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Title: Cohort consequences of drought and family disruption for male and female African elephants

Running Title: Long-term consequences of adversity for elephants

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Author contributions

PCL & CM conceived the initial project, VF carried out the initial project and contributed to theoretical development, JP contributed to theory and long-term data, NN and KS contributed to the long-term data gave feedback on ideas. PCL & VF analyzed the data and drafted the paper; CM & JP commented on the analyses and draft.

(see www.elephantvoices.org). The mission of our research is to promote knowledge about elephants so as to better effect their conservation in the wild. We thank three reviewers for their thoughtful comments on the original draft.

Ethics statement

The work reported on here is based on non-invasive observations carried out in accordance with the ASAB / ABS guidelines for field work with wild animals. Individual recognition was by photographs. Vehicle presence was a source of potential disturbance, but elephants were well habituated to tourist and research vehicles. Ethical clearance for recent work was granted to PCL by the University of Stirling's Animal Welfare and Ethical Review Body (AWERB/1718/018/New Non ASPA). All research was conducted from the start of the project with appropriate clearance and permissions from the Government of Kenya and representative bodies, the Kenyan National Commission for Science, Technology, and Innovation, the Kenya Wildlife Service, and the Maasai Community of Amboseli.

Data availability statement

Annual rainfall and population parameters are provided as an excel sheet in Supplementary materials. Basic individually based demographic information included in analyses up to 2019 is also provided as an excel sheet; this can be accessed via the University of Stirling DataStorre facility at http://hdl.handle.net/11667/186 (Lee et al. cohort demography data.xls). Further details of demography datasets or sightings of individuals are available upon request to CJ Moss or PC Lee.

Abstract:

Cohort effects, reflecting early adversity or advantage, have persisting consequences for growth, reproductive onset, longevity and lifetime reproductive success. In species with prolonged life histories, cohort effects may establish variation in age-sex structures, while social structure may buffer individuals against early adversity. Using periods of significant ecological adversity, we examined cohort effects for male and female elephants (*Loxodonta africana*) over almost 50 years in Amboseli, Kenya. Mortality spiked during severe droughts with highest mortality among calves under 2 years and females over 40 years. Deaths of oldest females resulted in social disruption via matriarch turnover, with potential impacts on resource acquisition for survivors. We predicted that survivors of high mortality and social challenges would have altered life history trajectories, with later age at first reproduction and reduced age-specific fertility for females and slow transitions to independence and late onset of potential mating or musth among males. Contrary to expectations, there were no persisting early drought effects on female age at first conception while matriarch loss around puberty accelerated reproductive onset. Experience of an early life drought did not influence age-specific reproductive rates once females commenced reproduction. Males who survived an early drought exhibited complex consequences: male age at family independence was later with larger peer cohort size, but earlier with drought in year of independence (13.9 vs 14.6 years). Early drought had no effect on age at first musth, but male reproductive onset was weakly associated with the number of peers (negative) and age at independence (positive).

Key words: elephant drought mortality, age-sex class variation, reproductive maturation, cohort effects, musth onset

Introduction

Extreme and prolonged droughts in sub-Saharan Africa are relatively rare but projected to become more common with a changing climate (Tan et al. 2020). When droughts occur, a short or non-existent growing season results in reduced vegetation availability (Vrieling et al. 2013), with negative consequences for the survival, health and fecundity of many grazing and browsing species (Western et al. 2015). The long-term consequences of population and individual responses to droughts are relatively poorly known for most large ungulates (Mduma et al. 1999; Ogutu and Owen-Smith 2003; Duncan et al. 2012). In Southern Kenya, where droughts occur at irregular intervals, these coincide with significant mortality in most grazing wildlife and livestock species, including elephants (Western et al. 2015; Wato et al. 2016). We focus on the consequences of these periods of adversity in early life for individual survivors, i.e. direct constraints (Monaghan 2008; Lea et al. 2015; Tung et al. 2016). We chose to examine adversity rather than advantage (e.g. silver-spoon effects; Pigeon and Pelletier 2018) as over an elephant's 5- to 10-year developmental period, any early advantage might be obscured by subsequent drought events or social adversity, such as matriarch loss. Conversely, early disadvantage could be "outgrown" (Hamel et al. 2017) or compensated for during periods of abundance and social cohesion later in life.

In species with slow rates of reproduction and long lifespan such as elephants, recovery time after population disruption can vary between the surprisingly rapid (Foley and Faust 2010; Goldenberg et al. 2016) and the extremely prolonged (Nyakaana et al. 2001; Gobush et al. 2008). The nature of population responses to high levels of mortality is of major significance for a population's ability to persist, especially when mortality exceeds reproductive rates, as in poached populations (Wittemyer et al. 2013; Chase et al. 2016) or after droughts (Foley et al. 2008; Wooley et al. 2008). Understanding the factors contributing to population resilience will therefore be fundamental in sustaining endangered elephant populations throughout their range.

Elephant kin units, called families, function as collaborative calf-rearing units (Lee 1987; McComb et al. 2011), led typically by the eldest female or matriarch. Loss of experienced

individuals due to droughts or poaching has the potential for social and reproductive disruption which may cascade through a population for at least a generation (Nyakaana et al. 2001; Gobush et al. 2008; Shannon et al. 2013). Males disperse from their natal family at adolescence, after which they develop their own social and ecological strategies and associate freely with other males and unrelated families (Lee & Moss 1999; Evans & Harris 2008; Lee et al. 2011; Murphy et al. 2020).

In addition to the immediate consequences of drought or familial disruption for individual survival and fertility, a poor start in life has long-term downstream consequences for elephants (Lee et al. 2013; Mumby et al. 2015). Thus, drought and disruption experiences might establish cohort variation in life history traits (e.g. Gaillard et al. 2003; Jones et al. 2005; Solberg et al. 2007) which could affect population resilience over decades (Tung et al. 2016; Rosenbaum et al. 2020). These downstream consequences could be exacerbated by intergenerational effects on offspring born to mothers who experience early adverse life effects (Zipple et al. 2019; Reichert et al. 2020; Rosenbaum et al. 2020). At the same time, any post-drought peak in infant production could produce additional long-term cohort effects through increased inter-individual competition.

The Amboseli region at the base of Kilimanjaro contains a small and well-protected elephant population where life histories based on individual recognition have been tracked since 1972. This population has increased gradually in size from ~600 to over 1800. Following 15 drought cohorts born between 1972 – 2019, we explore the short and long-term consequences of pre-reproductive drought experience for the Amboseli elephants. We first examined age-sex class vulnerability to drought mortality and then examined reproductive consequences for males and female survivors. We predicted that early drought experience would reduce future reproductive rates among female survivors due to reduced growth or other metabolic constraints (e.g. Lee et al. 2013). We also predicted that social disruption, due to loss of older leader females (matriarchs: McComb et al. 2001; Goldenberg and Wittemyer 2018) would exacerbate any effects of drought on mortality and fertility. Finally, we tested the consequences of early experience for age at first reproduction (females) or dispersal and musth onset (males). We expected that adversity-related late family independence, combined with delays to musth onset, would shorten male reproductive careers even for survivors. These are life history events with known potential for cohort variation

(Forchhammer et al. 2001; Gaillard et al. 2003), which subsequently impact population dynamics and population persistence.

Methods

Population monitoring

Individual elephants in the Amboseli population, southern Kenya, have been identified and observed continuously since 1972 (Moss et al. 2011). We recognize individuals using ear notches, veins and shape, as well as other body and tusk features (see Moss, 1996). Our current sample of individuals followed over the long-term is 3756 (1874 females, 1839 males, 43 of unknown sex who died young). Our ongoing population monitoring uses monthly re-sighting of individuals, with 100% annual re-sightings for females in ~65 families (0-12 sightings per month, median = 3.25 per month), and 87% annual re-sightings for 405 independent adult males (median = 8.8 sightings per year). Sightings of elephants (families, individual males) totaled 51,842 from 1972 to 2019, made by searching for elephants on an average of 24 days each month (see also Moss et al. 2011). Demographic data from these regular sightings consist of births recorded to females, with an accuracy of ±1 month for 79.6% of births among 1919 animals alive at the end of 2020, and deaths, either observed when carcasses could be located and identified for all age- and sex-classes, or inferred through the disappearance of a female or calf when the rest of the family was seen. Carcass identity was based on known ear attributes, body size and genitalia. Some males (n = 20) were known to have dispersed from the population after ~15 years of age and were therefore "lost" to further monitoring, and a few known males (n = 29) have been re-sighted after periods of 5 to 8 years away from the population. Typically, these re-sightings occurred when the males were in the sexually active state of musth, although for some males we missed first musth onset. A small proportion (6.7% n=124) of the study populations' known males (n = 1847) have dispersed, died or returned unrecognized and are scored as "fate unknown" and excluded from long-term demographic analyses. These males were distributed across all birth years at a mean of 5 "lost" per year, with a rise in 2011-2012 (20 lost) when staff turnover led to reduced monitoring.

The accuracy of births and deaths within families is therefore high in general, while statistics for males over 15 years of age rely on a specific subset of well-known individuals. Longevity calculations were restricted to individuals with well-established mortality dates and repeated sightings within a year.

Age categories were based on known (<1 month) ages for 2571 animals, confident (<6 months) age estimates for 473 individuals born since 1972, and estimates of ±1 to 5 years for 640 (330 females and 310 males) mostly born prior to 1972. Since elephants grow for a substantial proportion of their lives (up to 25-35 years for females and 50 years for males; see Lee and Moss 1995) it is possible to visually age calves (<6 months) and older individuals with some accuracy (within 2 to 5 years). Our estimates are also validated using tooth progression at death against known-aged individuals (Laws 1966; Lee et al. 2012). We defined age-classes as: calves (<2 years – dependent on milk), juveniles (2-4.9 years – dependent on mothers and families), adolescents (5 – 8.9 years – weaned but not yet reproductive), young adults (9-19.9 years – female first reproduction / male dispersal), prime adults (20-39.9 years) and old adults (40+ years).

Defining adversity events

We defined ecological and social adversity events (see Zipple et al. 2019) using rainfall patterns and death events for mothers and matriarchs. Annual rainfall and its monthly distribution within a rainfall year (Oct-Sept) was categorized using a dry season severity index (DSI) calculated as the number of consecutive dry season months with <20mm rainfall divided by total annual rain, multiplied by 100 for visualization (e.g. Alley 1984; Croze and Lindsay 2011). DSI ≥2.5 was considered as "drought" (52-year mean ± 0.5 CI), and typically represented >6 consecutive months with <20mm rain, and a total annual rainfall <250mm, compared to 405 mm for non-drought years. The semi-arid ecosystem has experienced 15 drought years with seven being extremely dry (DSI > 3) or prolonged over two years between 1972 to 2020. These low rainfall periods have been validated against remote sensing analyses of vegetation greenness (NDVI: Western et al. 2016; Boult et al. 2018). Events (births, deaths) were assigned to the rainfall year in which they occurred and then coded as drought or not drought using DSI for that rainfall year. Drought experience (yes/no) was also assigned to the 22-month gestation period preceding a birth.

Social adversity (disruption following matriarch death) was assigned as the date that a matriarch's death was recorded; the 12 following months were coded as the "disruption period". We considered the first year after a matriarch's death to be key since calves are most vulnerable to all-cause mortality in their first year of life (Lee & Moss 1986), and associations between females shift over at least a year, if not longer, after social disruption (Goldenberg & Wittemyer 2018). We also coded whether an individual who survived past 2 years experienced mother loss prior to the age 9 years (mean minimum first birth or dispersal age for males). Calves were coded as first-born or not first, as birth order affects survival (Lee et al. 2013).

Survival of consequences of adverse events

We used a binomial General Linear Mixed Model (run in SPSS V25, ©IBM Corp) to assess the probability of dying (yes, no) between birth and 12 months, with drought experience in the first year of life, sex, first born, gestational experience of drought and social disruption in the first year of life as fixed factors. Interactions between fixed factors were included in the initial model as drought * disruption, sex * drought, sex * first born and first born * drought. Mother ID was included as a random variable to account for the potential contribution of maternal factors such as parity, size, or age. We used random slopes and intercepts to reduce the incidence of Type I and II errors. Final model selection was based on excluding non-significant factors and interactions as long as these did not affect overall model fit or eliminate significant comparisons between factors. For these tests, a strongly censored sample was used (known birthdate, known early experience, death not due to humans, total N = 2259). We also calculated the proportion of calves that died in any year out of those available in two contexts: drought and social disruption.

We used a "time to event" approach to determine how long any elephant would be likely to live and thus calculated mortality hazard rates for each age. This approach also enabled us to assess average longevity from birth and from the onset of reproduction. Survival time across all ages for all study years was assessed using Cox proportional hazards regression (method: forward (Wald) with χ^2 for overall model fit), with cohort factors of gestational drought, drought in first 12 months of life, birth order, sex, disruption coded as matriarch death within 12 months of birth and maternal death prior to the calf attaining nine years of age. Human-caused mortality (n = 449) was

again excluded from survival analyses. Survival analysis included animals born prior to the study (left-censored) but whose fate was known. However, given that elephant lifespan can be >70 and the study has only considered <50 years of life to date, 49.6% of the samples in the longevity analysis were right-censored (i.e. still living).

Reproductive consequences of adversity

We used the same "time to event" approach for the analysis of reproductive onset for both females (defined as first conception resulting in a live birth) and males (first known musth) in order to include those yet to have an event (censored individuals). If individuals yet to experience an event are excluded, results can be biased towards early event detection (see Landes et al. 2020). Cox's proportional hazard regression models are considered robust to censored samples and allow for the inclusion of a number of covariates (see Zipple et al. 2019). Proportionality was assessed through visual inspection of residuals for crossover. We checked that covariates were uncorrelated and time-independent. Disruption, which co-occurred with droughts, was also found in non-drought periods (45.8% of 343 events). We used the forward (Wald) model design to be able to assess the contribution of each covariate to the overall model fit.

Female reproductive parameters

All known-age females who survived to nine years of age (n = 702) were included in the time-to-event analysis of age at first reproduction, defined as first known birth (accurate to within 1 month) minus 22 months for approximate age at first conception (AFC). Females who may have conceived but did not carry a calf to term were not included as successful reproducers and the frequency remains unknown for this population. Backdating from birth events also allowed us to determine when a female was available for a conception overall and in relation to the age of her current calf.

Cox's proportional hazards regression on age at first conception included birth order, matriarch death at birth and/or at age nine, maternal death prior to age nine, drought at birth and drought at age nine as covariates. Females were assigned to matriarch death (yes or no) for their year of birth, and for the year that they reached nine years of age (96% of first conceptions occur >9

yrs old), maternal death prior to age nine (yes or no), drought in first 12 months of life (yes or no), drought in the year when the female became nine (yes or no), and finally birth order (first born, not first born) as these factors are known to affect growth, survival and reproduction (Lee et al. 2013; Lee et al. 2016). Matriarch age (young, <30; yes or no) was also considered, as matriarch death could result in a young replacement, lacking leadership or competitive skills (Goldenberg and Wittemyer 2018). We also entered study decade from 1 to 5 to check for effects of changes in population size over time, representing potential competitor effects. Forward (Wald) models were again used to determine final fit and covariate effects on time to first conception. Females who had yet to conceive by the end of 2019 (n=142) were entered into the model at their current age or age of death.

Population level fertility was examined as a proportion of females conceiving out of those available to do so. Females were available when they were not already pregnant using backdated calf birthdates, and their surviving calf was over the age of 12 months (the average period of potential lactational anestrus; Lee, Lindsay and Moss 2011). Females who lost their calf in its first year of life were assumed to become available immediately after death of the calf. This fertility measure does not correct for the proportion of females at each age: females <20 and >40 have reduced conception probabilities (Lee et al. 2016). It therefore provides an indication of population level conception rate rather than an individual's conception risk, which varies with lactation demands due to offspring sex, individual condition and size, as well as her age.

We examined individual probabilities of giving birth in any year (fecundity) using a binomial GLMM, with birth (yes or no) and fixed factors of maternal age at calf birth, female early life experience, and drought experience at calf birth (drought: yes or no). Female ID was included as a random factor (N = 746). Matriarch and maternal death could not be assigned to each female's birth events since there were too few events for model stability (see Supplementary Materials for initial models).

We also used GLMM to examine factors affecting interbirth intervals (IBI) in months ($\log_{10}$ for normalization). Only IBI following a calf that survived to 12 months and which was not first born (n = 1493) were used. We assessed the effects of maternal age (young <20, prime 20-39, old 40+), calf

sex, drought, and matriarch age (young; yes or no) on overall fecundity, again with maternal ID as a random effect. Interactions of sex*drought were included in the initial model. Fixed factors and interaction were excluded when not significant.

Male life history events

Male independence, i.e. dispersal from the natal family, was defined as >80% of time not sighted with the family (Lee and Moss 1999). We assigned dispersal cohorts based on the male's year of independence for 354 males who left their natal families up to the end of 2019, with robust re-sighting frequencies and known fate (living or known date of death). Assigned ages for independence spanned 42 out of the 48 years of the study; for each male we counted the number of living population age-mates (± 2 years of the male's birthdate), called "peers" irrespective of whether the peer males were independent or still with their families. Male body size and dominance are associated (Poole 1989) so males aged within two years of each other are likely to be similar in size and relative dominance. These peer cohorts varied in number from 6 to 113 males, with a median of 61 males. Within-family peers (ranging from none to five) were not examined here as these were previously shown to be unrelated to age at independence (Lee and Moss 1999). The mean number of sightings of a male in any month of each year after independence was used to indicate presence within the main ecosystem. We conducted a *post hoc* Spearman's correlation to examine the effect of cohort size on independence age and resighting frequency due to non-normal distributions.

Factors influencing age at independence age were assessed using GLM (as the male sample for independence ages was uncensored, n = 324), with fixed factors of drought at birth, drought in year of independence, and number of peers ±2 years of the target's age. Matriarch death at birth or at independence were not used in male analyses due to limited sample sizes. No interactions were considered (see Supplementary Materials for model).

To assess the effects of ecological and social experience on male reproductive potential, we examined age at first musth (Poole et al. 2011). A total of 211 out of 320 males had reliable observations of first musth (month, year) between 1972 and 2019. Observations of musth represented sustained signaling (temporal gland secretion, urine dribbling) and association with

females and thus potential mating activity (Poole 1987). Musth has not been observed in Amboseli males prior to independence and occurs regularly after the age of 35 years in this population (Poole et al. 2011). For males who survived past independence but who had yet to experience musth (n=109), we included their age at the end of the sample period or death as censored in a Cox proportional hazard regression model for time to event analysis. We counted the number of musth-age male competitors (>35 years old), who had well established musth periods and could therefore potentially suppress other males' musth onset as these older males were larger and socially dominant (Hall-Martin and van der Walt 1984; Poole 1989; Slotow et al. 2000). We compared factors influencing time to first musth using the Cox's proportional hazards regression, with a forward (Wald) model. Fixed factors were the age at independence, drought experience at birth or independence, the number of peers in the population, and the number of musth age competitors (see Supplementary Materials for models). For *post hoc* two-way comparisons of factors associated with independence or musth age, we used Spearman correlations as data were not normally distributed.

Results

Survival by early experience

Natural mortality averaged 1.9% of the total population in non-drought periods (95% CI = 0.081, N = 41 years). Calves represent the majority of all mortality at any time but are especially affected by droughts (Figure 1). In an extreme drought during 2008-09, over 50% of dependent calves under two years of age died in the first drought year, while a total of 80% had died by the end of the following year. Some 60% of females (72/128) who gave birth in the first drought year of 2008 lost their calves. By contrast, in five preceding and five following non-drought years, an average of only 8.9% (± SD 3.99%) of calves died in their first year after birth. During the extreme 2008-09 drought, 35 of 64 females over the age of 45 years died, resulting in considerable turnover in family leadership. Nine of 35 families with matriarch deaths experienced multiple disruption events within a two-year period, losing successive matriarchs.
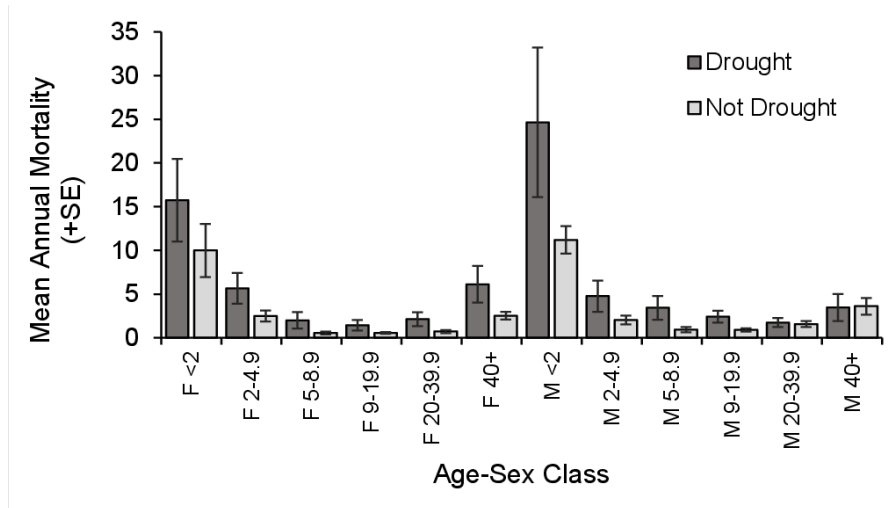
Figure 1. Mean (+SE) annual mortality per age-sex class (F = female, M = male; n drought = 15, n not drought = 33).

We analyzed survival probability specific to the first year of life for 2291 calves with known early life experiences. Drought experience in the first year of life was a significant predictor of the probability of early death (Table 1). The probability of a death was enhanced for males, for first born calves, and for those calves also lost their matriarch during a drought (Figure 2).

Table 1: Binomial logistic regression on the probability of dying in the first year of life (N Died = 351, Survived = 2212). Model factors: drought, first born, sex, disruption by matriarch death, with disruption * drought. Mother ID as a random factor, variance < 0.000002, NS. Excluded factor: gestational experience; excluded interactions: sex * drought, sex * first born, drought * first born, where exclusion had no effect on overall fit. Model details and sample sizes for factors in Supplementary Materials.

	Main effect, F, p value	Factor: t, p value	Coefficient (95% CI)
Overall model fit	$F_{5,2587} = 32.72$, p <0.001		
Drought	F = 68.68, p <0.001	Not Dry: t = -6.1, p < 0.001	-1.73 (-2.29 to -1.17)
Birth order	F= 24.07, p < 0.001	First: t = 4.9, p < 0.001	0.626 (0.38 to 0.88)
Sex	F = 11.5, p = 0.001	Female: t = -3.4, p = 0.001	-0.404 (-0.64 to -0.171)
Disrupted: Matriarch death in 12 mo	F = 24.91, p <0.001	Disrupted: t = 5.7, p <0.001	1.20 (0.79 to 1.61)

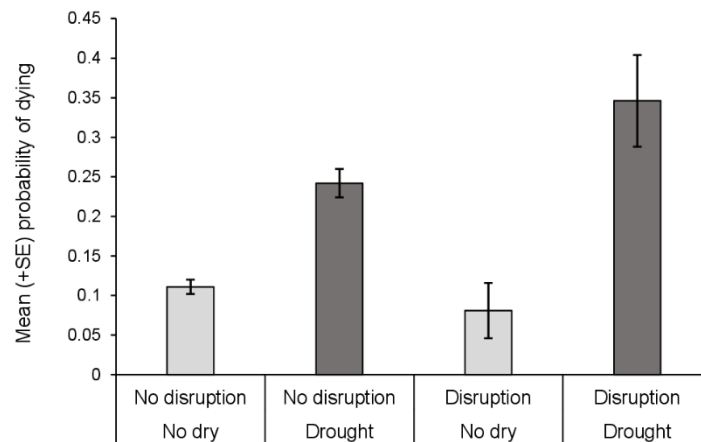|			
Drought * matriarch death	F = 6.53, p = 0.011	Neither: t = 2.6, p = 0.011	0.81 (0.19-1.44)

Figure 2. Risk of death in the first year of life for calves experiencing drought plus disruption to the family. (Risk = proportion of death specific to context out of all deaths for age).

Median longevity for all males was 24.9 years (21.4-28.4 95% CI, n = 1327) although longevity for males with early adverse experiences was only 16.75 years. For females, median longevity was 37.6 years (35.4-39.8 95% CI, n = 1562); that for females with early adverse experiences was 27.42 years. Of all the factors potentially influencing survival considered here, the strongest effects on longevity were those of maternal loss, matriarch death and birth order (Table 2). Regression coefficients were uncorrelated, with the exception of gestational experience and drought in first 12 months of life (r = -0.560) suggesting that those experiencing a drought during gestation were less likely to be born into a drought since droughts rarely last >2 years.

Table 2: Final Cox regression hazard model for social, ecological and maternal factors affecting survivorship of female (n = 479) and male (n = 474) elephants with known early experiences (natural mortality only). Forward (Wald) method in Cox's regression (Overall model fit χ^2 = 123.48, p<0.001).

Factor	B (Δ log hazard) (SE)	Wald, p	Exp (B) Hazard ratio (95% CI)
Sex (M < F)	-.245 (.065)	14.02 p<0.001	.783 (.688-.890)
Matriarch death in first 12 mo (< no disruption)	-.535 (.087)	37.67 p<0.001	.585 (.493-.695)
Mother died <9 (< mother survived)	-.648 (.076)	73.50 p<0.001	.523 (.451-.607)

Drought in 12 months (< no dry)	-.243 (.085)	8.11 p= 0.004	.784 (.663 -.927)
Birth order (First < not first)	-.461 (.075)	37.38 p<0.001	.631 (.544 -.731)
Drought in gestation (drought > no drought)	.358 (.080)	20.07 p<0.001	1.430 (1.22 -1.67)

Consequences of adversity for female reproduction

The majority of females in this population conceive successfully (i.e. result in a birth) for the first time between 9 and 12 years of age (mean age = 11.96 years, SD ± 1.99, N = 560). Mean age at first conception (AFC) changed significantly between the first decade of the study and later periods (early = 14.48, log rank = 72.4, p<0.001), possibly due to reduced accuracy in initial ageing or two years of extreme drought early in the study. Mean AFC was similar across subsequent years (11.57, log rank = 2.5, p = 0.287, NS) despite a doubling of the number of adult females in the population from 233 to 462 (r^2 = 0.024, NS).

Early drought and birth order did not influence AFC significantly, but matriarch death at age 9 did (Overall model fit: Wald X^2 = 4.85, p = 0.028). Females experiencing matriarch loss around the age of first reproduction matured slightly faster (ß = -0.294, 11.5 vs 12 years). Maternal death before 9 years, by contrast, slightly delayed age at first conception from 11.42 (n = 521) to 12.00 (n = 86) (ß = 0.407, p = 0.08). However, only 31% (77 of 251) of females who lost their mother survived to experience a first birth (with 14 yet to reproduce), compared to 52% of 973 females whose mothers survived (with 56 yet to reproduce).

On average, across 48 years of data, 37% of available females (9+ years, not pregnant, not in first 12 months of lactational anestrus) conceived in any year. Conceptions were reduced during extreme or prolonged droughts, followed by a significant increase in conceptions one year later (GLMM: estimate =0.427± SE 0.139, t=3.071 p=0.0042). There was a second peak at 5 years or one interbirth interval (estimate =0.499± SE 0.158, t=3.152, p=0.0034) after drought events (Figure 3). There was considerable variance in annual conceptions; in some years close to 80% of available females conceived, whereas during two extreme drought years of 2008 and 2009, only 2.5% of available females (n = 375) successfully conceived and carried a calf to term (Figure 4). Post-

drought peaks in calf production as well as persisting effects of drought deaths result in "missing" age-sex classes over time (Supplementary Figure 1).

Overall fecundity, as reflected in the duration of the interbirth interval (IBI) following a surviving, multiparous calf averaged 57 months and was unrelated to the occurrence of a matriarch death (Table 3). Maternal age was also unrelated to IBI, while IBI following the birth of a son or during good years was prolonged. Matriarch age was associated with IBI, with a longer IBI on average when a family's matriarch was under 30 years old.
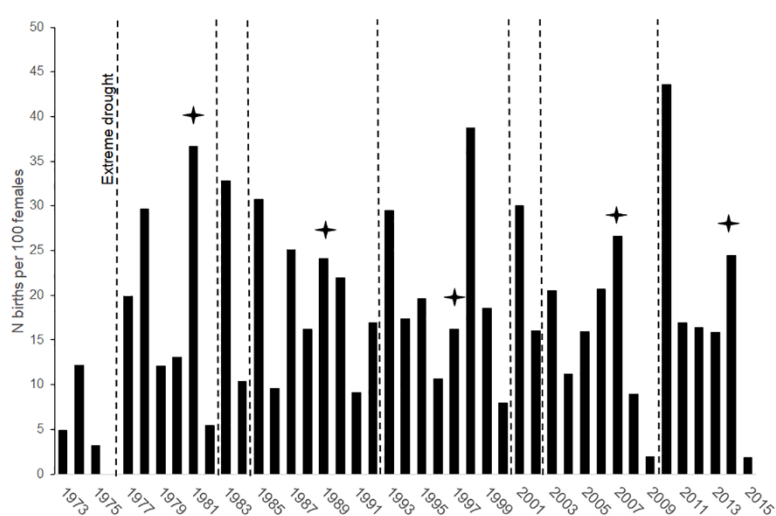

Figure 3. Temporal patterning of fertility (conceptions per 100 females) by year from 1973 to 2017 with 7 extreme droughts indicated by the dotted lines. Star indicates 5-years post-drought.
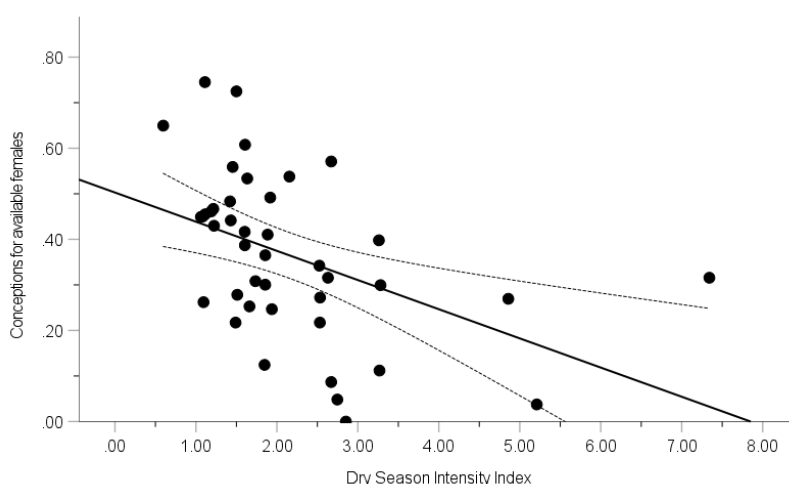

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Figure 4. Conceptions for available females from 1974 to 2017 in relation to Dry Season Intensity index (r = -0.452, n = 42, p = 0.003). Linear trend line with 95% CI shown.

Table 3: General linear mixed model on Log₁₀ IBI (months). Model factors: sex, drought at birth, matriarch age (<30 vs 30+). Mother ID as a random factor, variance (mother) Z= 3.632, p < 0.001, N mother = 746. Excluded: maternal age category (young <20, prime, old 45+), matriarch loss at birth, sex * drought. Overall model Fit $F_{5, 1495}= 8.50$.

Model terms	F p value	Factor: t, p value	Coefficient (95% CI)
Intercept		250.4 p<0.001	1.721 (1.709 to 1.734)
Sex	F= 11.05, p = 0.001	Male longer than female: t = -3.325, p < 0.001	-0.017 (-0.027 to -0.007)
Drought at birth	F = 7.87, p = 0.005	Drought shorter than no dry: t = 2.805, p = 0.005	0.017 (0.005 to 0.029)
Matriarch age	F = 5.39, p= 0.020	Old shorter than young: t = 2.321, p = 0.02	0.020 (0.003 to 0.036)

Adversity consequences for males

Male age at family independence ranged from 7.42 to 19.92 years, with a median age of 14.5 years. Experiencing a drought year around the age of independence was associated with a slightly earlier departure (13.1 years ± 1.70 SD vs 13.9 years ±1.89 SD; t = 3.28, p < 0.001). The median number of peers for males going independent was 30 (range 4-67). The number of male peers in the population (±2 years of target's age) was negatively associated with age at independence (t = -4.26, p <0.001): males tended to leave later when there were fewer close age mates in the population. In addition, there was a negative association between the size of dispersing cohorts and the likelihood of those males being resighted annually within the core population, suggesting greater movement away from core habitats with large cohorts (average cohort annual resighting rate and male cohort size, r_s = -0.665, p <0.01, n = 40).

Mean age at first musth was 29.3 ± .377 SE (range 16.4 – 38 years, n = 440 with 211 known events). The median number of musth-age competitors was 26 (range 11-47). Factors influencing time to first musth in the Cox proportional hazards model were number of peers at independence (ß = -.016, p = 0.005) and age at independence (ß = -.108, p = 0.011; full model in Supplementary Material), such that males who left families late were also those experiencing a later first musth (Fig. 5A), while larger peer cohorts were associated with younger ages at first musth (Fig. 5B). In *post hoc* comparisons for only known-aged musth males, the number of musth age competitors was also associated with a later age at first musth (r_s = 0.196, p = 0.004, n = 211); the effect was, however,

small and variance was constrained since relatively few well known males have yet reached musth age in the most recent larger birth cohorts. While the effect of drought at birth on the time to male reproductive onset could not be tested due to small and non-proportional samples, early adversity influenced male success through longevity: half of males die before the age of first musth, but for those that survived beyond a minimum age of first independence (10+), their median age at death was 39.3 (95% CI 36.0 – 42.5, n = 571).
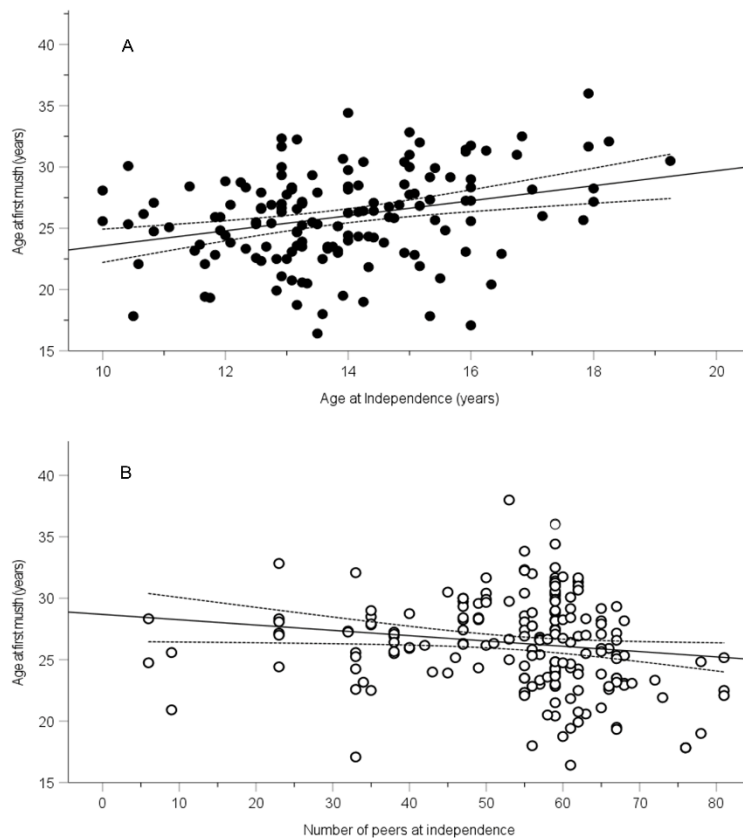

Figure 5. The association between age at first musth with (A) the age at independence from the family (n = 151); and (B) with the number of peers at mean independence age (14) (n = 192). Linear trend lines with 95% CI shown.

Discussion

As seen in other elephant populations (e.g. Dudley et al. 2001; Foley et al. 2008; Woolley et al. 2008; Wato et al. 2016) and other species (Caughley et al. 1985; Garel et al. 2004; Owen-Smith et al. 2005; Bourne et al. 2020), the most vulnerable age classes in Amboseli drought events were dependent infants (especially males) and the oldest females. Few males survive to the oldest ages and drought effects on older males were thus less likely to be detected (see Supplementary Figure

1). Droughts were associated with peaks of excess deaths; human-caused deaths follow similar patterns to drought deaths as in this area droughts bring elephants and livestock into close competition which can result in spearing (Sayialel & Moss 2011). Most natural deaths during droughts appeared to be the direct result of the drastic food limitation, possibly increasing susceptibility to other illness or infection, rather than starvation. Social disruption due to the loss of the matriarch also increased the probability of death for calves; whether this was related to loss of knowledge, loss of access to prime foods, reduced competitive ability with undisturbed families, or less protection for calves (e.g. McComb et al. 2001; Goldenberg and Wittemyer 2018) remains to be determined.

Like other long-lived species (chimpanzees: Stanton et al. 2020; Samuni et al. 2020; baboons: Zipple et al. 2019; Asian elephants: Lahdenperä et al. 2016), maternal death after weaning, but before reproductive onset, was an important influence on longevity; elephants who lost their mothers before they reached nine years old had a lifespan that was reduced by an average of 9 years (8 for males, 10 for females).

Female fertility onset, assessed by conceptions resulting in a live birth 22 months later, consistently occurred at ~12 years of age irrespective of early drought experience or increases in the number of female competitors over time. Density dependence effects on age at first reproduction are well established for some ungulate species (Hamel et al. 2010) but not for elephants (Trimble et al. 2009); its absence in these elephants might be associated with adequate nutrition for growth in early life (e.g. Jorgenson et al. 1993; Lee et al. 2013). We expected that matriarch loss would cause stress-related fertility disruption (e.g. Rosenbaum et al. 2020; Snyder-Mackler et al. 2020); but in this sample of 560 females over 5 decades, social disruption accelerated reproductive maturation, although the effect was small in terms of time at ~6 months. The observed earlier reproductive onset may have simply been related to covariation between a drought causing a matriarch's death, which was closely followed by higher food availability and therefore associated with a pulse in conceptions. Earlier reproductive onset is therefore likely to be food and/or body condition-related (e.g. Plard et al. 2015) rather than directly due to stress accelerating hormonal onset (e.g. Hochberg and Belsky 2013; Belsky et al. 2015).

We expected that females born in drought years and those approaching the minimum age for reproductive onset during a drought might suffer a condition loss or a delay between reproductive maturity and first conception due to restricted growth. Again, contrary to our predictions, females born in dry years who then survived to reproduce showed no disadvantages in terms of age-specific reproductive rates. Females who lost their mothers prior to reproductive onset had reduced longevity, as well as a slight trend for a later age at first birth. There were few such females due to excess early death, making interpretation difficult. We thus suggest that some effects of negative early experiences on female reproductive success are moderated by survival and growth (e.g. Douhard et al. 2014; Lee et al. 2016; Weibel et al. 2020) rather than by early adverse experiences alone. We cannot yet assess, however, whether adverse early experiences will have inter-generational consequences (Reichert et al 2020; Zipple et al. 2021).

Cohort density effects existed for males, as earlier male dispersal was associated with larger peer cohort size (see also Ridley 2012 for babblers). Smaller cohorts of drought survivors therefore dispersed later. When born into large cohorts, males dispersed younger, moved further and remained away from the core population for longer periods. We suggest that this greater dispersal allows males to access higher quality forage in rich habitats which enhances growth rates, and which may include crop foraging (e.g. Chiyo et al. 2014). Rapid growth then allows for earlier musth onset (Lee et al. 2013). Although a higher number of potential competitors over 35 years was weakly associated with a later musth onset (see also Markussen et al. 2019 for moose), the important influences were the interacting factors of number of peers and age at independence. The most recent male cohort (born after 1992, n = 153) has yet to reach 30 years old (mean onset of musth) so only nine of these young males, including one as young as 16, have been observed in musth. Thus, we could not test for cohort effects on first musth using either birth year or later periods of adversity. Our sample of musth males was limited in size and in effect sizes, as well as having an age structure skewed towards younger males, potentially influencing the extent of male-male competition (e.g. Mysterud et al 2005).

The association between early extreme droughts and male life events, e.g. an earlier age at independence but no association with age at first musth, may be mediated by growth. Some males

"outgrow" early disadvantages (Hamel et al. 2016) potentially by selecting better quality habitats (Chiyo et al. 2011). We did not test if drought at musth onset affected age at first musth since all males who experience a bad year with associated condition loss will simply skip a year before entering musth (Poole et al. 2011). In contrast to some ungulates where high densities create greater individual heterogeneity in male strategies (Markussen et al. 2019), here a larger number of peers was associated with younger dispersal suggesting that males may have had more opportunities for grouping in order to mitigate risks during activities such as crop foraging or moving to water (e.g. Evans and Harris 2008; O'Connell Rodwell et al. 2011; Chiyo et al. 2014; Srinivasaiah et al. 2019, Allen et al. 2020; Murphy et al. 2020). Although over 50% of Amboseli males die before the typical musth onset at age 30, survivors of early adversity who then reached independence were likely to live sufficiently long to experience on average ~10 years of musth experiences. Those males that use social strategies to improve survival and growth will ultimately achieve some reproductive success (Ganswindt et al. 2005; Hollister-Smith et al. 2007; Poole et al. 2011).

Elephants, both male and female, experience enduring consequences of early life disruption in the form of early mortality and reduced longevity, with direct impacts on reproductive output via the mechanism of a shorter lifespan. Fertility and musth onset were not directly impacted by adverse experiences that occurred in the first 2-5% of a lifespan, but were affected by the demographic consequences of such events; smaller cohort sizes and fewer competitors. Large body size, prolonged slow growth based on exploiting low quality foods, and cohesive social contexts may all act as buffers against the negative consequences of adverse life experiences over a long lifespan. As elephant populations face increasing drought challenges, such buffers will become more crucial for population persistence.

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