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Evolutionary developmental biology

Enduring consequences of early experiences: 40 year effects on survival and success among African elephants (*Loxodonta africana*)

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Growth from conception to reproductive onset in African elephants (*Loxodonta africana*) provides insights into phenotypic plasticity, individual adaptive plastic responses and facultative maternal investment. Using growth for 867 and life histories for 2652 elephants over 40 years, we demonstrate that maternal inexperience plus drought in early life result in reduced growth rates for sons and higher mortality for both sexes. Slow growth during early lactation was associated with smaller adult size, later age at first reproduction, reduced lifetime survival and consequently limited reproductive output. These enduring effects of trading slow early growth against immediate survival were apparent over the very long term; delayed downstream consequences were unexpected for a species with a maximum longevity of 70+ years and unpredictable environmental experiences.

1. Introduction

Individual variation in growth can have long-term consequences for adult survival and reproductive success in some large mammals [1,2], and studies on birds, rodents, humans and deer have demonstrated morbidity, mortality and reproductive consequences as a result of growth perturbations during early development [3]. Compensatory growth (‘catch up’) may reduce or eliminate the effects of early growth restriction [4,5], but an animal’s capacity to catch up will depend on its genotype and environmental quality. Without catch up, early growth restriction may determine the timing of subsequent events and susceptibilities to mortality risks [6], potentially leading to increased selection on specific cohorts or sexes seen in red deer [2], Soay sheep [1] or humans [6]. We ask whether elephants experiencing growth constraints compensate to ‘make the best of a bad start’ [7,8] or whether maternal bet-hedging—spreading risks at a cost to mean fitness—influences survival and reproduction.

Parental influences on offspring development, such as variance in maternal care allocation that affects growth trajectories [9,10], can represent either adaptive plasticity in investment (i.e. to maximize maternal fitness) [11] or non-adaptive variation in maternal quality or experience. The relative importance of these alternatives remains unclear [3], especially for long-lived species where maternal influences are likely to substantially precede the manifestation of their effects on offspring. To date, only humans have been shown to exhibit maternal effects over a prolonged time scale where relatively short perturbations early in life establish the onset and rates of metabolic processes over a lifespan [6]. Elephant mothers gain experience as well as grow in size over a series of events during approximately 50 reproductively active years

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Table 1. Parameter estimates of fixed effects from the minimal adequate linear mixed models describing the influence of birth order and drought on residual size-for-age. The minimal adequate models for female residual shoulder height and foot length included only the intercept (not shown).

model	source	estimate	s.e.	χ^2	*p*
male shoulder height	intercept	0.9269	3.0365		—
	birth order (not firstborn)	1.2243	3.4795		—
	drought in first 2 years (present)	−12.5407	4.3040		—
	birth order × drought in first two years	12.2977	4.8460	6.442	0.011
male foot length	intercept	0.0219	0.5416		—
	birth order (not firstborn)	1.4034	0.4889	7.307	0.007
	drought in first 2 years (present)	−1.0062	0.4424	4.955	0.026

[12]. We hypothesized that early-life stress owing to maternal inexperience might have profound and long-term consequences for growth and survival, especially for male elephants who face strong selection for rapid growth. We further evaluated changes in these consequences over consecutive births to test whether reduced care allocation was in fact adaptive plasticity or was a consequence of maternal inexperience.

2. Material and methods

2652 elephants have been recognized and assigned birth dates in Amboseli (see electronic supplementary material), with 1727 dates accurate to ± 2 weeks. We photogrammetrically assessed shoulder heights and measured hind footprint lengths for 431 males and 436 females across all ages. We determined relative growth (size-for-age) by extracting residuals from sex-specific nonlinear height and foot-length growth curves (see electronic supplementary material). We used linear mixed effects models (built separately for each sex using nlme 4 package for R) to assess changes in these residuals as a function of environmental experiences (drought or no drought) during gestation (for greater than six months during 22 months prior to birth) and separately during peak lactation (for greater than six months during the first 24 months of life; mean lactation duration = 57 months, $n = 949$). Our models included age, size and experience (first parity, $n = 464$, versus all subsequent births, $n = 1738$) of mothers at each birth. We also included interactions between drought during gestation, drought during lactation and maternal experience. In addition to fixed effects, we accounted for repeated measurements and genealogy by including individual ID nested within mother identity as random effects. We simplified models by iteratively removing the least significant, highest-order term, using likelihood ratio tests to determine whether its exclusion resulted in a significant increase in deviance [13].

We assessed the impact of early experiences on reproduction using female age at first parturition (median = 13.6 $\pm$ 0.104 s.e. years), categorized as early (less than or equal to 12), average or late (greater than or equal to 15; quartiles from proportional hazards analysis, $n = 455$). Similarly, we categorized the onset of male reproductive activity using age at first full musth (see electronic supplementary material; mean 28.2 $\pm$ 0.35, $n = 109$; hazards analysis): early musth males were less than 26 years (lowest 25%), average 27–31 and late greater than 31 (top 25%). Only relative size measured at ± 3 years (mean = 2.2) of age at first birth ($n = 81$) or age at first observed musth ($n = 124$) was used to minimize any growth constraints owing to the onset of reproductive activity.

Where data did not meet criteria for multi-level modelling, we used linear regression and ANOVA (Tukey post hoc tests). Probability of calf death owing to drought or maternal experience was assessed by logistic regression. Proportional hazards models provided mean and s.e. for longevity; we compared longevity between parity categories, drought experience in gestation and drought after birth using *z*-tests for independent effects of each factor in the minimal adequate model (R Package 'Survival').

3. Results

(a) Growth and its consequences

Growth occurs over a 50+ year period for males and 30+ years for females, with shoulder height and foot length highly correlated ($r^2 = 0.927$, $p < 0.001$, $n = 231$) and no significant difference in slopes between the sexes (ANCOVA, $F_{1,154} = 0.037$, $p = 0.9$, n.s.; electronic supplementary material, figure S1).

Parity affected offspring growth; firstborn calves under 5 (weaning) were small for their age ($F_{1,208} = 5.8$, $p = 0.017$), but growth varied by sex and environmental conditions during lactation (table 1). Sons (especially those firstborn) who experienced drought during lactation were also small for their age. For daughters, neither drought experience nor birth order had a significant effect on growth (figure 1).

Maternal age and size are highly correlated in elephants. However, maternal age alone was unrelated to offspring height-for-age among firstborn ($r^2 = -0.006$, d.f. = 110) or subsequent calves ($r^2 = 0.001$, d.f. = 353). The key risk factor in slow offspring growth was being a firstborn son.

Relative shoulder height ($F_{2,38} = 3.72$, $p = 0.04$) and foot length ($F_{2,124} = 7.69$, $p = 0.001$) were associated with age at first musth, and relative foot length was associated with female age at first birth ($F_{2,81} = 3.1$, $p = 0.05$). Early reproducers were large for their age (figure 2; males, early reproducers compared with average age at first musth, post hoc $p = 0.002$; females, all age comparisons $p < 0.05$). Some males apparently delayed musth, possibly until they were much larger than predicted for their age; thus, there was no significant size difference among early versus late reproducing males (post hoc $p = 0.16$). The effects of birth order and size on age at first reproduction cannot yet be compared for an adequate sample of firstborn males, but there was no parity × reproductive age interaction with size for females ($F_{3,81} = 1.35$, $p = 0.27$).

(b) Survival and longevity

Both drought and maternal inexperience influenced calf survival. Drought years with poor primary production doubled adult female probability of death ($t = 2.29$, $p = 0.03$,

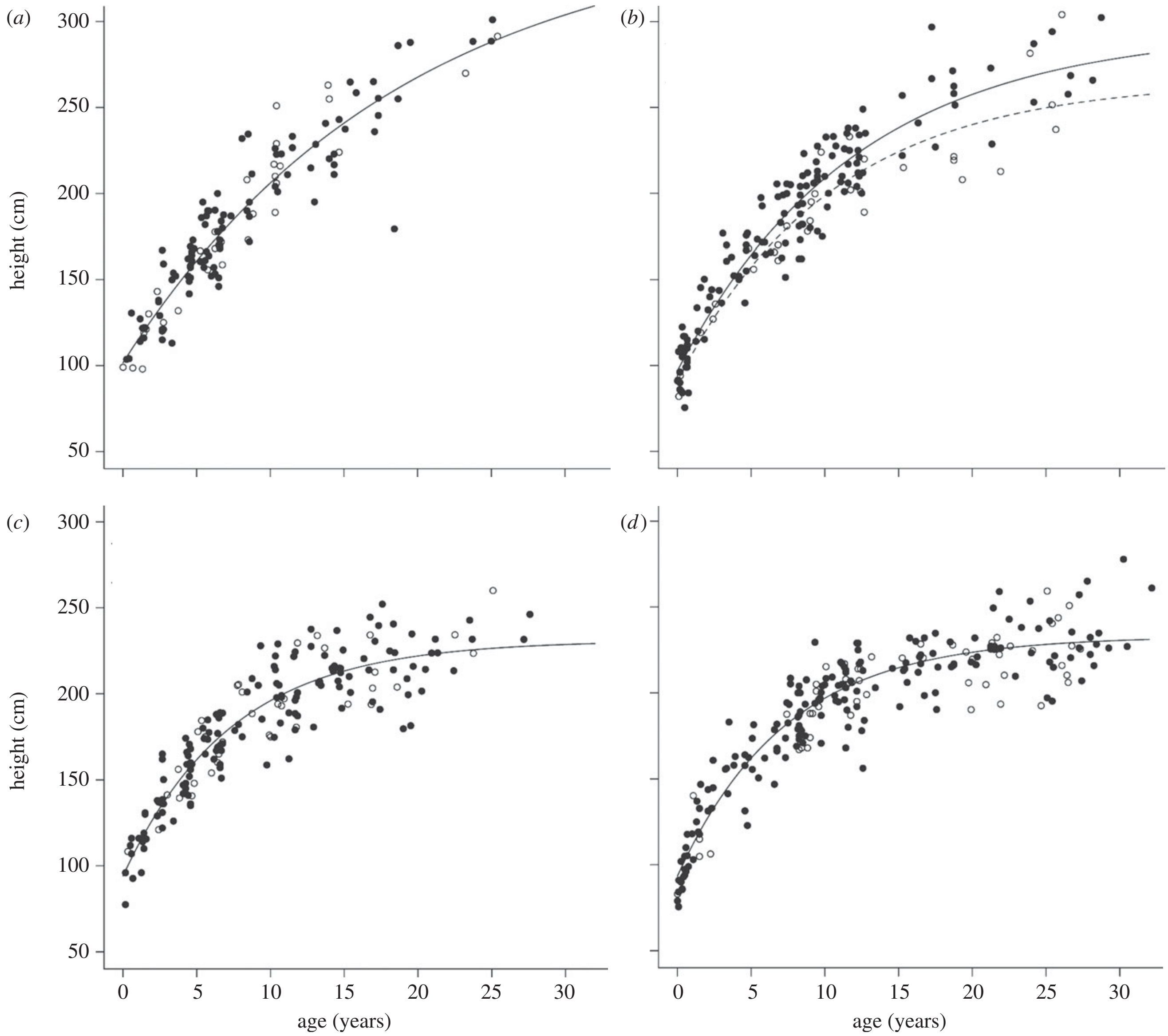

Figure 1. von Bertalanffy growth curves for height, estimated as a function of the presence of drought during the first 2 years of life and by birth order (see the electronic supplementary material for modelling approach). Males: (*a*) no drought in first 2 years, (*b*) drought in first 2 years and females: (*c*) no drought in first 2 years, (*d*) drought in first 2 years. Open circles represents firstborn and closed circles represents not firstborn.

3.8 versus 1.8%). Calves under 24 months were much more vulnerable in drought than non-drought years (backward logistic: overall model fit $\chi^2 = 78.9$, $r^2 = 0.04$, $p < 0.001$; drought: Wald $\chi^2 = 38.4$, d.f. $= 1$, $p < 0.001$; 29 versus 16% mortality). In addition, firstborn calves, and especially males, were more likely to die in their first year (first: Wald $\chi^2 = 30$, d.f. $= 2$, $p < 0.001$; sex: Wald $\chi^2 = 9.3$, d.f. $= 1$, $p = 0.002$; 25% males versus 17% females).

Firstborn survivors from 12 months of age (after peak calf mortality) had reduced longevity compared with later-born calves ($z = -2.77$, $p < 0.01$, mean longevity first $= 26.9 \pm 1.53$ years, not first $= 29.2 \pm 0.75$; see electronic supplementary material, figure S2) with no sex effects in the minimal adequate model. Calves surviving early drought experience past 12 months of age had an increased probability of death over the next 40 years, controlling for birth order ($z = 5.17$, $p < 0.001$; drought longevity $= 24.2 \pm 0.58$ years, no drought $= 26.7 \pm 0.79$). Calves experiencing gestational drought were only slightly more likely to die early (Wald $\chi^2 = 2.76$, d.f. $= 1$, $p = 0.09$), but survivors' mean lifespan was somewhat lengthened ($z = 3.77$, $p < 0.01$; dry $= 29.5 \pm 1.18$, no dry $= 27.9 \pm 2.02$).

4. Discussion

Both maternal and environmentally derived variation in early experience had enduring effects on elephant offspring. Maternal age, while a correlate of a mother's size at each birth, did not predict offspring growth independently of parity. The observed effect of maternal experience reflected learned responses to calf signals of need plus mothers' physical ability to sustain calves throughout an extended lactation [12]. Small, young mothers with low energy reserves were still growing (see the electronic supplementary material, figure S1), may have had dilute milk, and had yet to mesh with their calves' suckling demands. As a result, firstborn calves were smaller, with reduced growth potential and a higher risk of death. The sexes differed in their sensitivity to these constraints, with reduced growth and higher mortality among more rapidly growing sons, decades before reproductive onset. Because these associations with birth order relate to experience rather than maternal energy deprivation during droughts, the reduced growth of firstborn sons experiencing droughts early in life was unlikely to represent adaptive maternal plasticity, as has been suggested for human mothers experiencing famine [6,11].

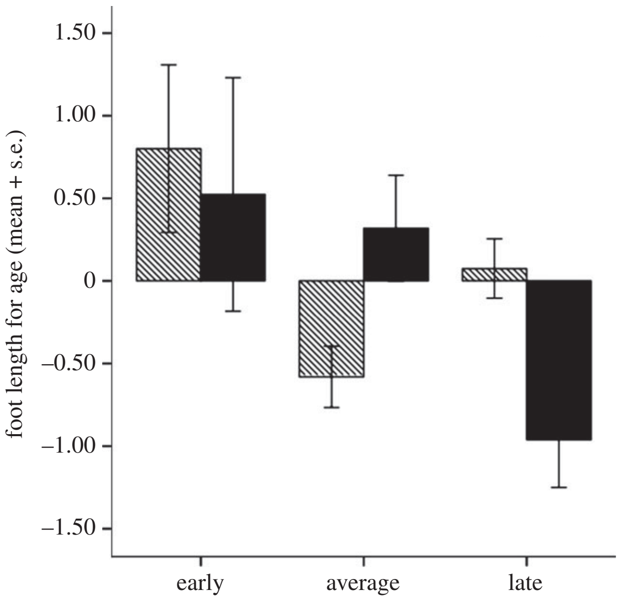

Figure 2. Size-for-age plotted for early, average or late reproductive onset for first musth ($n = 124$) and first birth ($n = 81$). Striped bar represents males and black bar represents females. Age categories defined in §2.

Persistent gestational 'stunting' was not seen, with a post-natal period of 5 years potentially allowing for compensatory growth. Thus, calves with drought-related *in utero* stunting either died early in life, especially when exposed to other risks, or if they survived, they overcame any potential stunting during lactation. However, like humans [11], drought-related energy deprivation affecting growth and metabolism during early lactation increased lifetime mortality hazards even for surviving calves. Given the duration of gestation (22 months) relative to the duration of droughts (greater than 6 months) and to elephant lifespan (approx. 70 years), gestationally mediated selection for alternative phenotypes seems unlikely [14].

Size interacted nonlinearly with the onset of male reproduction, possibly due to individual males trading reproductive time for growth. Smaller, poor-quality individuals generally reproduced later but some high-quality males may have delayed reproduction until they were older and very large. Variance in size was greater for early maturing males, contrary to predictions that individuals mature at the same size in poor conditions but with variance in maturation age [15]. Older males were more than 40 cm taller than males entering musth under 26, and size, age and genetic paternity frequency were all positively associated in this population [16]. Factors such as early growth that negatively impact on size-for-age and age at reproductive onset reduce male lifetime reproductive output.

Being born in a drought period to an inexperienced mother has adverse consequences for longevity, adult size and reproductive potential. A long, slow gestation, the capacity to learn calf-rearing skills over successive reproductive events, and indeterminate growth reflect adaptive responses to an inability to forecast ecological conditions in non-equilibrium savannah ecosystems.

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