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Is bigger better? The relationship between size and reproduction in female Asian elephants

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Abstract

The limited availability of resources is predicted to impose trade-offs between growth, reproduction and self-maintenance in animals. However, although some studies have shown that early reproduction suppresses growth, reproduction positively correlates with size in others. We use detailed records from a large population of semi-captive elephants in Myanmar to assess the relationships between size (height and weight), reproduction and survival in female Asian elephants, a species characterized by slow, costly life history. Although female height gain during the growth period overlapped little with reproductive onset in the population, there was large variation in age at first reproduction and only 81% of final weight had been reached by peak age of reproduction at the population level (19 years). Those females beginning reproduction early tended to be taller and lighter later in life, although these trends were not significant. We found that taller females were more likely to have reproduced by a given age, but such effects diminished with age, suggesting there may be a size threshold to reproduction which is especially important in young females. Because size was not linked with female survival during reproductive ages, the diminishing effect of height on reproduction with age is unlikely to be due to biased survival of larger females. We conclude that although reproduction may not always impose significant costs on growth, height may be a limiting factor to reproduction in young female Asian elephants, which could have important implications considering their birth rates are low and peak reproduction is young – 19 years in this population.

Introduction

Organisms distribute their finite supply of resources between growth, reproduction and survival, predicted to lead to trade-offs between these processes (Kirkwood & Rose, 1991). High investment in growth can reduce a female's fecundity (Lee *et al.*, 2012), and early reproduction and high reproductive investment have been found to suppress growth in some organisms, such as cod (*Gadus morhua*) (Folkvord *et al.*, 2014) and barn swallows (*Hirundo rustica*) (Saino *et al.*, 2014). Conversely, there is evidence from a number of seasonally breeding large mammals that fecundity positively correlates with size, with large individuals reaching reproductive onset first (Clutton-Brock *et al.*, 1988; Green & Rothstein, 1991; Jorgenson *et al.*, 1993). These findings lead to the contrasting hypotheses that size may either positively or negatively correlate with reproduction depending on the importance of size-related fitness, the care dependency of offspring and costs involved in reproduction (Jorgenson *et al.*, 1993). Further exploration of this relationship in natural systems is necessary to determine how body size and measures of reproductive success are associated in species that do

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not share the same life-history strategies as those previously studied.

In animals that reach a determinate size, such as birds and mammals, young individuals must invest more resources in somatic growth and maintenance than those that have ceased growing, and there may thus be a trade-off between growth and reproduction in younger individuals (Hamel & Côté, 2009). High early investment in reproduction has been found to reduce later-life fecundity and survival in many mammals (Nussey *et al.*, 2006; Hayward *et al.*, 2014) and birds (Reid *et al.*, 2003), although impacts on future growth are not widely studied, and often focus on experimental manipulation. For example, suppressed reproduction via experimental contraception improved later growth and body condition in the kangaroo (*Macropus giganteus*) (Gélin *et al.*, 2016). Some observational studies have also found that high early female fecundity is associated with stunted growth in humans (Rah *et al.*, 2008) and wild bison (*Bison bison*) (Green & Rothstein, 1991). Early reproduction also reduces later mass gain in bighorn ewes (*Ovis canadensis*), although this relationship may only prevail under high densities and therefore strong selection pressure (Festa-Bianchet *et al.*, 1995; Bérubé *et al.*, 1999).

Whereas reproductive investment can thus negatively impact growth, body size can also positively correlate with fecundity (Green & Rothstein, 1991; Festa-Bianchet *et al.*, 1995). This may explain why we do not see a negative impact of early reproduction on later fitness in some species if early reproduction is dominated by heavier, healthy females (Gjerde, 1986; Bérubé *et al.*, 1999). There is evidence from some species to suggest that only females with reduced condition may face substantial reproductive costs (Hamel *et al.*, 2009), which could introduce bias when assessing reproductive costs at a population level. Furthermore, studies often focus on seasonally breeding species, which could lead to a more marked difference between early and late reproducers (Jorgenson *et al.*, 1993). Exploration of the impact of early reproduction in species with a less restrictive breeding schedule could assess whether costs still persist when the differences between early and late reproduction are lessened.

Here, we investigate the association between size, reproduction and survival in female Asian elephants (*Elephas maximus).* Specifically, we examine the links between size and reproduction by (i) assessing the relationship between female height and weight gain during growth against age-specific reproductive rates at the population level; (ii) analysing the association between age at first reproduction (early/late reproducers) and later mature size (height, weight), building on past findings in Asian elephants that high early investment in reproduction trades off with later-life fecundity and survival (Robinson *et al.*, 2012; Hayward *et al.*, 2014); testing whether adult height and weight constrain reproduction: in terms of (iii) number of offspring produced or raised to age 5 or (iv) reproductive status (reproducer vs. nonreproducer); and (v) evaluating the impact of height on survival, to understand whether survival differences could underlie size or age variation in reproductive output.

Our study system presents a rare opportunity to examine the relationships between these life-history parameters in a species that grows for a prolonged period and reproduces until age 65 years or beyond (Lahdenperä *et al.*, 2014), with high investment in few offspring. This high investment includes a 22-month gestation period with conceptions occurring any time of the year (Mumby *et al.*, 2013), average birth intervals exceeding 5 years and an infant dependency period of 4–5 years (Hildebrandt *et al.*, 2006; Lahdenperä *et al.*, 2014). The Asian elephant's growth period spans two decades, with females reaching mature height (> 2 m) at around 20 years, and a weight exceeding 2 tonnes, which can continue to increase or fluctuate throughout life, reflecting changes in body condition (Mumby *et al.*, 2015). Such a growth pattern involves potential for overlap between growth and reproduction as average age at first reproduction has been reported to be around 13 years in wild Asian elephants in Sri Lanka (De Silva *et al.*, 2013), and working Asian elephants in Myanmar can begin reproducing from as young as 10 (Clubb *et al.*, 2009). Studying associations between size, reproduction and survival in female Asian elephants thus offers new insights in the little-studied context of a continuously breeding, nonhuman large mammal, with a very slow life history.

Materials and methods

Study population

Population estimates of wild Asian elephants in Myanmar range from 2000 to 5000, although the current number likely lies at the bottom end of this range (Sukumar, 2006; Leimgruber *et al.*, 2008, 2011). Around 5500 Myanmar elephants are semi-captive, and over half of these semi-captive individuals (around 2700 individuals) work in the timber industry, owned by the state-run Myanma Timber Enterprise (MTE). The workload of these state-owned elephants adheres to MTE regulations, with set hours per week, days per year and tonnage per individual (Mumby *et al.*, 2013). The MTE elephants are not provisioned for, but instead are allowed to forage freely in the forest (Gale, 1974). Similarly, breeding is not managed by humans, and most reproduction occurs in unsupervised hours during release into the forest at night either with other semi-captive individuals or with wild elephants. MTE ensures that detailed logbooks are kept for each individual elephant, which has led to the formation of the world's largest multigenerational life-history data set on semi-captive Asian elephants (Mar *et al.*, 2012; Mumby *et al.*, 2013). The logbooks contain detailed information including individual ID number, date of birth and death, sex, birth origin (captive born/wild caught) and work camp as well as offspring birth dates and survival, allowing us to investigate reproductive investment across a lifetime in individuals of known ages. The assignment of ages to wild-caught individuals is performed by experienced vets using body size, temporal/buccal depression, ear folds, pigmentation and tusk size (Arivazhagan & Sukumar, 2008); subadults can be aged very accurately. Elephants are weaned and begin training at 5 years old, whereupon they carry out light work tasks until they enter the workforce at 17, with retirement at 55 (Begley, 2006).

Data selection

This study uses a range of demographic data sets maintained by MTE over decades on individual working elephants, combined with information recorded on variation in individual size. For our body size measurements, we measured height from ground to shoulder to the closest centimetre or inch depending on region (inches were converted to centimetres for the purpose of analyses, and thus, measurements were accurate to within 2.54 cm), and weight to the nearest kg using Eziweigh 3000 scales. The measurements were taken in years spanning 1985–2017 for height and 2011–2017 for weight. Measurements were taken across different climatic seasons of the year (monsoon, cool and hot), and we account for such differences in measurement season where appropriate in weight models (height does not vary by season). Reproductive analyses focus on females with recorded size measurements, known reproductive history (date of birth and survival of any offspring born) and known birth origin (wild caught or captive born), and we only include wild-caught individuals captured under the age of 15 (capture age ranges: 0–5 years = 19, 6–10 = 31, 11–15 = 5) to ensure accurate age estimation and to reduce potential unknown reproductive events prior to capture (consistent with Leimgruber *et al.*, 2008). Specific details of data selection and sample breakdown are given in subsequent sections. The majority of the females included in the reproductive analyses are still alive, with only three known deaths, two of which were in the last 3 years. The elephants from this subset span five work regions in northern Myanmar, four in the Sagaing Region and one in the Mandalay region.

Statistical analyses

All statistical analyses were conducted using R version 3.3.1 (R Core Team, 2016). In analyses using *glmer*'s, continuous variables were scaled to a mean of zero and standard deviation of one to aid model convergence.

Population-level timing of growth and reproduction

First, we investigated the relationship between reproduction and growth in females by quantifying the overlap between the population-level increase in reproduction with age and the levelling off of the growth curve with age. We determined age-specific fertility of all reproductive females between the ages of 5–60 years in a sample of 1040 females. Age-specific fertility was calculated as the total number of offspring born each year divided by the total number of reproductive females alive at the end of each year for each age (see Lahdenperä *et al.*, 2014). We then compared this to height and weight gain over a lifetime for all females we had size data available for, adapted from Mumby *et al.* (2015), (average measurement and age over a 4-year measurement period: 1690 height measures from 240 females and 1474 weight measures from 243 females aged 0–72 years). Growth curves were produced from nonlinear least-squares models using the *nls* function in R, with a response variable of either height or weight. A self-starting von Bertalanffy growth function was used, with age in years as an input parameter – the von Bertalanffy curve was deemed a better fit than other commonly used growth curves (Gompertz and 3-parameter logistic) on the basis of their coefficients of determination (see Mumby *et al.*, 2015). Both wild-caught and captive-born females were included in these models, as previous studies found little difference in the growth curves of wild-caught and captive-born individuals (Mumby *et al.*, 2015).

Age at first reproduction and size

We then assessed the impact of age at first reproduction on subsequent age-specific height and weight by constructing linear mixed models using the *lme4* package version 1.1.12 (Bates *et al.*, 2015). Specifically, we aimed to contrast the subsequent size of females that reproduced for the first time before vs. after the population average peak age in reproduction – for this population, this is 19 years (age at first reproduction in our subset ranged between 9 and 35 years, with a mean of 18.5) (Hayward *et al.*, 2014). In this model, we included only reproductive females over the age of 20 (range 20–62) and used only size measurements taken from their first reproduction onwards (over 74% of ever-reproduced females had reproduced for the first time by 20). These models compared the continuous height of 62 ($n = 498$ height measurements) and weight of 61 ($n = 438$ weight measurements) reproductive females that started reproduction either before or after the population peak of 19 years (binary variable for before: height $n = 32$; weight $n = 30$, and after or equal to 19: height $n = 30$; weight $n = 31$). In these models, we fitted birth origin as a fixed effect (integer term: 1 for wild-caught individuals, height $n = 33$ and weight $n = 34$; 0 for captive-born individuals, height $n = 29$ and weight $n = 27$), to account for potential differences between wild-caught and captive-born females. We included an additional interactive term between this birth origin term and capture age (continuous variable, range 0–15), to account for the entry of wild-caught elephants into our study at variable estimated ages. We also included a continuous fixed term of age at measurement (range = 20–62) in all models and a fixed categorical term of measurement season in weight models (3-level factor: cool, dry, wet) to account for seasonally variable conditions (Mumby *et al.*, 2013). A quadratic age term was included in weight models, as weight gain neither ceases with age nor linearly increases (Mumby *et al.*, 2015). However, the measurement season term and quadratic age terms did not improve model fit and were subsequently removed from the final model. Random terms accounted for work camp (5-level factor), and birth cohort, using a term for 5-year interval of birth (9-level factor from 1950 to 95). We also included a random term for individual ID, as the effects were tested using multiple measurements of the same individual at different ages over the total measurement period (maximum 32 years of measurements, mean 3.8 for height and a maximum of 4 years of weight measurements, mean 1.2). All models included an additional random slope of age at measurement by ID to allow the slope of any age effects to differ between individuals. Comparisons between models were based on the lowest Akaike information criteria (AIC) values comparing models with and without the term in question (following a selection procedure similar to Hamel & Côté, 2009). Appreciating the complexity of mixed models, we carried out thorough model selection before proceeding to AIC comparisons and terms were dropped in the case of model convergence issues to reduce complexity, although biologically significant terms were retained (following Bolker *et al.*, 2008). These model terms and comparison methods were replicated for each of the subsequent analyses unless stated otherwise.

Size and lifetime reproductive output

We next investigated whether a female's reproductive success is constrained by her height or weight, first measured by the number of offspring produced, followed by the number raised to weaning age. Measurements were taken from 102 females ($n = 687$ height and $n = 541$ weight measurements). Only females aged 30 and older (range 30–62) were included to allow females the opportunity to have produced multiple offspring. We fitted generalized linear mixed models, again from the *lme4* package in R, with a Poisson distribution to account for the zero-inflated skew caused by including nonreproductive females in the model. We first used a continuous term of number of calves birthed by the age of measurement (range 0–9) as a measure of reproductive output. The other terms controlled for in the models were identical to those described above, although in all subsequent models we did not include the measurement season term in weight models as it is not relevant to reproduction as the dependent variable, and the capture age term was dropped as it did not improve model fit. We also tested for an interactive effect of height/weight and age at measurement on reproductive output as size effects may vary depending on the age of a female. We then repeated these models on the same subset of females using number of calves raised to age 5 (range 0–5) as the measure of reproductive output. This was to account for maternal investment differences in lactation and maternal care – mothers may require more resources to ensure survival of offspring. We split the calf variable into categories for visual representation in figures (0 = none; 1–3 = low; 3–5 = medium; 5+ = high), and findings from analyses run with these categorical variables were consistent with the continuous term reported.

Size and reproductive status

Because a large proportion of females in our study population fail to reproduce at all in their lifetime, to further explore the general relationship between size and reproduction across different ages, we fitted binomial generalized linear mixed models (*lme4* package) to assess whether a female's reproductive status (1/0) at the time of measurement depended on her height or weight. Comparisons were made between 147 and 145 females measured over the age of 20 for (i) height and (ii) weight, respectively, totalling (i) 498 and (ii) 438 observations of reproductive and (i) 406 and (ii) 418 observations of nonreproductive females. Reproductive status was coded as the status at the age of measurement (had vs. had not produced any calves by this age), so some females would be coded as 0 at younger ages and 1 later – we account for this difference between individuals with the random slope for age at measurement by individual. The models controlled for the same terms as above analyses, with an interaction similar to that in (iii), between age and height or weight, to investigate whether the effect of size on reproduction depended on age (i.e. whether size limited reproduction more at certain ages).

Survival and size

To assess whether a female's survival during reproductive years depends on her height, we fitted a Cox proportional hazards mixed-effects model using the *coxme* package in R (Therneau, 2015). The model included 104 females (18 dead and 86 censored), measured between ages 20 and 50 of prime reproduction (mean 35 years). We focused only on height for this analysis, as weight measurements only started in 2011, and there are insufficient numbers of measurements of individuals that have subsequently died. We used a continuous measure of height for this analysis, but split the height variable into binary quantiles for easier visual representation in figures (split into even quantiles, above and below 218 cm, $n = 52$, $n = 52$, respectively). We included fixed terms of reproductive status (binary: reproduced; did not reproduce aged 20–50), age at measurement (continuous variable) and birth origin (wild caught vs. captive born). Decade of birth was included as a random term (4-level factor: 60s, 70s, 80s, 90s) to control for any differences in birth conditions.

Results

Population-level timing of growth and reproduction

We first compared the timing of female fertility with their height and weight gain in our study population. From our growth curves (shown in Fig. 1), we found that by the peak fertility of this population – 19 years – females have reached approximately 96.6% of their mature (final) height, but only 81.4% of their mature weight. As over half (52%) of the reproductive females in our sample started reproducing younger than 19, there may be potential for overlap between reproductive investment and both body size parameters. However, height is unlikely to be greatly affected by early reproduction; at the ages of 10 and 15 years, on average 87% and 93.7% of height gain are complete, respectively. However, weight gain could be subject to reproductive costs: only 60.3% and 73.9% of the average 'final' weight is gained at the same ages.

Age at first reproduction and size

Of our 147 females over 20, 55% of measurements were taken from reproductive females, and their age at first reproduction ranged between 9 and 35 years, with a mean and median of 18.5 years. We investigated how their age at the onset of reproduction (before vs. after the population peak age of reproduction of 19) was associated with subsequent size. Although females starting to reproduce earlier than the peak tended to be taller and lighter, these trends were not significant (height: $\chi^2 = 0.313_1$, $P = 0.576$, $n = 62$; weight: $\chi^2 = 2.657_1$, $P = 0.103$, $n = 61$; see Fig. 2 and Table 1).

Size and lifetime reproductive output

We then investigated whether an individual's size affected her reproductive success, measured first as the total number of offspring produced and then as the total number raised to the weaning age of 5. We found no significant relationship between a female's height and the total number of offspring produced ($\chi^2 = 0.01_{1,}$ $P = 0.90$, $n = 102$) or raised to 5 ($\chi^2 = 0.088_1$, $P = 0.77$, $n = 102$), see Figure S1; Tables S1.1 & S1.2. Similarly, the number of offspring born was not significantly associated with body weight ($\chi^2 = 0.001_1$, $P = 0.98$, $n = 102$), nor was number of calves raised to 5 ($\chi^2 = 0.018_1$, $P = 0.894$, $n = 102$). There was a significant quadratic relationship between age and number of calves surviving to 5 in the weight model ($\chi^2 = 0.3.94_1$, $P < 0.05$, $n = 102$) but not for number of calves born. There was no interaction between age at measurement and height on number of offspring born ($\chi^2 = 0.330_1$, $P = 0.55$, $n = 102$), or raised to 5 ($\chi^2 = 0.277_1$, $P = 0.599$, $n = 102$), nor was there an interactive effect of age and weight on either the number of calves born ($\chi^2 = 0.022_1$, $P = 0.882$, $n = 102$) or raised to 5 ($\chi^2 = 0.024_1$, $P = 0.877$, $n = 102$).

Size and reproductive status

Given that a large proportion of females in the population forego reproduction altogether, we also investigated whether size is an important factor influencing the probability of reproducing at all for these large mammals. We found there to be a significant negative interaction between height and age on reproductive status, indicating that during peak reproductive years,

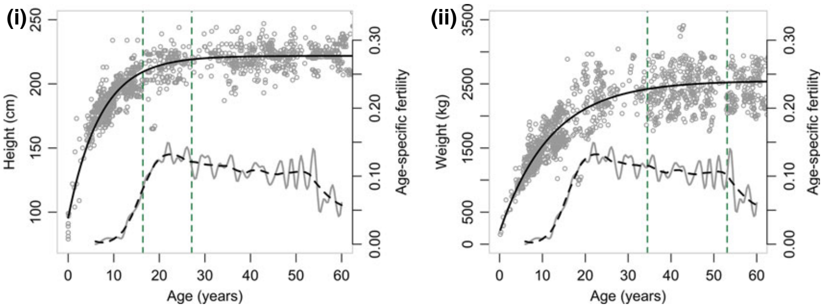

Fig. 1 Growth curves of (i) height and (ii) weight gain over a lifetime in relation to age-specific fertility. The filled black line represents the growth curve for (i) height ($n = 240$) and (ii) weight ($n = 243$), with grey points showing repeated measurements of individuals used to construct the population-level curve. The dashed black line shows the smoothed age-specific fertility of reproductive females, whereas the grey line represents raw fertility data ($n = 1040$). The vertical green lines show the ages at which 95% and 99% of (i) height and (ii) weight is achieved.

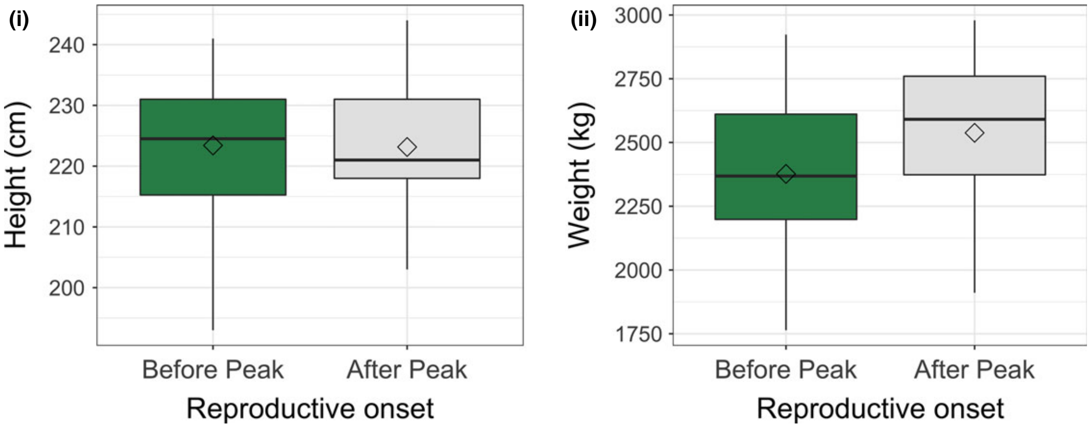

Fig. 2 Age at first reproduction and subsequent size. Comparisons of the subsequent height (i) and weight (ii) of females who started reproducing before (green) or after (grey) the peak of population reproduction (age 19). Box limits show upper and lower quartiles, vertical line shows range, midline the median and diamond the mean.

Table 1 *Lmer* output of the effects of first calving (early/late reproducers) on the height and weight of females measured over 20. Estimates are expressed on the logit scale. Colon (:) represents an interaction. Reference corresponds to late reproducers and captive-born females.

	Height		Weight	
Fixed effects	Estimate ± SE	*t*-value	Estimate ± SE	*t*-value
Intercept	226.55 ± 3.45	65.66	2063.06 ± 247.03	8.35
First rep (early)	1.12 ± 1.99	0.56	−143.29 ± 85.88	−1.67
Age	−0.12 ± 0.07	−1.65	14.03 ± 5.83	2.41
Origin (Wild)	−8.11 ± 3.65	−2.22	−116.79 ± 165.13	−0.71
Origin: Capture Age	1.32 ± 0.44	2.98	−6.42 ± 22.10	−0.29

Random effects	Variance ± SD	Corr	Variance ± SD	Corr
ID (Intercept)	53.23 ± 7.30	–	570 585.7 ± 755.37	–
Age	0.02 ± 0.15	−0.56	463.80 ± 21.54	−0.97
Birth Cohort	0.00 ± 0.00	–	0.00 ± 0.00	–
Camp	0.00 ± 0.00	–	9177.50 ± 95.80	–
Residual	26.77 ± 5.17	–	33 978.90 ± 184.33	–

taller females were more likely to have reproduced, but such effects of height on the probability to reproduce diminished with age ($\chi^2 = 9.702_1$, $P < 0.01$, $n = 147$; Fig. 3; Table 2). Weight was unrelated to reproductive status at all ages, as indicated by a nonsignificant interaction between weight and age ($\chi^2 = 0.00_1$, $P = 1.00$, $n = 145$).

Survival and size

Finally, we tested for differences in survival of reproductive-aged females by height to investigate whether there was selective disappearance of smaller females at older ages, which could underlie the lessened impact of height on reproduction with age. Between the ages of 20 and 50, there was no evidence in our sample for differences in mortality by height (HR = 1.05, $z = 1.44$, $P = 0.15$, $n = 104$; see Fig. 4; Table S2).

Discussion

This study applied life-history theory to assess the association between size and reproduction in the context of a continuously breeding, nonhuman large mammal, with a slow life history. We found there to be a potential for overlap between reproductive investment and height gain at the population level and a substantial potential for an overlap with weight gain (a marker of body condition). Our results showed that early onset of reproduction was associated with taller later height of females and lower later weight, but these associations were not significant. Importantly, however, taller females were more likely to be reproductive across all ages as compared to shorter ones, but the effect of height on reproductive status reduced with age, indicating that taller females had an advantage particularly during peak reproductive years. Our survival analysis indicated no evidence of a link between height and survival in females of reproductive ages, suggesting that the declining importance of height on reproduction in older females is not due to size-biased survival.

Our first question, assessing the extent of overlap between reproduction and growth, was to determine whether there was potential investment competition between the two. Our results (see Fig. 1), show that although the majority of growth, as indicated by height gain (almost 97%), is complete by 19 years – the age of peak fecundity – only 81% of weight is gained by this age. Weight gain continues to increase and fluctuate

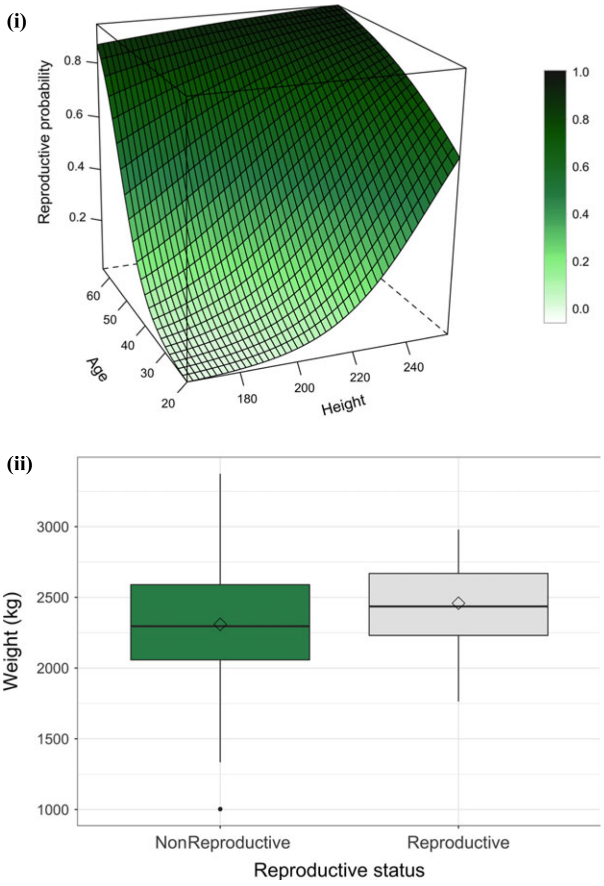

Fig. 3 Size and reproductive status. (i) The positive association between female height and reproductive status significantly declines with age. Plane is plotted from predictions generated from a simplified model of the interaction of height and age on reproduction. (ii) The association between female weight and reproductive status in females over 20. Box limits show upper and lower quartiles, line shows range, midline the median and diamond the mean.

throughout life, reflecting variation in resources (Mumby *et al.*, 2013, 2015). Consequently, there is potential for an overlap mostly between reproductive investment and weight gain, but also height gain in individuals with early reproductive onset. There is substantial individual variation in reproductive onset, ranging from 9 to 35 years in our subset, and with such variation, we found 52% of reproductive individuals in our subset had their first calf prior to the population peak of 19 years. There may be population-level differences too – average reproductive onset has been reported to be as early as 13 in wild Asian elephants, so there may be a larger potential for overlap in other, unmanaged populations of this species (De Silva *et al.*, 2013).

We next considered the association between age at first reproduction and later size, to assess whether starting to reproduce early might negatively impact your height or weight gain, following from previous findings that early reproductive investment reduces later survival in this population (Robinson *et al.*, 2012; Hayward *et al.*, 2014). We found that early reproducers were taller and lighter later in life, but these correlations were not significant. The lack of association between early reproduction and weight is perhaps most surprising due to the larger overlap between weight gain and reproduction. Weight is known to fluctuate throughout life as a reflection of body condition, and it also varies between seasons, being lowest during the hot, dry period of the year (Mumby *et al.*, 2013), so it could be that this sensitivity of weight masks long-term effects. It is also possible that “poorer quality” females, which would be more likely to experience negative impacts to body condition, are holding off on reproduction until later ages to save resources (Leimgruber *et al.*, 2008). Furthermore, past studies finding costs of early reproduction on growth focussed on species with seasonal breeding (Jorgenson *et al.*, 1993), for which the distinction between early and late breeders is large and defined. Asian elephants, with continuous breeding throughout the year (16-week ovulation cycle with no specific breeding season), and spanning decades, may not face the same restrictions on reproductive timing and subsequent costs of early reproduction on their later body size as seasonal breeders. However, our associative approach cannot provide direct causative evidence for lack of a trade-off (Van Noordwijk & De Jong, 1986). Future studies would gain from comparing longitudinal measures of growth within individuals specifically before and after reproduction. The long lifespan of Asian elephants and measurement bias to recent years limited our access to such data, although we had height measurements for two individuals taken in the year of first reproduction (at 19 and 20), followed by subsequent measures in later life. We found that these individuals continued to grow following reproduction, both gaining 5 cm in the 2 years following first reproduction. Although it is not possible to conclude general growth patterns from such a limited sample, this reinforces our finding that early reproduction does not fully limit skeletal growth.

We next tested whether a female’s height or weight constrained their reproductive output as has been shown in a number of other mammal species such as Soay sheep (*Ovis aries*), bison (*B. bison*) and moose (*Alces alces*) (Green & Rothstein, 1991; Clutton-brock *et al.*, 1996; Sand, 1996). We found no evidence that female size in terms of their height or their weight was associated with lifetime number of calves produced. The slow life history of the Asian elephant means they have prolonged care for their young, not weaning calves sometimes for 4–5 years (De Silva *et al.*, 2013). Further analysis therefore took into account whether offspring survived to the age of 5, but again there was no significant effect of female size

Table 2 *Glmer* output of the effect of height and weight on female reproductive status (reproducers/nonreproducers). Estimates are expressed on the logit scale, and continuous variables were scaled to have a mean of 0 and a standard deviation of 1 so effect sizes are comparable. Colon (:) represents an interaction.

	Height		Weight	
Fixed effects	Estimate ± SE	*z*-value	Estimate ± SE	*z*-value
Intercept	−15.43 ± 5.14	−3.00	−20.98 ± 6.69	−3.14
Height/Weight	1.67 ± 1.78	0.94	0.48 ± 1.25	0.38
Age	29.30 ± 5.97	4.91	39.00 ± 8.69	4.49
Birth Origin	1.76 ± 3.16	0.56	5.63 ± 4.15	1.36
Height: Age	−6.50 ± 2.45	−2.66	–	–

Random effects	Variance ± SD	Corr	Variance ± SD	Corr
ID (Intercept)	2197.54 ± 46.88	–	3163.31 ± 56.24	–
Age	6284.78 ± 79.28	−1.00	16 753.33 ± 129.44	−1.00
Camp	49.37 ± 7.03	–	79.31 ± 8.91	–
Birth Cohort	0.00 ± 0.00	–	0.00 ± 0.00	–

on her total number of surviving offspring. It is possible that once a female produces a calf, the sociality of the species and their tendency for cooperative breeding mask post-partum size effects due to 'social facilitation' by helpers and allomothers (Lee, 1987; Rapaport & Haight, 1987; Schulte, 2000; Lahdenperä *et al.*, 2016). It must also be noted that our limited sample size of body height and weight measures that date back sufficiently long in time to cover full reproductive histories of females may have restricted our current ability to detect an association between size and lifetime reproductive output.

Although female size was unrelated to variation in the total number of calves produced to date, many females within our population forego reproduction altogether – only 42% of reproductive-aged females in our sample with measures of size available to them had reproduced – so we next studied whether female size dictates their likelihood to reproduce at all. We found a positive association between height and the chance of having reproduced by a given age, which significantly declined with age (Fig. 3(i)). Consequently, taller females were more likely to be reproductive than shorter ones, but the effect of size declined with age, suggesting that size is more important for reproduction in younger ages, which could be an important limitation considering peak reproduction is at only 19 years in this population. A similar effect has been found in bison; reproduction is positively correlated with size (weight in this case) in young females, but this effect declines with age (Green & Rothstein, 1991). This size constraint to reproduction lessening in older ages could reflect lack of competition with growth at later ages, or selective disappearance of smaller females at older ages.

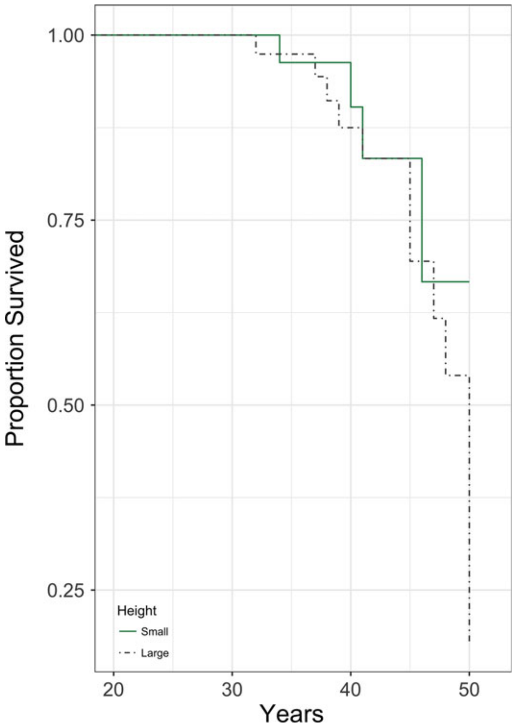

Fig. 4 Survival of female elephants by height. The survival of adult female elephants depending on their height, split into binary quantiles for visual representation (Small (< 218 cm), shown in green: *n* = 52; Large (≥ 218 cm), shown in black: *n* = 52).

We therefore subsequently explored the link between height and survival for females in their reproductive prime (20–50), to examine whether this lessening size effect with age could be due to selective disappearance of smaller females – or biased survival of large "high-quality" females. We found no effect however of height on survival, suggesting that selective disappearance is unlikely to drive the lessening effect of size on reproduction when females grow older. This result should be interpreted with caution however as it was conducted on a limited sample due to the long lifespan of our study species, and therefore cannot provide conclusive evidence for a lack of size-biased survival.

Our study provides novel insight into age-dependent effects of female height on reproduction in the Asian elephant, a species with a very slow life history and high costs associated with both reproduction and growth. This informs evolutionary theory around how reproduction and size relate to each other – we provide evidence that the significance of female size for reproduction is context dependent, along with the findings of other studies (Albon *et al.*, 1983; Jorgenson *et al.*, 1993; Clutton-brock *et al.*, 1996). These findings could also have interesting implications in terms of elephant management, as they could help to explain variation in reproductive output in this species; indicating the importance of food availability for young elephants. This can be applied both in this and other species of endangered animals, or other large-bodied mammals that are similarly characterized by low fertility.

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Conflict of interest

The authors declare there are no conflict of interests in the creation of this work.

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Supporting information

Additional Supporting Information may be found online in the supporting information tab for this article:

Table S1.1 *Glmer* output comparing the reproductive output of females over 30 of varying sizes, measured as the number of offspring produced at time of measurement

Table S1.2 *Glmer* output comparing the reproductive output of females over 30 of varying sizes, measured as the number of offspring survived to the age of 5 at time of measurement

Table S2 Coxme proportional hazards model output showing survival of female adult elephants (20–50), depending on height as a continuous variable

Figure S1 Constraints of size on reproduction

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