

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

2

3 **Short running title: Size and reproduction in Asian elephants**

4

5 Jennie A. H. Crawley¹, Hannah S. Mumby^{*2}, Simon N. Chapman¹, Mirkka Lahdenperä¹, Khyne U.
6 Mar³, Win Htut⁴, Aung Thura Soe⁴, Htoo Htoo Aung⁴, Virpi Lummaa¹

7

8 ¹Department of Biology, University of Turku, Turku, Finland.

9 ²Department of Zoology, University of Cambridge, Downing Street, Cambridge, U.K.

10 ³Department of Animal and Plant Sciences, Alfred Denny Building, University of Sheffield, Western
11 Bank, Sheffield, U.K.

12 ⁴Myanma Timber Enterprise, Ministry of Environmental Conservation and Forestry, Gyogone Forest
13 Compound, Bayint Naung Road, Insein Township, Yangon, Myanmar.

14

15 ***Correspondence:** Hannah S. Mumby, Department of Zoology, University of Cambridge, Downing
16 Street, Cambridge, CB2 3EJ U. K. Tel: +44 (0)1223 331698, E-mail: hsm29@cam.ac.uk

17

18 **Acknowledgements**

19 We thank the Branco Weiss- Society in Science fellowship administered by the ETH, Pembroke
20 College Cambridge, the Leverhulme Trust, the Kone foundation and the European Research Council
21 for funding. We thank Myanma Timber Enterprise for giving us access to the elephants and their
22 records and we particularly thank the staff that assisted in data collection. We thank R. Goodsell, J.
23 Jackson, and V. Berger for statistical guidance and the anonymous reviewers for their helpful advice.

24

25 **Abstract**

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

43

44 *Keywords: Life History; Growth; Trade-offs; Long-lived; Working elephants; Elephas maximus*

45

46

47

48

49

50 **Introduction**

51 Organisms distribute their finite supply of resources between growth, reproduction and survival,
52 predicted to lead to trade-offs between these processes (Kirkwood & Rose, 1991). High investment in
53 growth can reduce a female's fecundity (Lee *et al.*, 2012), and early reproduction and high reproductive
54 investment have been found to suppress growth in some organisms, such as cod (*Gadus morhua*)
55 (Folkvord *et al.*, 2014) and barn swallows (*Hirundo rustica*) (Saino *et al.*, 2014). Conversely, there is
56 evidence from a number of seasonally breeding large mammals that fecundity positively correlates with
57 size, with large individuals reaching reproductive onset first (Clutton-Brock *et al.*, 1988; Green &
58 Rothstein, 1991; Jorgenson *et al.*, 1993). These findings lead to the contrasting hypotheses that size
59 may either positively or negatively correlate with reproduction depending on the importance of size-
60 related fitness, the care-dependency of offspring, and costs involved in reproduction (Jorgenson *et al.*,
61 1993). Further exploration of this relationship in natural systems is necessary to determine how body
62 size and measures of reproductive success are associated in species that do not share the same life-
63 history strategies as those previously studied.

64 In animals that reach a determinate size, such as birds and mammals, young individuals must
65 invest more resources in somatic growth and maintenance than those that have ceased growing, and
66 there may thus be a trade-off between growth and reproduction in younger individuals (Hamel & Côté,
67 2009). High early investment in reproduction has been found to reduce later-life fecundity and survival
68 in many mammals (Nussey *et al.*, 2006; Hayward *et al.*, 2014) and birds (Reid *et al.*, 2003), though
69 impacts on future growth are not widely studied, and often focus on experimental manipulation. For
70 example, suppressed reproduction via experimental contraception improved later growth and body
71 condition in the kangaroo (*Macropus giganteus*) (Gélin *et al.*, 2016). Some observational studies have
72 also found that high early female fecundity is associated with stunted growth in humans (Rah *et al.*,

73 2008) and wild bison (*Bison bison*) (Green & Rothstein, 1991), and early reproduction also reduces
74 later mass gain in bighorn ewes (*Ovis canadensis*), though this relationship may only prevail under
75 high densities, and therefore strong selection pressure (Festa-Bianchet *et al.*, 1995; Bérubé *et al.*, 1999).

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

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

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

110

111 **Materials and methods**

112 ***Study Population***

113 Population estimates of wild Asian elephants in Myanmar range from 2000-5000, although the current
114 number likely lies at the bottom end of this range (Sukumar, 2006; Leimgruber *et al.*, 2008, 2011).

115 Around 5500 Myanma elephants are semi-captive, and over half of these semi-captive individuals
116 (around 2,700 individuals) work in the timber industry, owned by the state-run Myanma Timber
117 Enterprise (MTE). The workload of these state-owned elephants adheres to MTE regulations, with set
118 hours per week, days per year and tonnage per individual (Mumby *et al.*, 2013). The MTE elephants
119 are not provisioned for, but instead are allowed to forage freely in the forest (Gale, 1974). Similarly,

120 breeding is not managed by humans, and most reproduction occurs in unsupervised hours during
121 release into the forest at night either with other semi-captive individuals or with wild elephants. MTE
122 ensures that detailed logbooks are kept for each individual elephant, which has led to the formation of
123 the world's largest multigenerational life history dataset on semi-captive Asian elephants (Mar *et al.*,
124 2012; Mumby *et al.*, 2013). The logbooks contain detailed information including individual ID number,
125 date of birth and death, sex, birth origin (captive born/wild caught) and work camp as well as offspring
126 birth dates and survival, allowing us to investigate reproductive investment across a lifetime in
127 individuals of known ages. The assignment of ages to wild caught individuals is done by experienced
128 vets using body size, temporal/ buccal depression, ear folds, pigmentation and tusk size (Arivazhagan
129 & Sukumar, 2008); subadults can be aged very accurately. Elephants are weaned and begin training at
130 5 years old, whereupon they carry out light work tasks until they enter the workforce at 17, with
131 retirement at 55 (Begley, 2006).

132 *Data selection*

133 This study uses a range of demographic datasets maintained by MTE over decades on individual
134 working elephants, combined with information recorded on variation in individual size. For our body
135 size measurements, we measured height from ground to shoulder to the closest centimetre or inch
136 depending on region (inches were converted to centimetres for the purpose of analyses, thus
137 measurements were accurate to within 2.54cm), and weight to the nearest kg using Eziweigh 3000
138 scales. The measurements were taken in years spanning 1985-2017 for height and 2011-2017 for
139 weight. Measurements were taken across different climatic seasons of the year (monsoon, cool and hot)
140 and we account for such differences in measurement season where appropriate in weight models
141 (height does not vary by season). Reproductive analyses focus on females with recorded size
142 measurements, known reproductive history (date of birth and survival of any offspring born) and
143 known birth origin (wild caught or captive born), and we only include wild caught individuals captured

144 under the age of 15 (capture age ranges: 0-5 years=19, 6-10=31, 11-15=5) to ensure accurate age
145 estimation and to reduce potential unknown reproductive events prior to capture (consistent with
146 Leimgruber *et al.*, 2008). Specific details of data selection and sample breakdown are given in
147 subsequent sections. The majority of the females included in the reproductive analyses are still alive,
148 with only 3 known deaths, 2 of which were in the last 3 years. The elephants from this subset span five
149 work regions in northern Myanmar, four in the Sagaing region, and one in the Mandalay region.

150 *Statistical Analyses*

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

154 (i) *Population-level timing of growth and reproduction*

155 First, we investigated the relationship between reproduction and growth in females by quantifying the
156 overlap between the population-level increase in reproduction with age and the levelling off of the
157 growth curve with age. We determined age-specific fertility of all reproductive females between the
158 ages of 5-60 years in a sample of 1040 females. Age-specific fertility was calculated as the total
159 number of offspring born each year divided by the total number of reproductive females alive at the
160 end of each year for each age (see Lahdenperä *et al.*, 2014). We then compared this to height and
161 weight gain over a lifetime for all females we had size data available for, adapted from Mumby *et al.*
162 (2015), (average measurement and age over a 4 year measurement period: 1690 height measures from
163 240 females and 1474 weight measures from 243 females aged 0-72yrs). Growth curves were produced
164 from non-linear least squares models using the *nls* function in R, with a response variable of either
165 height or weight. A self-starting von Bertalanffy growth function was used, with age in years as an
166 input parameter - the von Bertalanffy curve was deemed a better fit than other commonly used growth
167 curves (Gompertz and 3-parameter logistic) on the basis of their coefficients of determination (see

168 Mumby *et al.* 2015). Both wild- and captive-born females were included in these models, as previous
169 studies found little difference in the growth curves of wild and captive-born individuals (Mumby *et al.*
170 2015).

171 (ii) *Age at first reproduction and size*

172 We then assessed the impact of age at first reproduction on subsequent age-specific height and weight
173 by constructing linear mixed models using the *lme4* package version 1.1.12 (Bates *et al.*, 2015).
174 Specifically, we aimed to contrast the subsequent size of females that reproduced for the first time
175 before vs after the population average peak age in reproduction – for this population, this is 19 years
176 (age at first reproduction in our subset ranged between 9 and 35 years, with a mean of 18.5) (Hayward
177 *et al.*, 2014). In this model we included only reproductive females over the age of 20 (range 20-62), and
178 used only size measurements taken from their first reproduction onwards, (over 74% of ever-
179 reproduced females had reproduced for the first time by 20). These models compared the continuous
180 height and weight of 62 (n=498 height measurements) and 61 (n=438 weight measurements)
181 reproductive females that started reproduction either before or after the population peak of 19 years
182 (binary variable for before: height n=32; weight n=30, and after or equal to 19: height n=30; weight
183 n=31). In these models we fitted birth origin as a fixed effect (integer term: 1 for wild caught
184 individuals, height n=33 & weight n=34; 0 for captive borns, height n=29 & weight n=27), to account
185 for potential differences between wild and captive born females. We included an additional interactive
186 term between this birth origin term and capture age (continuous variable, range 0-15), to account for
187 the entry of wild-caught elephants into our study at variable estimated ages. We also included a
188 continuous fixed term of age at measurement (range= 20-62) in all models and a fixed categorical term
189 of measurement season in weight models (3 level factor: cool; dry; wet) to account for seasonally
190 variable conditions (Mumby *et al.*, 2013). A quadratic age term was included in weight models, as
191 weight gain neither ceases with age nor linearly increases (Mumby *et al.*, 2015). However, the

192 measurement season term and quadratic terms did not improve model fit and were subsequently
193 removed from the final model. Random terms accounted for work camp (5 level factor), and birth
194 cohort, using a term for five-year interval of birth (9 level factor from 1950-95). We also included a
195 random term for individual ID, as the effects were tested using multiple measurements of the same
196 individual at different ages over the total measurement period (maximum 32 years of measurements,
197 mean 3.8 for height and a maximum of 4 years of weight measurements, mean 1.2). All models
198 included an additional random slope of age at measurement by ID to allow the slope of any age effects
199 to differ between individuals. Comparisons between models were based on the lowest akaike
200 information criteria (AIC) values comparing models with and without the term in question (following a
201 selection procedure similar to Hamel & Côté, 2009). We appreciate that mixed model comparisons are
202 complex, and we carried out thorough model selection before proceeding to AIC comparisons and
203 terms were dropped in the case of model convergence issues to reduce model complexity, though
204 biologically significant terms were retained (Bolker *et al.*, 2008). These model terms and comparison
205 methods were replicated for each of the subsequent analyses unless stated otherwise.

206 (iii) *Size and lifetime reproductive output*

207 We next investigated whether a female's reproductive success is constrained by her height or weight,
208 first measured by the number of offspring produced, followed by the number raised to weaning age.
209 Measurements were taken from 102 females (n=687 height and n=541 weight measurements). Only
210 females aged 30 and older (range 30-62) were included to allow females the opportunity to produce
211 multiple offspring. We fitted generalised linear mixed models, again from the *lme4* package in R, with
212 a Poisson distribution to account for the zero inflated skew caused by including non-reproductive
213 females in the model. We first used a continuous term of number of calves birthed by the age of
214 measurement (range 0-9) as a measure of reproductive output. The other terms controlled for in the
215 models were identical to those in the models above, although in all subsequent models we did not

216 include the measurement season term in weight models as it is not relevant to reproduction as the
217 dependent variable, and the capture age term was dropped as it did not improve model fit. We also
218 tested for an interactive effect of height/weight and age at measurement on reproductive output as size
219 effects may vary depending on the age of a females. We then repeated these models on the same subset
220 of females using number of calves raised to age 5 (range 0-5) as the measure of reproductive output.
221 This was to account for maternal investment differences in lactation and maternal care- mothers may
222 require more resources to ensure survival of offspring. We split the calf variable into categories for
223 visual representation in figures (0=none; 1-3=low; 3-5=medium; 5+=high), and findings from analyses
224 run with these categorical variables were consistent with the continuous term reported.

225 (iv) *Size and reproductive status*

226 Because a large proportion of females in our study population fail to reproduce at all in their lifetime,
227 to further explore the general relationship between size and reproduction across different ages, we
228 fitted binomial generalised linear mixed models (*lme4* package) to assess whether a female's
229 reproductive status (1/0) at the time of measurement, depended on her height or weight. Comparisons
230 were made between 147 and 145 females measured over the age of 20 for (i) height and (ii) weight
231 respectively, totalling (i) 498 (ii) 438 observations of reproductive and (i) 406 (ii) 418 observations of
232 non-reproductive females. Reproductive status was coded as the status at the age of measurement (had
233 vs had not produced any calves by this age), so some females would be coded as 0 at younger ages and
234 1 later- we account for this difference between individuals with the random slope for age at
235 measurement by individual. The models controlled for the same terms as above analyses, with an
236 interaction similar to that in (iii), between age and height or weight, to investigate whether the effect of
237 size on reproduction depended on age (i.e. whether size limited reproduction more at certain ages).

238 (v) *Survival and size*

239 To assess whether a female's survival during reproductive years depends on her height, we fitted a Cox
240 proportional hazards mixed effects model using the *coxme* package in R (Therneau, 2015). The model
241 included 104 females (18 dead and 86 censored), measured between ages 20-50 of prime reproduction
242 (mean 35 years). We focused only on height for this analysis, as weight measurements only started in
243 2011, and there are insufficient numbers of measurements of individuals that have subsequently died.
244 We used a continuous measure of height for this analysis, but split the height variable into binary
245 quantiles for easier visual representation in figures (split into even quantiles, above and below 218cm,
246 n=50, n=51 respectively). We included fixed terms of reproductive status (binary: reproduced; did not
247 reproduce aged 20-50), age at measurement (continuous variable) and birth origin (wild caught vs
248 captive born). Decade of birth was included as a random term (4 level factor: 60s; 70s; 80s; 90s) to
249 control for any differences in birth conditions.

250

251 **Results**

252 (i) *Population-level timing of growth and reproduction*

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

262 (ii) *Age at first reproduction and size*

263 Of our 147 females over 20, 55% of measurements were taken from reproductive females, and their age
264 at first reproduction ranged between 9 and 35 years, with a mean and median of 18.5 years. We
265 investigated how their age at the onset of reproduction (before vs. after the population peak age of
266 reproduction of 19) was associated with subsequent size. Although females starting to reproduce earlier
267 than the peak tended to be taller and lighter, these trends were not significant (height: $\chi^2=0.313_1$,
268 $p=0.576$ $n=62$; weight: $\chi^2=2.657_1$, $p=0.103$, $n=61$; see Figure 2 and Table 1).

269 (iii) *Size and lifetime reproductive output*

270 We then investigated whether an individual's size affected her reproductive success, measured first as
271 the total number of offspring produced, and then as the total number raised to the weaning age of 5. We
272 found no significant relationship between a female's height and the total number of offspring produced
273 ($\chi^2=0.01_1$, $p=0.90$, $n=102$) or raised to 5 ($\chi^2=0.088_1$, $p=0.77$, $n=102$), see Figure S1; Tables S1.1 &
274 S1.2. Similarly, the number of offspring born was not significantly associated with body weight
275 ($\chi^2=0.001_1$, $p=0.98$, $n=102$), or number of calves raised to 5 ($\chi^2=0.018_1$, $p=0.894$, $n=102$). There was a
276 significant quadratic relationship between age and number of calves surviving to 5 ($\chi^2=0.3.94_1$, $p<0.05$,
277 $n=102$) but not for number of calves born. There was no interaction between age at measurement and
278 height on number of offspring born ($\chi^2=0.330_1$, $p=0.55$, $n=102$), or raised to 5 ($\chi^2=0.277_1$, $p=0.599$,
279 $n=102$), nor was there an interactive effect of age and weight on either the number of calves born
280 ($\chi^2=0.022_1$, $p=0.882$, $n=102$) or raised to 5 ($\chi^2=0.024_1$, $p=0.877$, $n=102$).

281 (iv) *Size and reproductive status*

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

286 have reproduced, but such effects of height on the probability to reproduce diminished with age
287 ($\chi^2=9.702_1$, $p<0.01$, $n=147$; Figure 3; Table 2). Weight was unrelated to reproductive status at all ages,
288 as indicated by a non-significant interaction between weight and age ($\chi^2=0.00_1$, $p=1.00$, $n=145$).

289 *(v) Survival and size*

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

295

296 **Discussion**

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

308 Our first question, assessing the extent of overlap between reproduction and growth, was to
309 determine whether there was potential investment competition between the two. Our results (see Figure
310 1), show that whilst the majority of growth, as indicated by height gain (almost 97%), is complete by
311 19 years- the age of peak fecundity- only 81% of weight is gained by this age. Weight gain continues to
312 increase and fluctuate throughout life, reflecting variation in resources (Mumby *et al.*, 2013, 2015).
313 Consequently, there is potential for an overlap mostly between reproductive investment and weight
314 gain, but also height gain in individuals with early reproductive onset. There is substantial individual
315 variation in reproductive onset, ranging from 9 to 35 years in our subset, and with such variation, we
316 found 52% of reproductive individuals in our subset had their first calf prior to the population peak of
317 19 years. There may be population level differences too -average reproductive onset has been reported
318 to be as early as 13 in wild Asian elephants, so there may be a larger potential for overlap in other,
319 unmanaged populations of this species (De Silva *et al.*, 2013).

320 We next considered the association between age at first reproduction and later size, to assess
321 whether starting to reproduce early might negatively impact your height or weight gain, following from
322 previous findings that early reproductive investment reduces later survival in this population (Robinson
323 *et al.*, 2012; Hayward *et al.*, 2014). We found that early reproducers were taller and lighter later in life,
324 but these correlations were not significant. The lack of association between early reproduction and
325 weight is perhaps most surprising due to the larger overlap between weight gain and reproduction.
326 Weight is known to fluctuate throughout life as a reflection of body condition, and it also varies
327 between seasons being lowest during the hot, dry period of the year (Mumby *et al.*, 2013), so it could
328 be that this sensitivity of weight masks long term effects. It is also possible that “poorer quality”
329 females, which would be more likely to experience negative impacts to body condition are holding off
330 on reproduction until later ages to save resources (Leimgruber *et al.*, 2008). Furthermore, past studies
331 finding costs of early reproduction on growth focussed on species with seasonal breeding (Jorgenson *et*

332 *al.*, 1993), for which the distinction between early and late breeders is large and defined. Asian
333 elephants, with continuous breeding throughout the year (16-week ovulation cycle with no specific
334 breeding season), and spanning decades, may not face the same restrictions on reproductive timing and
335 subsequent costs of early reproduction on their later body size as seasonal breeders. However, our
336 associative approach cannot provide direct causative evidence for lack of a trade-off (Van Noordwijk &
337 De Jong, 1986). Future studies would gain from comparing longitudinal measures of growth within
338 individuals specifically before and after reproduction. The long lifespan of Asian elephants and
339 measurement bias to recent years limited our access to such data, although we had height
340 measurements for two individuals taken in the year of first reproduction (at 19, and 20), followed by
341 subsequent measures in later life. We found that these individuals continued to grow following
342 reproduction, both gaining 5cm in the 2 years following first reproduction. Although it is not possible
343 to conclude general growth patterns from such a limited sample, this reinforces our finding that early
344 reproduction does not fully limit skeletal growth.

345 We next tested whether a female's height or weight constrained their reproductive output as has
346 been shown in a number of other mammal species such as soay sheep (*Ovis aries*), bison (*Bison bison*)
347 and moose (*Alces alces*) (Green & Rothstein, 1991; Clutton-brock *et al.*, 1996; Sand, 1996). We found
348 no evidence that female size in terms of their height or their weight was associated with lifetime
349 number of calves produced. The slow life-history of the Asian elephant means they have prolonged
350 care for their young, not weaning calves sometimes for 4-5 years (De Silva *et al.*, 2013). Further
351 analysis therefore took into account whether offspring survived to the age of 5, but again there was no
352 significant effect of female size on her total number of surviving offspring. It is possible that once a
353 female produces a calf, the sociality of the species and their tendency for cooperative breeding masks
354 post-partum size effects due to 'social facilitation' by helpers and allomothers (Lee, 1987; Rapaport &
355 Haight, 1987; Schulte, 2000; Lahdenperä *et al.*, 2016). It must also be noted that our limited sample

356 size of body height and weight measures that date back sufficiently long in time to cover full
357 reproductive histories of females may have restricted our current ability to detect an association
358 between size and lifetime reproductive output.

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

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

378 Our study provides novel insight into age dependent effects of female height on reproduction in
379 the Asian elephant, a species with a very slow life history and high costs associated with both

380 reproduction and growth. This informs evolutionary theory around how reproduction and size relate to
381 each other- we provide evidence that the significance of female size for reproduction is context
382 dependent, along with the findings of some other studies (Albon *et al.*, 1983; Jorgenson *et al.*, 1993;
383 Clutton-brock *et al.*, 1996). These findings also inform management decisions in terms of the costs
384 associated with reproductive investment at younger ages in this species, which has been shown to reach
385 their reproductive peak in early years. This can be applied both in this and other species of endangered
386 animals, or other large-bodied mammals that are similarly characterised by low fertility, such as in zoo
387 settings, in which many species experience both rapid growth and early reproduction.

388

389 **Conflict of interest**

390 The authors declare there are no conflicts of interest in the creation of this work.

391

392 **References**

- 393 Albon, S.D., Mitchell, B. & Staines, B.W. 1983. Fertility and body weight in female red deer: a
394 density-dependent relationship. *J. Anim. Ecol.* **52**: 969–980.
- 395 Arivazhagan, C. & Sukumar, R. 2008. Constructing Age Structures of Asian Elephant Populations : A
396 Comparison of Two Field Methods of Age Estimation. **29**: 11–16.
- 397 Bates, D., Maechler, M., Bolker, B. & Walker, S. 2015. Fitting Linear Mixed-Effects Models Using
398 Lme4. *J. Stat. Softw.* **67**: 1–48.
- 399 Begley, C. 2006. A Report on the Elephant Situation in Burma. *Eleaid*.
- 400 Bérubé, C.H., Festa-Bianchet, M. & Jorgenson, J.T. 1999. Individual differences, longevity, and
401 reproductive senescence in bighorn ewes. *Ecology* **80**: 2555–2565.
- 402 Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., *et al.* 2008.
403 Generalized linear mixed models : a practical guide for ecology and evolution. *Trends Ecol. Evol.*

404 **24**: 127–135.

405 Clubb, R., Rowcliffe, M., Lee, P., Mar, K.U., Moss, C. & Mason, G.J. 2009. Fecundity and population
406 viability in female zoo elephants: Problems and possible solutions. *Anim. Welf.* **18**: 237–247.

407 Clutton-brock, A.T.H., Stevenson, I.R., Marrow, P., Maccoll, A.D., Houston, A.I. & Mcnamara, J.M.
408 1996. Population Fluctuations , Reproductive Costs and Life-History Tactics in Female Soay
409 Sheep. **65**: 675–689.

410 Clutton-Brock, T.H., Albon, S.D. & Guinness, F.E. 1988. Reproductive success in male and female red
411 deer. In: *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems*,
412 pp. 325–343.

413 De Silva, S., Elizabeth Webber, C., Weerathunga, U.S., Pushpakumara, T. V., Weerakoon, D.K. &
414 Wittemyer, G. 2013. Demographic variables for wild Asian elephants using longitudinal
415 observations. *PLoS One* **8**.

416 Festa-Bianchet, M., Jorgenson, J., Lucherini, M. & Wishart, W.D. 1995. Life history consequences of
417 variation in age of primipary in bighorn ewes. *Ecology* **76**: 871–881.

418 Folkvord, A., Jørgensen, C., Korsbrekke, K., Nash, R.D.M., Nilsen, T. & Skjæraasen, J.E. 2014. Trade-
419 offs between growth and reproduction in wild Atlantic cod. *Can. J. Fish. Aquat. Sci.* **71**: 1106–
420 1112.

421 Gale, U.T. 1974. *Burmese Timber Elephant*. Trade Corporation, Yangon, Burma.

422 Gélin, U., Wilson, M.E., Cripps, J., Coulson, G. & Festa-Bianchet, M. 2016. Individual heterogeneity
423 and offspring sex affect the growth-reproduction trade-off in a mammal with indeterminate
424 growth. *Behav. Ecol.* **180**: 1127–1135. Springer Berlin Heidelberg.

425 Gjerde, B. 1986. Growth and reproduction in fish and shellfish. *Aquaculture* **57**: 37–55.

426 Green, W.C.H. & Rothstein, A. 1991. Trade-offs between growth and reproduction in female bison.
427 *Oecologia* 521–527.

- 428 Hamel, S. & Côté, S.D. 2009. Foraging decisions in a capital breeder: Trade-offs between mass gain
429 and lactation. *Oecologia* **161**: 421–432.
- 430 Hamel, S., Gaillard, J.M., Festa-Bianchet, M. & Côté, S.D. 2009. Individual quality, early-life
431 conditions, and reproductive success in contrasted populations of large herbivores. *Ecology* **90**:
432 1981–1995.
- 433 Hayward, A.D., Mar, K.U., Lahdenperä, M. & Lummaa, V. 2014. Early reproductive investment,
434 senescence and lifetime reproductive success in female Asian elephants. *J. Evol. Biol.* **27**: 772–
435 783.
- 436 Hildebrandt, T.B., Göritz, F., Hermes, R., Reid, C., Dehnhard, M. & Brown, J.L. 2006. Aspects of the
437 reproductive biology and breeding management of Asian and African elephants. *Int. Zoo Yearb.*
438 **40**: 20–40.
- 439 Jorgenson, J.T., Festa-Bianchet, M., Lucherini, M. & Wishart, W.D. 1993. Effects of body size,
440 population density, and maternal characteristics on age at first reproduction in bighorn ewes. *Can.*
441 *J. Zool.* **71**: 2509–2517.
- 442 Kirkwood, T.B. & Rose, M.R. 1991. Evolution of senescence: late survival sacrificed for reproduction.
443 *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **332**: 15–24.
- 444 Lahdenperä, M., Mar, K.U. & Lummaa, V. 2016. Nearby grandmother enhances calf survival and
445 reproduction in Asian elephants. *Sci. Rep.* 1–10. Nature Publishing Group.
- 446 Lahdenperä, M., Mar, K.U. & Lummaa, V. 2014. Reproductive cessation and post-reproductive
447 lifespan in Asian elephants and pre-industrial humans. *Front. Zool.* **11**: 1–15.
- 448 Lee, P.C. 1987. Allomothering among African elephants. *Anim. Behav.* **35**: 278–291.
- 449 Lee, W.S., Monaghan, P. & Metcalfe, N.B. 2012. The pattern of early growth trajectories affects adult
450 breeding performance. *Ecology* **93**: 902–912.
- 451 Leimgruber, P., Oo, Z.M., Aung, M., Kelly, D.S., Wemmer, C. & Senior, B. 2011. Current Status of

452 Asian Elephants in Myanmar. **35**: 76–86.

453 Leimgruber, P., Senior, B., Uga, Aung, M., Songer, M. a., Mueller, T., *et al.* 2008. Modeling
454 population viability of captive elephants in Myanmar (Burma): Implications for wild populations.
455 *Anim. Conserv.* **11**: 198–205.

456 Mar, K.U., Lahdenperä, M. & Lummaa, V. 2012. Causes and correlates of calf mortality in captive
457 asian elephants (*elephas maximus*). *PLoS One* **7**: 1–9.

458 Mumby, H.S., Chapman, S.N., Crawley, J.A.H., Mar, K.U., Htut, W., Thura Soe, A., *et al.* 2015.
459 Distinguishing between determinate and indeterminate growth in a long-lived mammal. *BMC*
460 *Evol. Biol.* **15**: 214. BMC Evolutionary Biology.

461 Mumby, H.S., Courtiol, A.C., Mar, K.. U. & Lummaa, V. 2013. Climatic variation and age-specific
462 survival in Asian elephants from Myanmar. *Ecology* **94**: 1131–1141.

463 Nussey, D.H., Kruuk, L.E.B., Donald, A., Fowlie, M. & Clutton-Brock, T.H. 2006. The rate of
464 senescence in maternal performance increases with early-life fecundity in red deer. *Ecol. Lett.* **9**:
465 1342–1350.

466 R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for
467 Statistical Computing, Vienna, Austria.

468 Rah, A.B., Christian, J.H., Shamim, P., Arju, A.A. & Labrique, U.T. 2008. Pregnancy and lactation
469 hinder growth and nutritional status of adolescent girls in rural Bangladesh. *J. Nutr.* **138**:
470 1505–1511.

471 Rapaport, L. & Haight, J. 1987. Some Observations regarding Allomaternal Caretaking among Captive
472 Asian Elephants (*Elephas maximus*). *Am. Soc. Mammologists* **68**: 438–442.

473 Reid, J.M., Bignal, E.M., Bignal, S., McCracken, D.I. & Monaghan, P. 2003. Age-specific reproductive
474 performance in red-billed choughs *Pyrrhocorax pyrrhocorax*: Patterns and processes in a natural
475 population. *J. Anim. Ecol.* **72**: 765–776.

476 Robinson, M.R., Mar, K.U. & Lummaa, V. 2012. Senescence and age-specific trade-offs between
477 reproduction and survival in female Asian elephants. *Ecol. Lett.* **15**: 260–266.

478 Saino, N., Romano, M., Rubolini, D., Ambrosini, R., Romano, A., Caprioli, M., *et al.* 2014. A trade-off
479 between reproduction and feather growth in the barn swallow (*Hirundo rustica*). *PLoS One* **9**.

480 Sand, H. 1996. Life history patterns in female moose (*Alces alces*): the relationship between age ,
481 body size , fecundity and environmental conditions. *Oecologi* **106**: 212–220.

482 Schulte, B.A. 2000. Social structure and helping behaviour in captive elephants. *Zoo Biol.* **19**: 447–459.

483 Sukumar, R. 2006. A brief review of the status , distribution and biology of wild Asian elephants. 1–8.

484 Therneau, T.M. 2015. *coxme: Mixed Effects Cox Models*.

485 Van Noordwijk, A.J. & De Jong, G. 1986. Acquisition and Allocation of Resources : Their Influence
486 on Variation in Life History Tactics. *Am. Nat.* **128**: 137–142.

487

488

489

490

491

492

493

494

495

496

497

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

	Height		Weight	
Fixed effects				
	Estimate ± S.E	t-value	Estimate ± S.E	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 ± S.D	Corr	Variance ± S.D	Corr
ID (Intercept)	53.23 ± 7.30	-	570585.7 ± 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	-	33978.90 ± 184.33	-

501

502

503

504

505

506

507

508

509

510

511

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

	Height		Weight	
Fixed effects:				
	Estimate ± S.E	z-value	Estimate ± S.E	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 ± S.D	Corr	Variance ± S.D	Corr
ID (Intercept)	2197.54 ± 46.88	-	3163.31 ± 56.24	-
Age	6284.78 ± 79.28	-1.00	16753.33 ± 129.44	-1.00
Camp	49.37 ± 7.03	-	79.31 ± 8.91	-
Birth Cohort	0.00 ± 0.00	-	0.00 ± 0.00	-

516

517

518

519

520

521

522

523

524

525 **Figure Legends**

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

532

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

537

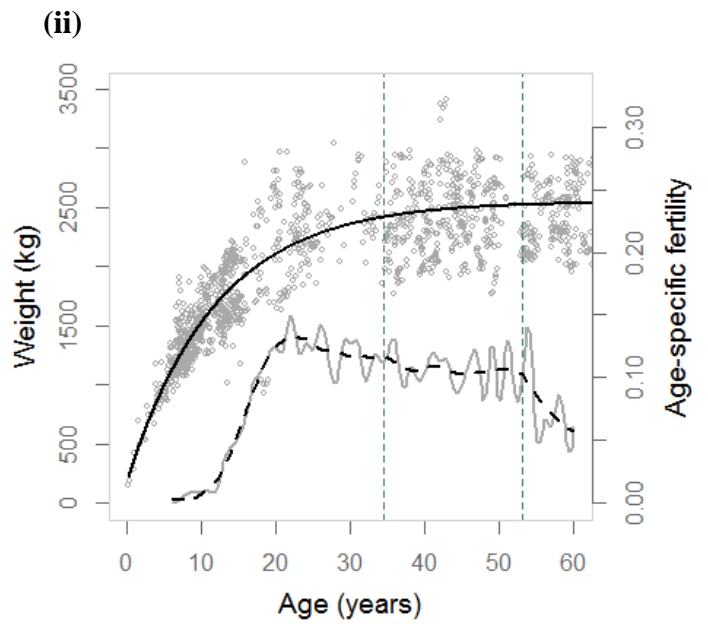
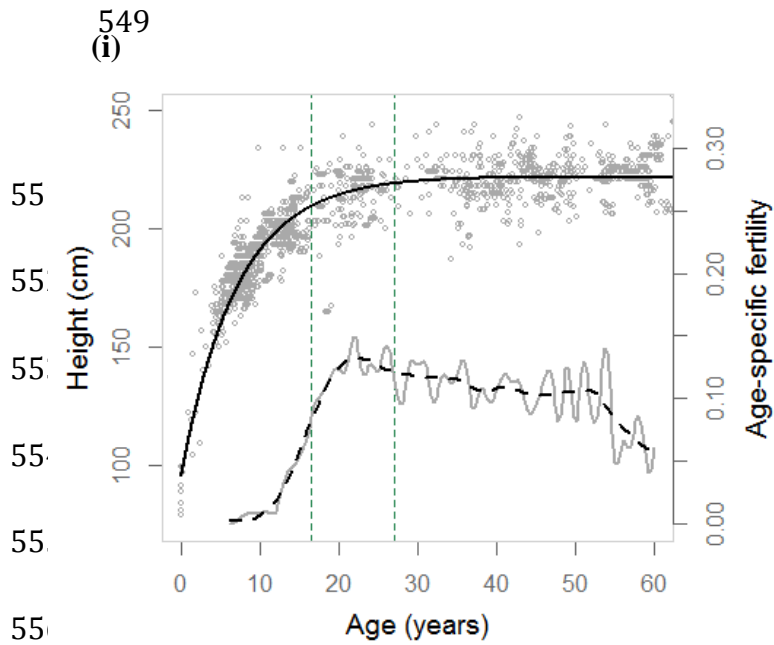
538 **Figure 3. Size and reproductive status.** (i) The positive association between female height and
539 reproductive status significantly declines with age. Plane is plotted from predictions generated from a
540 simplified model of the interaction of height and age on reproduction. (ii) The association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

543

544 **Figure 4. Survival of female elephants by height.** The survival of adult female elephants depending
545 on their height, split into binary quantiles for visual representation (1= small (<218cm), shown in
546 green: n=52; 2=large (\geq 218cm), shown in black: n=52).

547

548 **Figure 1**



557

558

559

560

561

562

563

564

565

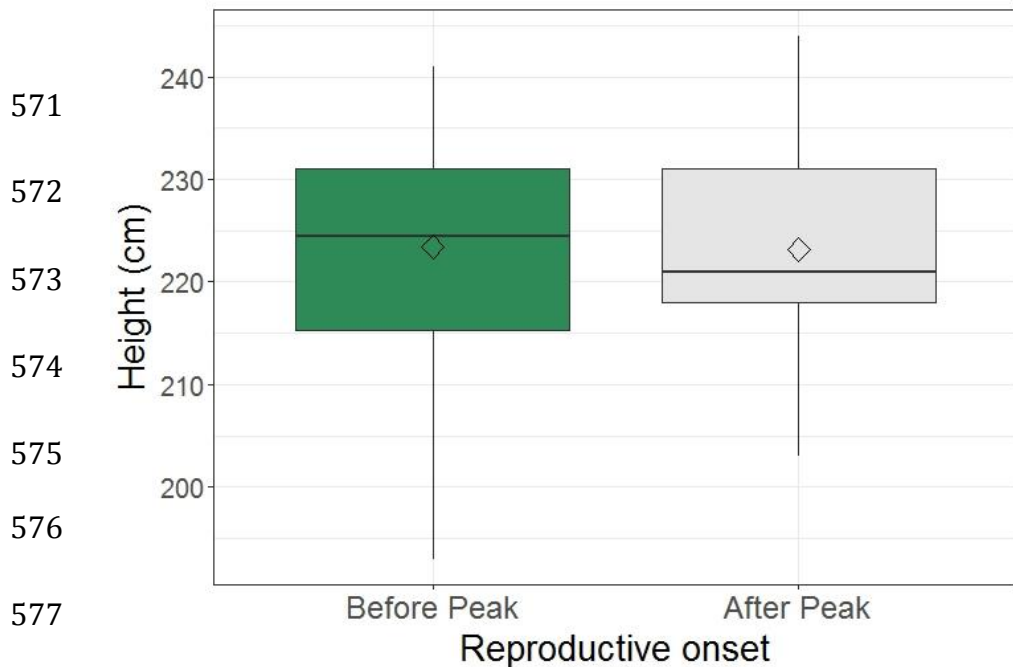
566

567

568 **Figure 2**

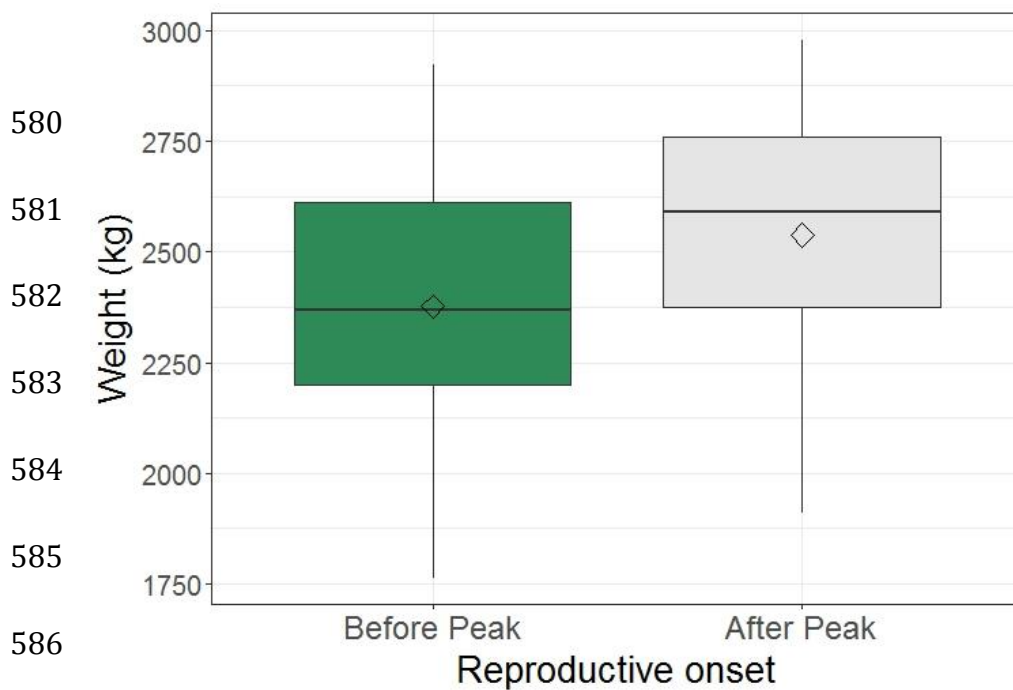
569

(i)



578

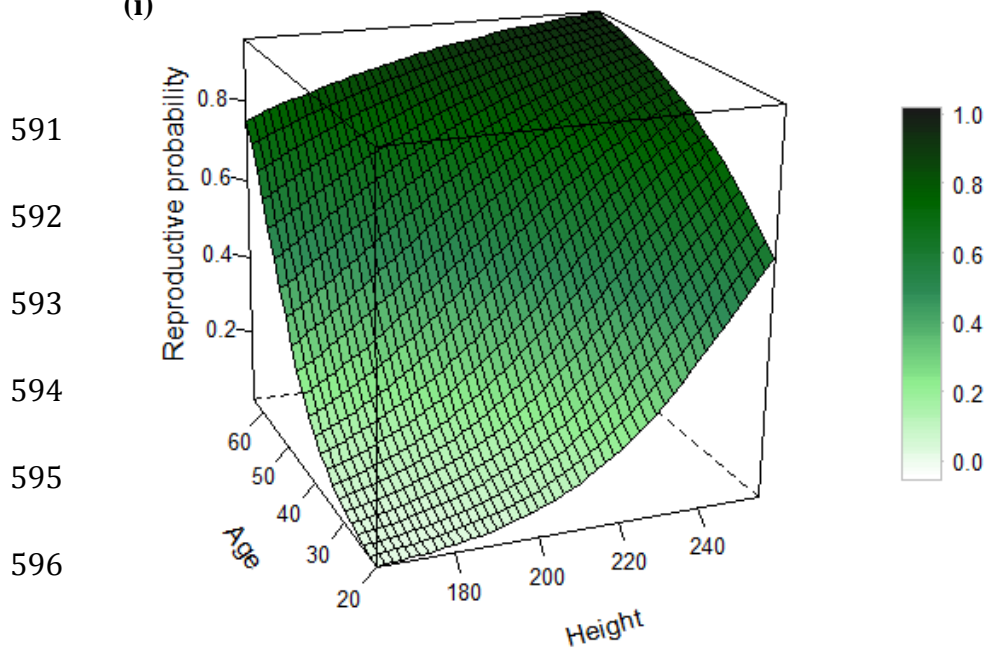
(ii)



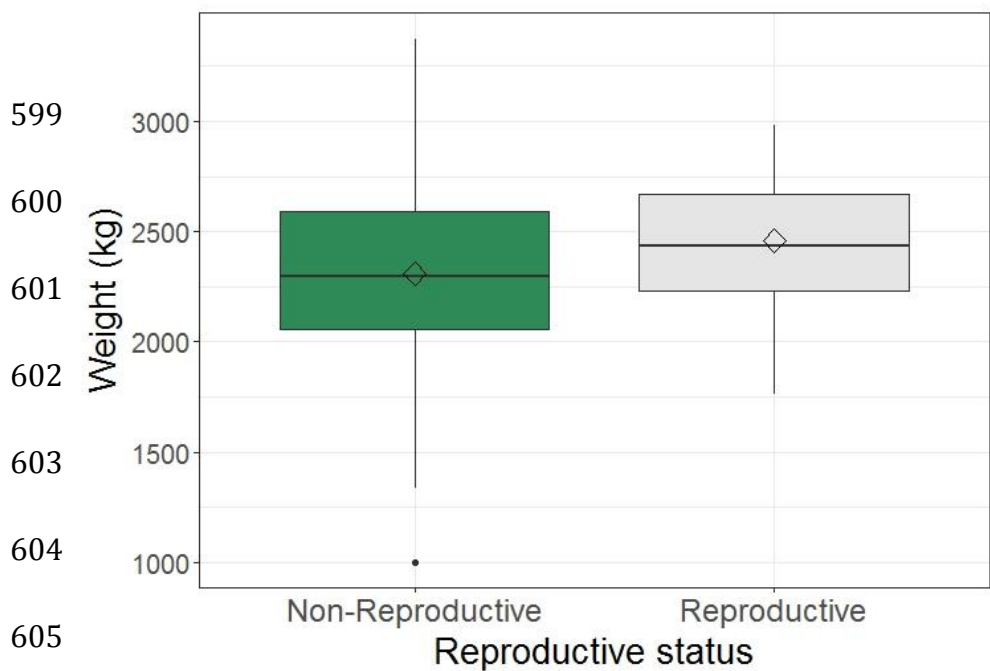
588 **Figure 3**

589

(i)



(ii)



608 **Figure 4**

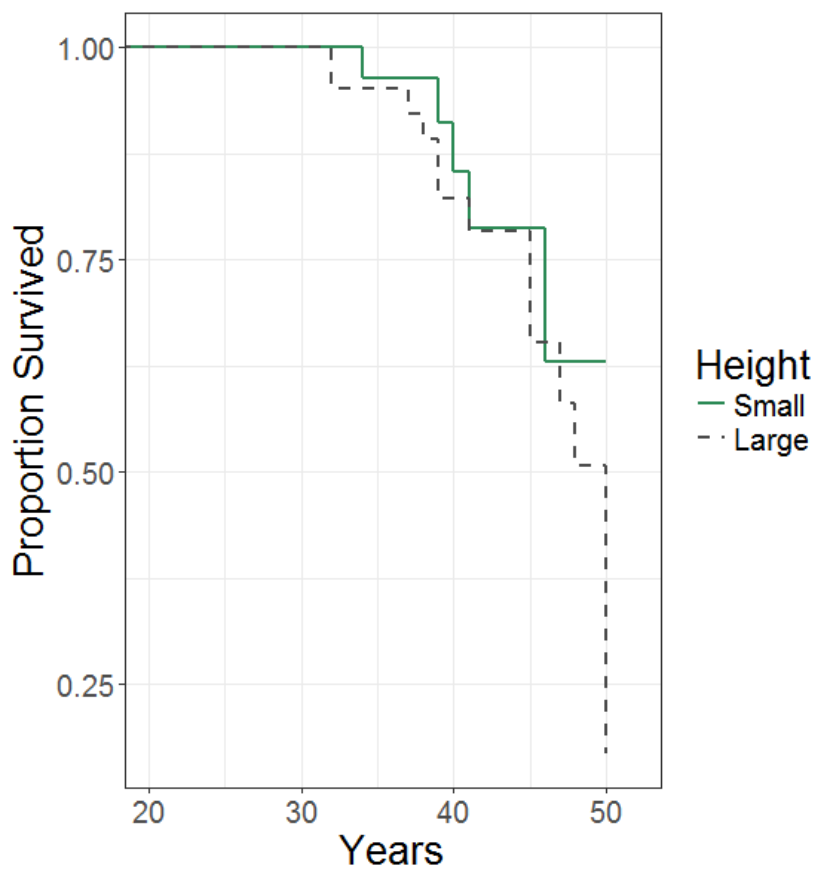


Table S1.1. *Glm*er output comparing the reproductive output of females over 30 of varying sizes, measured as the number of offspring produced at time of measurement. Estimates are expressed on the log scale and continuous variables were scaled to have a mean of 0 and a standard deviation of 1 so effect sizes are comparable.

	Height		Weight	
Fixed effects				
	Estimate ± S.E	z-value	Estimate ± S.E	z-value
Intercept	-0.82 ± 0.47	-1.74	-7.01 ± 1.12	-6.29
Height/ Weight	0.01 ± 0.06	0.12	-0.01 ± 0.42	-0.03
Age	0.84 ± 0.42	2.00	5.90 ± 0.75	7.89
Origin	-0.05 ± 0.32	-0.17	-0.08 ± 0.29	-0.28
Random effects				
	Variance ± S.D	Corr	Variance ± S.D	Corr
ID (Intercept)	3.72 ± 1.93	-	30.98 ± 5.57	-
Age	0.67 ± 0.82	-1.00	12.87 ± 3.59	-1.00
Birth Cohort	0.31 ± 0.55	-	0.00 ± 0.00	-
Camp	0.04 ± 0.21	-	0.00 ± 0.00	-

Table S1.2. *Glm*er 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. Estimates are expressed on the log scale and continuous variables were scaled to have a mean of 0 and a standard deviation of 1 so effect sizes are comparable.

	Height		Weight	
Fixed effects				
	Estimate ± S.E	z-value	Estimate ± S.E	z-value
Intercept	-1.28 ± 0.34	-3.78	-1.99 ± 0.44	-4.46
Height/ Weight	0.02 ± 0.07	0.28	-0.01 ± 0.08	0.89
Age	1.45 ± 0.20	7.30	6.04 ± 2.26	2.68
Age ²	-	-	-3.54 ± 1.78	-1.98
Origin	-0.36 ± 0.24	-1.47	-0.41 ± 0.26	-1.56
Random effects				
	Variance ± S.D	Corr	Variance ± S.D	Corr
ID (Intercept)	4.39 ± 2.10	-	4.31 ± 2.08	-
Age	1.15 ± 1.07	-1.00	1.15 ± 1.07	-1.00
Birth Cohort	0.00 ± 0.06	-	0.00 ± 0.00	-
Camp	0.00 ± 0.00	-	0.00 ± 0.00	-

Table S2. Coxme proportional hazards model output showing survival of female adult elephants (20-50), depending on height as a continuous variable. Reference corresponds to non-reproducers.

<i>Fixed effects</i>	coef ± S.E.	exp (coef) Hazard Ratio	z value	p value	Variance ± S.D
Height	0.04 ± 0.03	1.05	1.44	0.15	
Reproductive status (Rep)	-1.04 ± 0.55	0.35	-1.91	0.06	
Age at measurement	-0.13 ± 0.04	0.87	-3.08	0.002	
Origin (Wild)	-0.01 ± 0.52	0.99	-0.02	0.98	
<i>Random effects</i>					
Birth cohort					0.18 ± 0.42

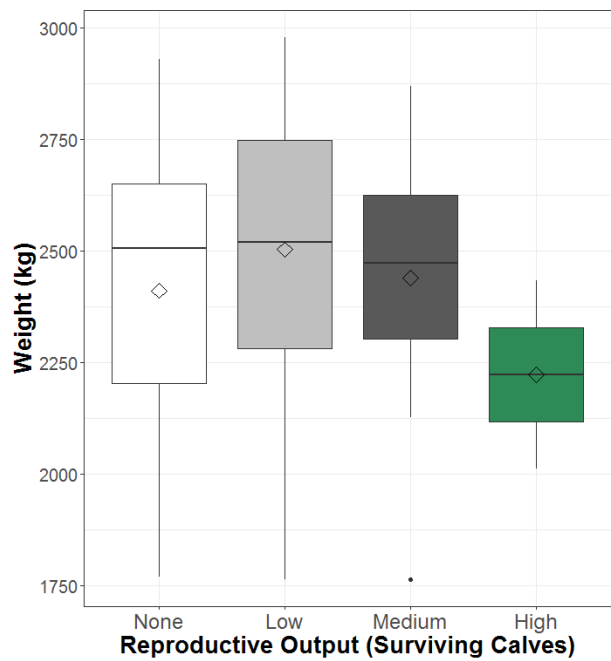
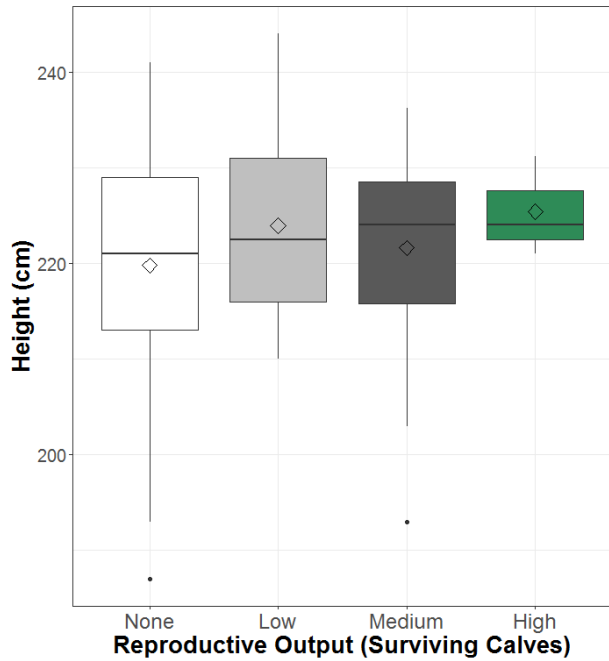
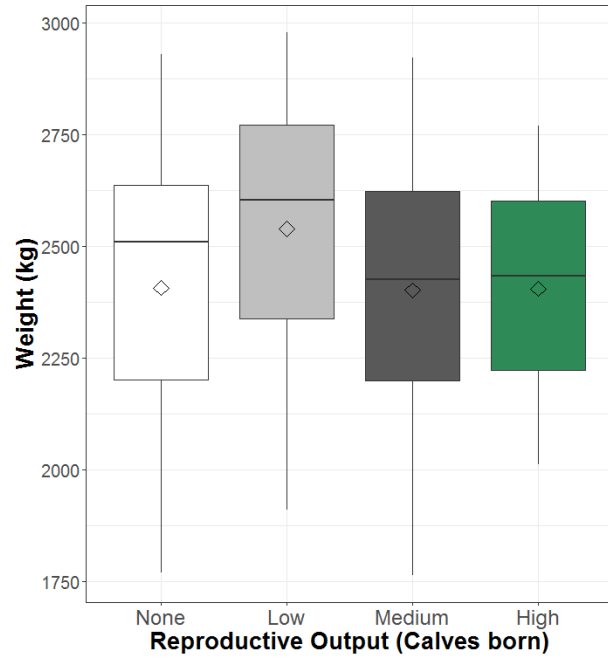
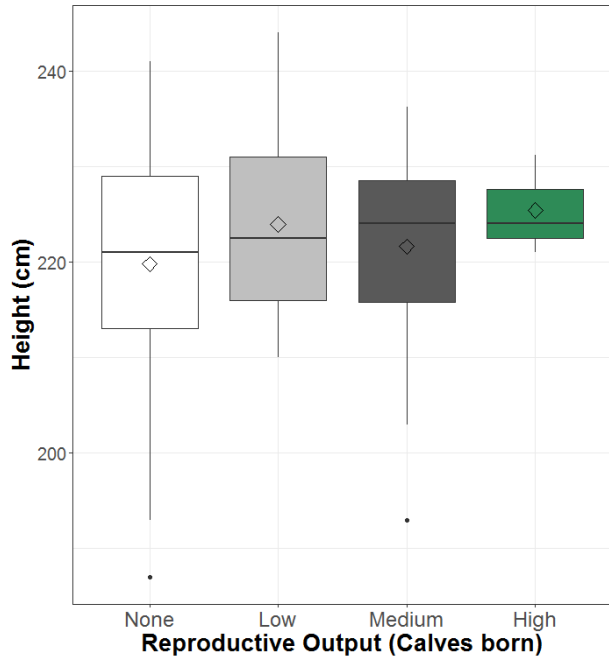


Figure S1. Constraints of size on reproduction: Reproductive output shown as (a) number of calves produced and (b) number of calves raised to 5, of females of varying height (i) and weight (ii) (Reproductive output scale: none=0, low=1-3, medium=3-5, high=5+).

