ($\hat{g}$) was calculated. Two survey estimates were compared with a two-tailed t-test, with the null hypothesis that the population number had not changed. Other statistical tests followed Zaiontz (2025).

When a plot suggested that the rate of population change decreased with time, a logistic curve was fitted to the survey estimates. Sibly et al. (2005) suggested that, in a wide range of animal species, population regulation was generally the result of a concave relationship between the growth rate of a population and its size, in which case the theta-logistic model was more appropriate than the simple Ricker model used here. However, after a recent simulation study comparing models, Koetke et al. (2020) suggested that the Ricker model is appropriate for population survey data of species with slow life histories. It is not the intention here to compare various forms of the logistic model to determine their fit to the Gonarezhou survey data, and the Ricker logistic is used here merely to illustrate the general form of the logistic curve.

Population model

A model of an elephant population, which would mimic the real Gonarezhou population, was constructed using an MS Excel spreadsheet. The model population was divided into males and females and into 60 age classes, each representing one year (0–1,….. 59–60) and commenced immediately after the 1993 captures. The age structure of the non-adults, and the ratio of non-adult elephants to adult females, in the model at that time were proportionally the same as those observed amongst the captured elephants (Dunham 2024). The ages of the adult females could not be estimated from their shoulder heights. Hence, the age structures of the adult females and adult males <40 years of age were estimated approximately from the adult female and adult male age structures during the 1986 Gonarezhou cull (GP Sharp, unpubl. data, Gonarezhou NP files, May 2008), with each age class advanced seven years. Entire female herds and bull groups were included in this cull; hence it provided representative samples of both adult females and adult males. In the model, it was assumed that no elephants >40 years of age survived the 1992 drought. Leggett (1994) found few carcasses of elephants older than 40 years. This observation was taken as indicating that there were few elephants >40 years of age in the population immediately before the 1992 drought and that the older elephants present died during the drought. In Amboseli, Kenya, researchers also noted the high mortality for females >40 years of age during droughts (Lee et al. 2022).

In the model, each year starts at the beginning of the rainy season. The population number then increased with births. The proportion of fertile females in each age class followed the fertility versus age graph of Sherry (1975), but with ages adjusted to the schedule of Jachmann (1988). The proportion of females in each age class that gave birth annually was calculated as the proportion that were fertile divided by the mean CI, in years. This interval was assumed to be constant between years. The sex ratio at birth was assumed to be 1:1 (Sherry 1975). The elephants in each age/

sex class advanced to the next (older) age class, while the newborn elephants moved into age class 0–1.

The number of elephants in each age/sex class of the model was then reduced by any recorded deaths, such as trophy hunting or PAC in areas bordering Gonarezhou, or poaching (although there are no poaching records for 1992–2008). It was assumed that all poached elephants were males. It was further assumed that both trophy hunters and poachers would preferentially kill elephants with larger tusks, and so, in the model, the numbers of animals in the oldest age classes were reduced until the total number of reductions for each year was equal to the total recorded offtake in and around Gonarezhou that year. Information on offtakes in the Mozambique border zone is not available. In the model, it was assumed that there was negligible immigration to Gonarezhou.

Based on the survey results, it was assumed in the model that: a) some female herds emigrated to Mahenye from 2010 and to Malipati from 2015 (Fig. 5); b) some bulls emigrated to Mahenye from 2013 and to Malipati from 2017; and c) elephant movements into Naivasha were temporary and did not constitute emigration. In the model population, elephants that emigrated were removed annually, with elephants in female herds removed proportionally to their presence (in the model population).

It is reasonable to assume that the elephants in the Mozambique border zone moved there from Gonarezhou. Estimating the number of elephants that have died in the border zone during the past ~20 years depends on the mean duration of the period that an elephant carcass remains visible to a survey observer. The conservative option is to assume that all carcasses remained visible to a survey observer during subsequent surveys, and so the lower trend line (Fig. 6) was used to estimate the number of elephants emigrating annually to Mozambique from 2013. No female herds were seen in the border zone during the 2014, 2018, or 2022 surveys and the few herds seen here during earlier surveys were assumed to have returned to Gonarezhou. In the model population, it was assumed that only elephant bulls moved there from Gonarezhou.

After births and emigration, the total number of animals in the 60 x 2 age/sex classes of the model population was the predicted population number for that year, at the time when surveys are often conducted. The model population was divided into two sections: bull groups, which comprised all males older than 16 years; and breeding or female herds, which comprised males aged 1 to 16 years and all females. The model was run for 29 years, mimicking the period 1993–2022.

After surveys and at the end of the dry season, when food and water are the most limiting, the number of elephants in each age/sex class was reduced by age- and sex-specific annual mortality rates. For simplicity, the number of animals in each age/sex class was not constrained to be an integer. The Gonarezhou elephant population increased at a mean exponential rate of 6.2% annually immediately after the 1992 drought (Dunham 2012), which is a relatively high rate (Cumming 1981). Hence, it was assumed that the age and sex-specific annual mortality rates were relatively low, and the rates in the model (except that for first-year calves) were set to be identical to the mortality rates observed for South Africa's Addo elephant population, which also increased rapidly in number (Whitehouse and Kerley 2002).

First-year mortality in the model was negatively related to rainfall, as suggested by elephant carcass records from ranger patrols in Gonarezhou for 2014–2023 (GCT unpubl. data) and as noted in Amboseli (Lee et al. 2011a). If the observed rainfall during the preceding January–June was greater than the long-term mean (393 mm), the first-year mortality rate was the same as the Addo figure (6.2 %). However, if the observed rainfall was less than this mean, the first-year mortality increased by a factor that was negatively and curvilinearly related to rainfall. Hence, first-year mortality increased to 9.0% when the January–June rainfall was 300 mm, to 18.4% when it was 200 mm, and to 25.7% when the rainfall was 150 mm.

Among the elephants captured in female herds during 1993, the numbers of males in the 13–14, 14–15 and 15–16–year–age classes were similar (13, 7 and 12, respectively (Dunham 2024)). This was taken to indicate that the males left their natal female herds after their approximate sixteenth birthday. Hence, bull recruitment in any model year was defined as the number of males transferring from the 15–16–year–age class to the 16–17–year class. As they transferred between these two model age classes, males also transferred from the female herds to the bull groups. For simplicity, the age when males in the population model transferred to the bull groups coincided with their transfer between age classes, but in reality, male independence is not sudden (Lee et al. 2011b).

The real numbers of elephants in bull groups and female herds during 1993 were not known. Hence, these numbers were initially set to be 819 and 3,324, respectively, which were the 1995 survey estimates, with the constraints (for these numbers) set to be the same as the confidence limits for these estimates. The mean calving interval (CI) was also not known. It was initially set to be 4.1 years, the mean value for Gonarezhou during the early 1970s (Sherry 1975), with constraints of 2.9 and 9.1 years, which are the minimum and maximum values reported for East African elephant populations (Hanks and McIntosh 1973).

The MS Excel add-in, Solver *Evolutionary*, was used to determine the starting values (i.e. 1993) that resulted in the predicted numbers of bulls and elephants in female herds providing the closest fit to all the survey estimates for years when the Gonarezhou population was actually censused. Running the Solver add-in was equivalent to running numerous models with different starting values for the three unknowns (initial number of elephants in bull groups, initial number of elephants in female herds, and mean CI). Each model was assessed by comparing the fit of the predicted elephant numbers with the actual survey estimates. Martin's estimator (Martin 1992; Dunham 2008) was used to compare the fit of the different models. Each survey estimate was compared with the predicted population number for that year by relating the difference between the two numbers to the variance of the survey estimate. There were 12 aerial surveys of the Gonarezhou elephant population during 1995–2022, and each provided estimates of the numbers of elephants in bull groups and in female herds. Hence, the predicted population numbers were compared with 24 survey estimates for each combination of the three unknowns, 12 for bull groups and 12 for female herds. The product of the 24 comparisons gave a single 'index value', which was minimized using the Solver add-in. The robustness of this model was determined by repeating the above procedure 12 times, each time removing a different year of survey from the fit.

The Solver *Evolutionary* can find a sound solution, but not necessarily one which is optimal (Frontline Systems 2024). To increase the likelihood that Solver found a solution that was close to optimal, the default options were changed, with the convergence reduced (to 0.0000001) and the mutation rate increased (to 0.15). Solver found an identical solution even if the initial values for the three unknowns were changed, either to their minimum or maximum constraints.

Population model starting with 'normal' age structure

A revised version of the above model was run starting in 1993, with a 'normal' age structure (i.e. not affected by drought) for the population. A normal age structure was obtained by running the original model until 2093. After 100 years, all drought survivors were dead and the 2093 model age structure was determined by the fecundity and mortality schedules used in the model and assumed to be 'normal'.

This normal age structure was used as the starting (1993) age structure in another model that was, in other respects, the same as the original model with the drought-impacted age structure. The population trends from the model starting with a normal age structure were compared with both the survey estimates and the trends from the original model with the drought-impacted age structure.

Population model incorporating unrecorded poaching

The original population model, with the age structure impacted by drought, was rerun under the assumption that a certain number of adult males were poached each year from 1994 to 2007. The model was run multiple times, each time assuming a different number of poached males (1, 2, 3, 4, 5, 6, 7, 10, 15, or 20 per annum). The fit of the modelled trends to the observed trends for each scenario, as indicated by the index value, was compared to a model that assumed no adult males were poached during this period. In the model used here, poaching, trophy hunting and emigration of adult males would all have a similar impact as they all contribute to an increase in the number of adult males removed from the population each year.

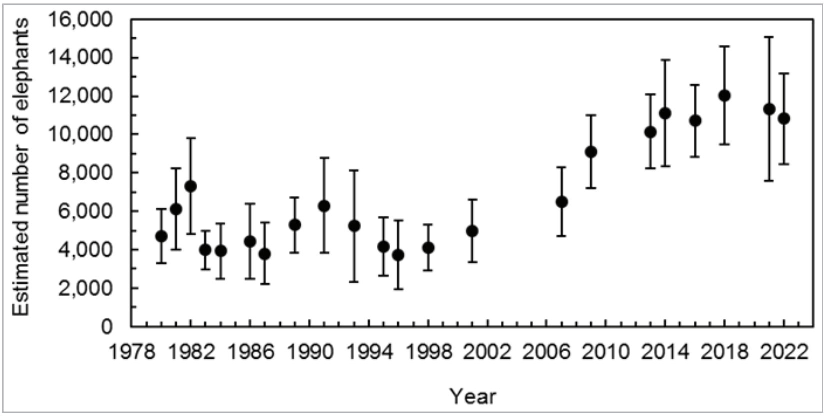

Figure 2. Temporal trend in the estimated number of elephants in Gonarezhou. Points are survey estimates with 95% CI. During 1983, 1986 and 1987, a total of >4,000 elephants were culled in response to concerns about the impact of elephants on the vegetation. A severe drought occurred in 1992, and 670 elephants were captured and translocated during 1993.

Results

Surveys of the Gonarezhou elephant population

The mean estimate of the number of all elephants in Gonarezhou increased during 1995–2018 at a mean exponential rate of 5.3% per annum (n = 10 surveys; CL 4.2 and 6.5%) (Fig. 2). But during 2013–2022, the estimated number of all elephants changed little and averaged 11,031 (n = 6 surveys), more than three times any model estimate of the number immediately after the 1993 captures (Table 1).

The mean estimate of the number of elephants in female herds increased during 1995–2018 at a mean rate of 5.7% per annum (n = 10; CL 4.4 and 7.0%) (Fig. 3). But for the entire study period, a logistic curve was a better fit to the survey estimates than an exponential curve. The apparent decline in the estimated number of elephants in female herds between 2018 and 2022 was not statistically significant (two-tailed t-test, t = 0.90, p = 0.37). Nonetheless, the last survey estimate in the time series (that for 2022) had a greater impact on the parameters of the logistic equation than other survey estimates. During 1995–2007, the number of elephants in bull groups appeared to decline, but not significantly (Fig. 4). However during 2007–2022, the number in bull groups increased exponentially, at a mean rate of 6.3% per annum.

The surveys revealed an increase in the number of elephants in Zimbabwean areas adjacent to Gonarezhou (Fig. 5). The estimated number of elephants (alive or dead) in the border zone of Mozambique also increased with time (Fig. 6). The temporal trends in the estimated numbers of all elephant carcasses and of fresh or recent carcasses in Gonarezhou gave no indication of large-scale or unusual elephant mortality in Gonarezhou during the years following the 1992 drought. The all-carcass ratio (including 'unidentified' carcasses, which are likely to have been elephant carcasses) was relatively high during the years immediately after the drought (>10% for five surveys during 1993–1998), presumably a reflection of the 1992 drought mortality. But from 2001 onwards, it averaged 5.9% (n=7, range 3.6–8.5%) and showed no significant trend (linear regression slope = -0.09, p = 0.4). From 1996 onwards, the 1+2 carcass ratio (an index of elephant mortality during the survey year) averaged 0.13% (n=12, range 0–0.39), and also showed no significant trend (slope = 0.001, p = 0.7).

Population model starting with drought-impacted age structure

Temporal trends in the numbers of elephants in bull groups and female herds modelled were within the confidence limits of all the survey estimates for the Gonarezhou population (12 estimates for elephants in female herds and 12 estimates for elephants in bull groups), except for the estimate of elephants in female herds during 2022 (Fig. 7).

The population model which predicted elephant numbers that best fit the survey estimates, started

Table 1. Estimates from aerial surveys during 1995 to 2022 of the numbers of all elephants, elephants in bull groups and elephants in female herds for Gonarezhou. CI = 95% confidence interval of estimate. Discrepancies between the estimate for all elephants and the sum of the estimates for bulls and females are usually rounding errors.

Year	All elephants		Elephants in bull groups		Elephants in female herds		Source
	Estimate	CI	Estimate	CI	Estimate	CI	
1995	4,156[a,b]	1,509	819[a]	281	3,324[a]	1,408	a Davies et al. (1996); ʙ Douglas-Hamilton (1995) ([a,b] merged estimate)
1996	3,742	1,796	663	222	3,064	1,687	See Dunham (2012)
1998	4,132	1,198	762	274	3,369	1,169	
2001	4,987	1,637	718	228	4,272	1,623	
2007	6,516	1,790	577	213	5,939	1,778	
2009	9,123	1,902	757	195	8,366	1,892	
2013	10,151	1,922	1,145	229	9,007	1,909	See Appendix S1 of O'Connor and Shimbani (2024)
2014	11,120	2,764	1,179	372	9,940	2,741	
2016	10,715	1,878	983	195	9,734	1,867	
2018	12,046	2,555	1,489	378	10,559	2,527	Dunham and van der Westhuizen (2018); Dunham (2022)
2021	11,339	3,746	1,329	475	10,010	3,718	Dunham et al. (2022); Dunham (2022)
2022	10,812	2,371	1,810	458	9,001	2,328	Dunham (2022)

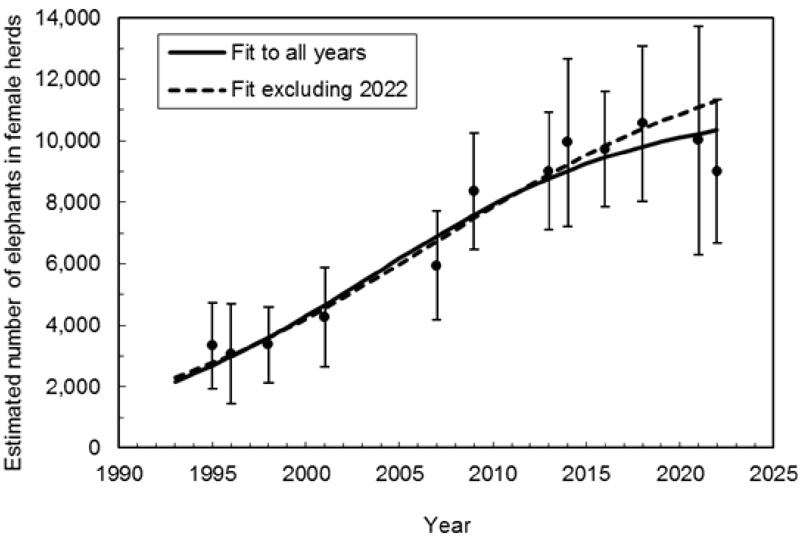

Figure 3. Temporal trend in the estimated number of elephants in female herds in Gonarezhou. Points are survey estimates with 95% CI. Lines indicate best-fit logistic curves, one fitted to all survey estimates (solid line) and the second fitted to all survey estimates except that for 2022 (dashed line). For the first line: N_0 = 2,161, r_m = 0.137 and K = 11,142. For the second curve: N_0 = 2,310, r_m = 0.113 and K = 13,317. The MS Excel add-in Solver was used to determine the N_0, r_m and K values that minimized the differences between the survey estimates and the values predicted by the equation, with each difference related to the variance of the appropriate survey estimate (Martin 1992).

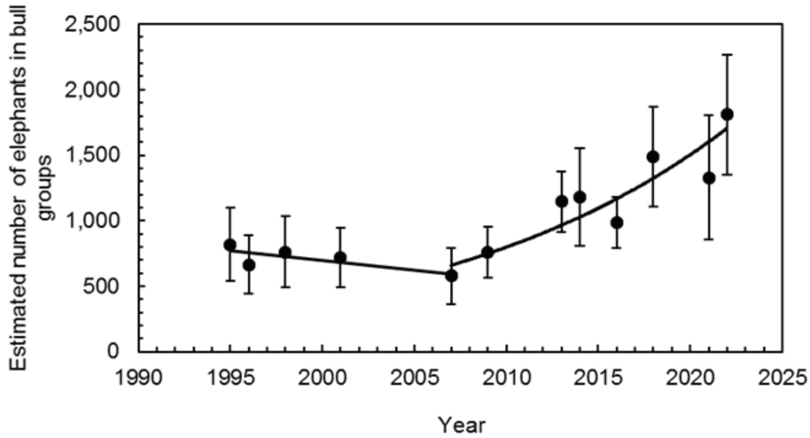

Figure 4. Temporal trend in the estimated number of elephants in bull groups in Gonarezhou. Points are survey estimates with 95% CI. Bold lines indicate the likely trends. During 1995–2007, the mean linear rate of change ($\hat{g}$) was 14 bulls per annum (CL = -37.3 and 9.3; n = 5 surveys). During 2007–2022, the number of elephants in bull groups increased at a mean exponential rate (r) of 6.3% per annum (CL = 4.2 and 8.5%; n = 8).

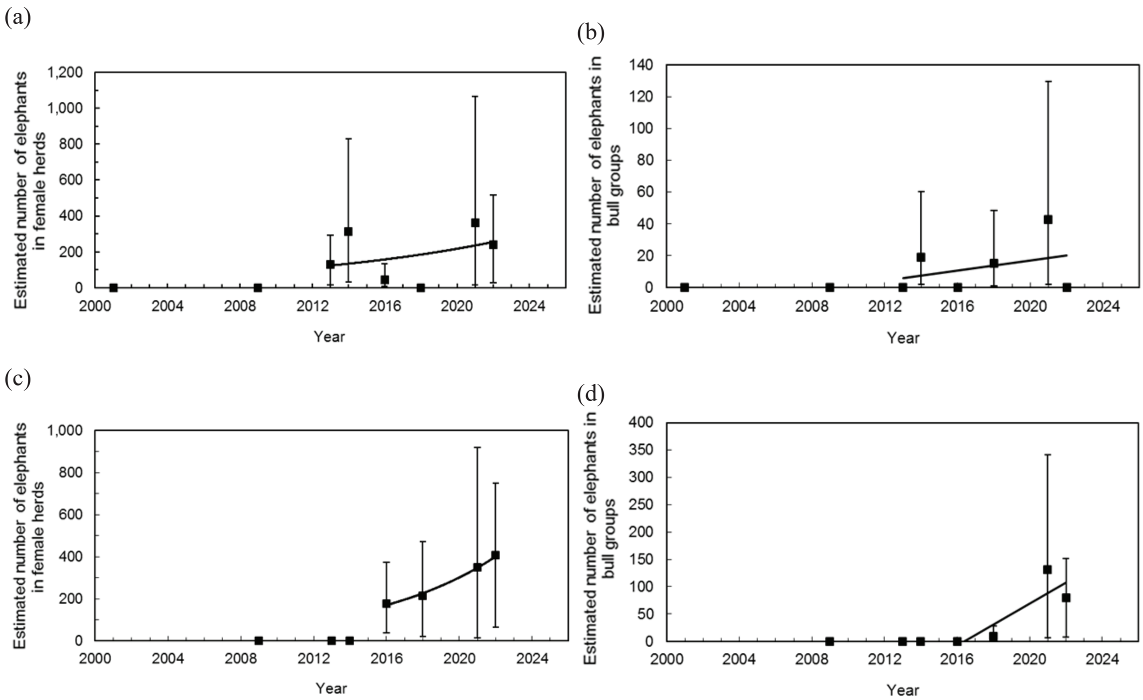

Figure 5. Temporal trends in the estimated numbers of elephants in Mahenye communal area and Malipati, which border Gonarezhou. The points are survey estimates with 95% CI: (a) female herds and (b) bulls in Mahenye; and (c) female herds and (d) bulls in Malipati. Bold lines indicate assumed trends used in the population model: exponential for female herds and linear for bulls.

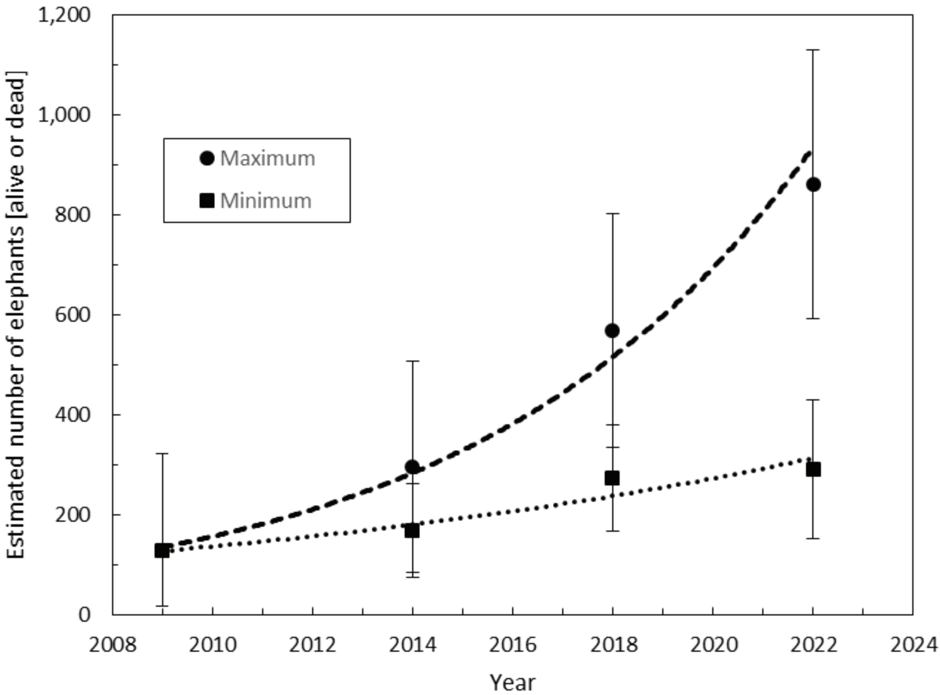

Figure 6. The temporal trend in the accumulative number of elephants estimated to have emigrated to the Mozambique border zone from Gonarezhou. Points are survey estimates with 95% CI. The lower (dotted) line is an exponential curve through estimates calculated on the assumption that all elephant carcasses seen during surveys remained available to be seen during later surveys (minimum estimates). The upper line (dashed) is an exponential curve through estimates calculated on the assumption that the elephant carcasses seen during any survey were not available to be seen during any subsequent survey (maximum estimates). For the upper line, r = 14.3% per annum (CL = 6.7 and 22.4%); and for the lower line, r = 7.0% per annum (CL = -0.8 and 15.4%).

with 2,892 elephants in female herds and 658 in bull groups after the 1993 captures and had a mean CI of 3.9 years. Even when one survey was removed from the fit, these parameters barely changed. However, the 2022 survey estimate had the most influence because that survey produced a relatively low population estimate for both elephants in female herds (less than the estimates of the four previous surveys during 2014–2021) and elephants in bull groups. (This was less than the estimates of the two previous surveys during 2018 and 2021) (Table 1).

In the model populations, the recruitment of males to the bull groups, as they transferred from the female herds, was low from 1994 until 2003 (Fig. 8) and declined further during 2004–2008, before a significant rise during 2009. Thereafter, there was generally a small increase in recruitment annually.

Population model starting with the 'normal' age structure

Temporal trends in the numbers of elephants in bull groups and female herds from a model with a normal age structure were within the confidence limits of most survey estimates, but a poorer fit (Fig. 9) than the trends from the model with the drought-impacted age structure (Fig. 7). The normal age structure model which predicted elephant numbers that best fit the survey estimates, started with 2,995 elephants in female herds and 599 in bull groups after the 1993 captures and had a mean CI of 3.1 years. Noticeably, the model trend in the number of elephants in bull groups did not show the constant or declining number observed from 1995 to 2007, but instead the modelled number increased throughout the 30 years of the model run (Fig. 9b).

Population model incorporating unrecorded poaching

For models which assumed that some adult males were poached annually between 1994 and 2007, the index value was used to compare the fit of the trends from these models to the survey estimates, with the fit for a model that assumed that no males were poached during this period. When the fit to the survey estimates for both elephants in female herds and elephants in bull groups was considered, the fit was similar whether one elephant or none was poached, but the fit declined if two or more elephants were poached (Fig. 10a). When only the fit to the survey estimates for elephants in bull groups was considered during those model runs, the fit was similar if five or fewer, or no adult males were poached; however it declined if six or more were poached. The trends produced by these models differed little from each other, whether 0, 5, 10, 15, or 20 adult males were assumed to have been poached annually (Figs 10b and c). The main difference was in the model estimate of the number of elephants in bull groups during 1993 at the start of the model, with this starting number increasing as the assumed number of poached males increased.

Discussion

Long-term effect of the 1992 drought

Temporal trends in the numbers of elephants in bull groups and female herds of a model with a drought-impacted age structure were a credible fit to the survey estimates for the Gonarezhou population during the 20 years after drought. Trends from a model with a normal age structure were a poorer fit to the observed trends and, in particular, did not reflect the observed absence of an increase in the number of elephants in bull groups from 1995 to 2007. Also, the model with the normal age structure required a notably small (implausible?) mean ICI (3.1 years) over 30 years. This compares with 3.9 years for the model with the drought-impacted age structure and, consequently, a high proportion of adult females (Dunham 2024).

Alone, the unusual age structure of the elephant female herds that survived the 1992 drought (Dunham 2024) can explain the differing observed post-drought trends for elephants in female herds and those in bull groups. No additional explanation is required, as shown by models that started with that unusual age structure, but also assumed that, during 1994–2007, a few (5 or fewer) adult males were lost annually from the Gonarezhou population (by unrecorded poaching, trophy hunting, emigration, or any combination of these), being an equally good, but no better fit to the survey estimates. This implies that the trend observed after the drought for elephants in bull groups cannot be accounted for primarily by unrecorded hunting (legal or illegal) or emigration.

The age structure of the drought survivors revealed that relatively few non-adults survived and that, among younger non-adults, males suffered greater mortality than females. This pattern of mortality due to drought has been observed elsewhere (Foley et al. 2008; Lee et al. 2022). In the absence of immigration, the only recruitment of elephants to the bull groups in any population is when males leave their natal female herds, with most leaving before they are 17 years of age (Lee et al. 2011b). At any time, annual recruitment to bull groups during the next ~16 years can usually be estimated from the number of males in each year/class, from 15 to 16 years down to 0 to 1 year. During the ~16 years after the 1992 drought, recruitment to bull groups, both in the model and likely in the real Gonarezhou population, declined until it was very low between 2003 and 2008, when recruits consisted of the few males who were aged <5 years during the drought and survived it.

When males born in Gonarezhou in 1993, (the year after the drought) left their natal female herds during 2009, there would have been a notable increase in recruitment to the bull groups. Following 2009, annual recruitment to bull groups was largely determined by the number of males born ~16 years earlier, during 1994, 1995, 1996, etc. After 2007, the estimates of elephants in bull groups in the survey increased at a similar annual rate as the number of elephants in female herds had increased 16 years earlier. With an elephant having a potential lifespan of >60 years, it will take another 30 years for the impact of the drought mortality on the young elephants in Gonarezhou to progress through the age profile of the population, as has been shown for the Amboseli elephants (Lee et al. 2022). In Gonarezhou, the gap in the male age profile resulting from drought mortality now (2025) coincides with the group aged 30–45 years old. Elephant tusk mass is proportional to age (Whyte and Hall-Martin 2018), and so the gap in this age group will impact the number of elephants with sizeable tusks available for trophy hunting around Gonarezhou.

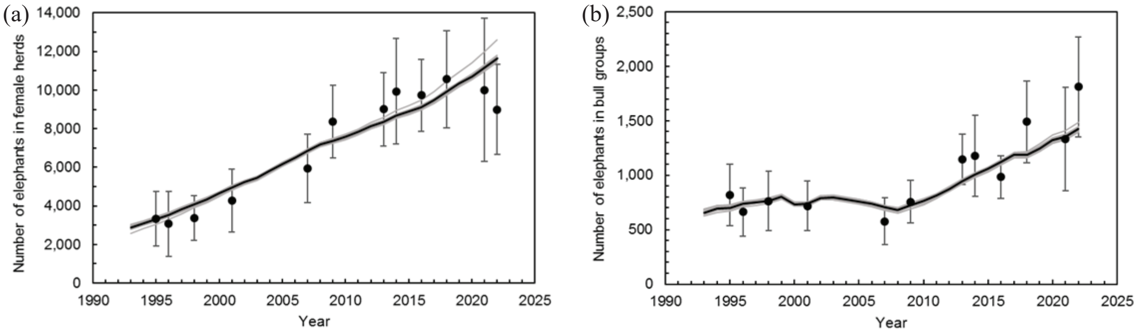

Figure 7. Temporal trends in the number of elephants in Gonarezhou: (a) elephants in female herds; (b) elephants in bull groups. Trends (lines) of a model with a drought-impacted age structure and survey estimates (points) with 95% CI are shown. Bold lines indicate the best-fit modelled trends when the model estimates are fitted to all survey estimates; and grey lines indicate the trends when the model is run 12 times, each time excluding the estimates for a different survey from the fit. The apparent grey bands are individual grey lines, most of which differ little from each other. The grey line, which diverges from the others (after 2013 for elephants in female herds and after 2019 for elephants in bull groups), is the best-fit model when the 2022 survey estimates are excluded from the fit. These models assumed that no bulls were poached during 1994–2007.

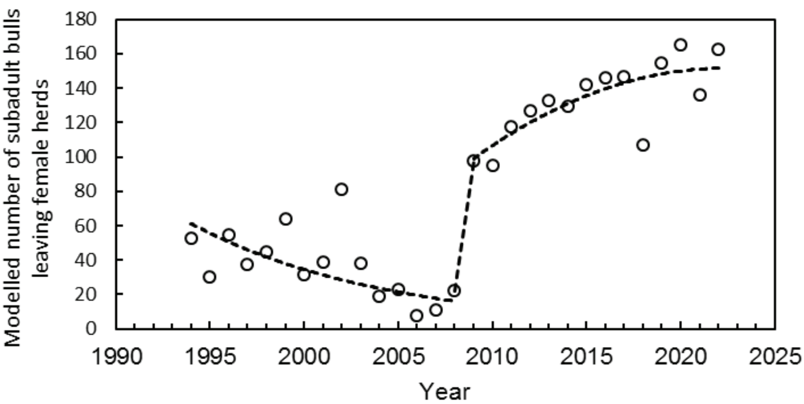

Figure 8. Temporal trend in the modelled annual recruitment of bull elephants in Gonarezhou after the 1992 drought. Recruitment occurs when males leave the female herds and transfer to the bull groups, when they are ~16 years of age. Points are not data points, but model outputs representing the number of bulls moving into the 16–17–year–old class. For illustrative purposes, the broad trend in recruitment is summarized with three (dashed) regression lines (the first a negative exponential, the second linear, and the third a two-order polynomial). Relatively low recruitment during 2018 and 2021 reflects the model-predicted high juvenile mortality during the low rainfall years when these recruits were born (2002 and 2005).

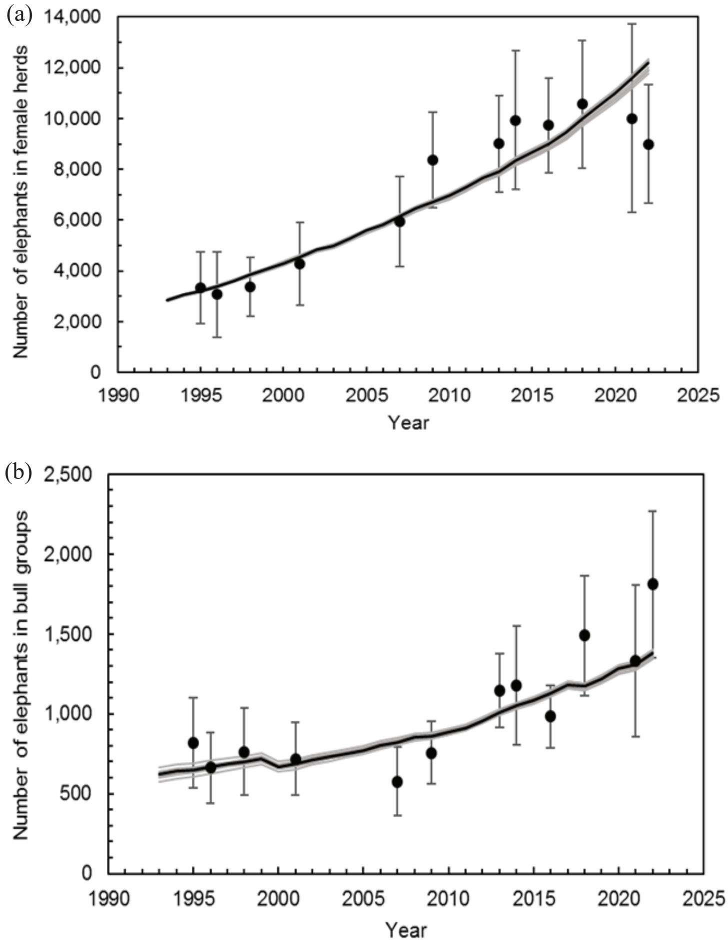

Figure 9. Temporal trends in the number of elephants in Gonarezhou: (a) elephants in female herds; (b) elephants in bull groups. Trends (lines) of a model with a normal age structure and survey estimates (points) with 95% CI are shown. Bold lines indicate the best-fit modelled trends when the model estimates are fitted to all survey estimates; and grey lines indicate the trends when the model is run 12 times, each time excluding the estimates for a different survey from the fit. The apparent grey bands are individual grey lines, most of which differ little from each other.

Trend in the number of elephants in female herds

The high rate of increase in the survey estimate of the number of elephants in female herds after the drought probably reflected the high proportion of adult females among drought survivors. But for 15 years (the approximate time for a female to reach maturity) following the drought, the proportion of adult females in the female herds would have declined, as non-adult age classes were filled by youngsters born after the drought. The rate of increase in the number of elephants in female herds decreased in both the real and model populations as a result of this changing age structure. But the rate continued to decline after that period (i.e. after 2007), as is indicated by a logistic curve being a credible fit to the survey estimates. The recorded removals from the Gonarezhou elephant population are mostly of adult males. The decline in the rate of increase of elephants in female herds within Gonarezhou revealed by the surveys is at least partly due to emigration to areas bordering the park. There were often a few elephants seen in Malipati and Mahenye, but recent movement into Malipati

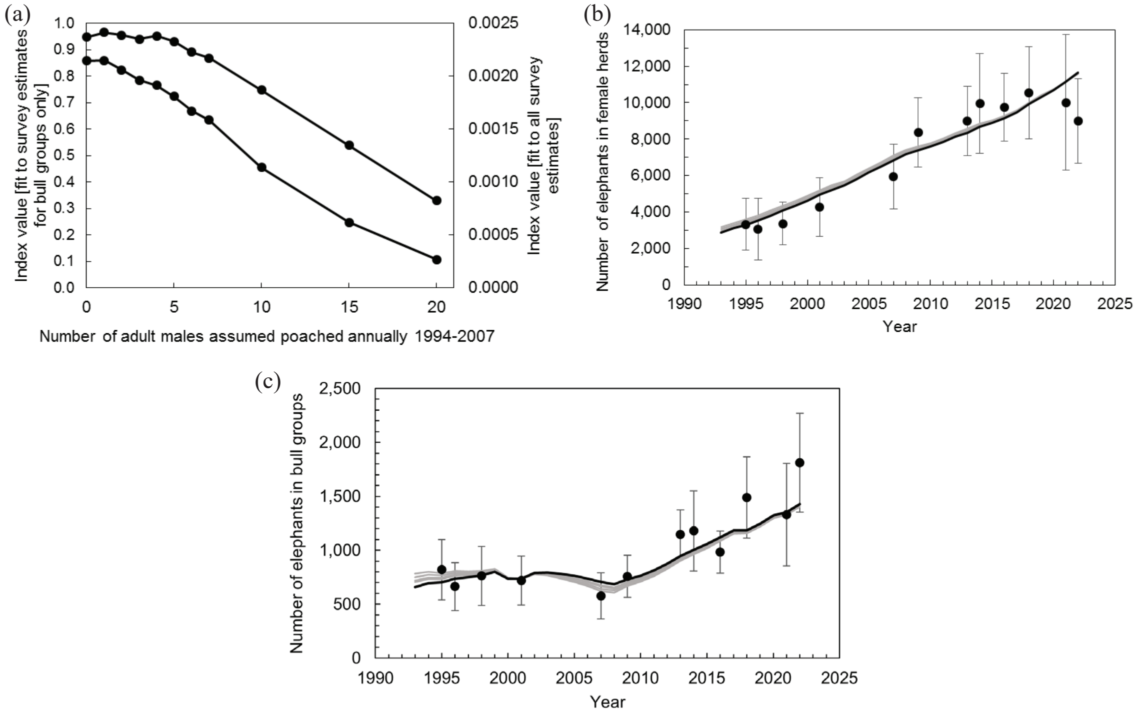

Figure 10. (a) The fit to the survey estimates of trends from models that assumed that some adult males were poached annually during 1994–2007. Each point represents a run of the model, with the indicated number of adult males assumed to have been poached. The lower line indicates the fit to all 24 survey estimates, 12 for elephants in female herds and 12 for elephants in bull groups (right scale). The upper line indicates the fit from the same model runs, to the 12 estimates only for elephants in bull groups (left scale). The greater the index value, the better the fit. The left and right scales differ and are not comparable with each other (because the left index is based on the product of 12 numbers, while the right is based on the product of 24 numbers).
Temporal trends in the number of elephants in Gonarezhou for (b) elephants in female herds and (c) elephants in bull groups. Trends from these same models (lines) and survey estimates (points) with 95% CI are shown. Bold lines indicate the best-fit modelled trends when the model estimates were fitted to all survey estimates, and it was assumed that no adult males were poached between 1994 and 2007. The grey lines indicate the trends when the model was run four times, each time assuming that 5, 10, 15, or 20 adult males were poached annually. The apparent grey band is composed of several individual grey lines (which merge), most of which differ little from each other.

has probably been encouraged by the cessation of trophy hunting there after 2017. Movements into Mahenye may have been encouraged by the establishment of a 70 km^2 wildlife area, fenced to reduce HEC, but open to Gonarezhou across the Save River.

The discrepancy between the estimate of elephants in female herds in 2022 and the predicted number is large. In the absence of any evidence of major mortality of elephants between the 2021 and 2022 surveys, or of undetected emigration, it is likely that the 2022 estimate of elephants in female herds in Gonarezhou is simply a low estimate. The planned 2025 survey should reveal whether this is the case.

Emigration at least partly accounts for the decline during the last decade in the rate of increase in the number of elephants in female herds in Gonarezhou. There appears to have been no increase in subadult or adult mortality within the Park, because the aerial surveys recorded that the carcass estimates and carcass ratio there have not increased. The surveys do record a large increase in mortality in the Mozambique border zone, but most of these dead elephants were likely adult males. The levelling off of the number of elephants in female herds may have involved changes in the female age at first conception, the inter-calving interval (ICI), or juvenile survival, or any combination of these factors. This would be in line with expectations that these parameters would change before any increase in non-anthropogenic adult mortality (Eberhardt 2002). But Gonarezhou data are not available to test for changes in these parameters. For elephant populations, a change in the ICI is an important population regulating mechanism (Hanks and McIntosh 1973).

Assumptions of model

The model is intentionally a simple one and includes various assumptions. The mean ICI was assumed to be constant for the ~30 years that the model runs simply because there is no information available for Gonarezhou to indicate if or how the interval has changed, or even what the mean interval has been since 1992. Carcass records from ranger patrols since 2014 suggest that the mortality of juvenile elephants in Gonarezhou was negatively related to rainfall, with the relationship being curvilinear, as also in Amboseli (Lee et al. 2011a). A similar relationship between first-year mortality and rainfall was assumed to apply for the duration of the model, although possibly, during the decade or so after the drought, when elephant density was relatively low, there was a weaker relationship, or none at all.

During surveys after 2009, no female herds were seen in the Mozambique border zone, but numerous elephant carcasses, indicative of the illegal killing of elephants, were observed. Given that elephant female herds are more risk-averse than bull groups (Smit et al. 2023), it was assumed in the model that, while female herds from Gonarezhou may have visited Mozambique occasionally, no female herds emigrated there. Therefore, in the model, it was assumed that all elephant carcasses seen in Mozambique were of elephant bulls. If some female herds did emigrate to Mozambique, the effect of this would be to improve the fit of the Gonarezhou model estimates of the number of elephants in female herds to the survey estimates for the years after emigration commenced.

Estimating how many elephant bulls have moved into the Mozambique border zone depends on the duration of the period after the death of an elephant that its carcass remains visible to a survey observer. In the model, it was conservatively assumed that all the carcasses remained potentially visible during subsequent surveys. But if it is assumed that, on average, a carcass remained visible to a survey observer for four years (Booth and Dunham 2016), the number of elephants estimated to have moved to Mozambique during 2009–2022 almost triples, from 291 (+/- CI 48%) (if no carcasses disappeared) to 860 (+/- 31%). If the number of bulls that moved to Mozambique was greater than assumed in the model, the effect of this would be to reduce the fit of the model estimates of the number in bull groups to the survey estimates after 2009.

The model assumed that there was no immigration into Gonarezhou; however, Kruger NP lies ~30 km south of Gonarezhou, and elephants are known to move between the two PAs, although at present there is no evidence that the moves are permanent and hence would constitute immigration/emigration (Sherry 1978; Henley et al. 2023; Mandinyenya et al. 2024). Studies of bull movements in Kruger NP and the wider ecosystem have tended to focus on adult bulls with large tusks, i.e. older individuals. If there are annual dispersal movements of younger bulls from Kruger NP northwards, the effect of this immigration would be consistent with an increase in the estimated number of bulls emigrating from Gonarezhou to Mozambique.

Management implications

Since 1993, the number of elephants in Gonarezhou has increased threefold. The mean rate of population increase of 5.3% per annum over 23 years compares with 4.1% annually in Kruger NP (Louw et al. 2021). The increase in the Gonarezhou population contrasts with the situation elsewhere in Zimbabwe (Dunham 2015) and much of Africa (Thouless et al. 2016), where poaching has caused significant population declines. The contrast with other Zimbabwean subpopulations follows the formation in Gonarezhou of a conservation partnership between the national wildlife management authority and an INGO (FZS), with resulting increases in local law enforcement capacity and in economic engagement with local households (Kuiper et al. 2023).

Since 2013, the Gonarezhou population has numbered ~11,000 elephants, with the levelling off of the population coinciding with the movement of some female herds into the Mahenye community lands and Malipati. For many years, the number of elephants in the areas bordering Gonarezhou was small, but now it is necessary to consider a larger population in Gonarezhou that includes not only the elephants in Gonarezhou, but also those in neighbouring areas, including the Mozambique border zone. At present, the Mozambique border zone acts as a sink area, where the rate of elephant mortality remains high, in contrast to the situation in Gonarezhou, which is the source. There is little cultivation or human settlement in this border zone, which suggests that the high mortality rate is not a consequence of conflict, but of the illegal killing of elephants.

Significant drought-induced mortality of non-adult elephants during 1992 resulted in female herds the following year that contained a high proportion of adult females and few immatures. Immature females significantly outnumbered immature males among the survivors (Dunham 2024). The models presented here show how a low proportion of immature males in female herds can cause a significant decline in adult male recruitment during a period of ~16 years after a drought and, therefore, a decline during that period in the number of adult bulls in the population, likely because bull mortality exceeds recruitment. Similar lag effects, induced by poaching, are probably occurring in the populations of elephants of the Sebungwe and Zambezi Valley in Zimbabwe. The estimated number of elephants in female herds in Sebungwe declined by >9,000 (79%) between 2006 and 2014 as a consequence of poaching (Dunham 2008; Dunham et al. 2015). Even if poaching has reduced or stopped, a similar magnitude decrease in annual recruitment of adult males would be expected for ~16 years after 2014.

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