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Sex-specific body mass ageing trajectories in adult Asian elephants

Running title: Sex-specific ageing in Asian elephants

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Abstract

In species with marked sexual dimorphism, the classic prediction is that the sex which undergoes stronger intrasexual competition ages earlier or quicker. However, more recently, alternative hypotheses have been put forward, showing that this association can be disrupted. Here, we utilise a unique, longitudinal dataset of a semi-captive population of Asian elephants (*Elephas maximus*), a species with marked male-biased intrasexual competition, with males being larger and having shorter lifespans, and investigate whether males show earlier and/or faster body mass ageing than females. We found evidence of sex-specific body mass ageing trajectories: adult males gained weight up to the age of 48 years old, followed by a decrease in body mass until natural death. In contrast, adult females gained body mass with age until a body mass decline in the last year of life. Our study shows sex-specific ageing patterns, with an earlier onset of body mass declines in males than females, which is consistent with the predictions of the classical theory of ageing.

Keywords: Elephas maximus, long-term data, senescence, sex-differences, terminal decline

Introduction

Ageing – a decline in organismal functioning with age (Monaghan et al., 2008) – has been observed in many species (Jones et al., 2014). However, the onset and rates of ageing differ both between (Jones et al., 2014) and within species (Nussey et al., 2007) and between sexes (Clutton-Brock & Isvaran, 2007; Lemaître et al., 2020; Tidière et al., 2015). A main challenge in ageing research is to quantify and explain such differences in the onset and rates of ageing (Rando & Wyss-Coray, 2021).

In species with sex-specific intrasexual competition, the classical theory of ageing predicts that the sex with the highest intrasexual competition has a shorter lifespan and an earlier onset and/or higher rate of ageing (Williams, 1957). The rationale is that high intrasexual selection often results in one sex showing conspicuous displays or aggressive intrasexual behaviours, leading to increased mortality and a *live fast, die young* pace of life (Bonduriansky et al., 2008; Clutton-Brock & Isvaran, 2007; Maklakov & Lummaa, 2013). For that sex, antagonistically pleiotropic genes or deleterious mutations are not counter selected due to a weakened force of selection in late-life (Williams, 1957). Accordingly, in polygynous species with male-biased intrasexual competition, males often die earlier (Lemaître et al., 2020) and age earlier or faster than females (Beirne et al., 2015; Clutton-Brock & Isvaran, 2007; Douhard et al., 2017; Nussey et al., 2009; Tidière et al., 2015). However, recent conceptual developments have shown that this association can be disrupted. This can occur for example because of condition-dependent extrinsic mortality selecting particularly high-performing individuals in the population (Chen & Maklakov, 2014) or canalisation (*i.e.* the more a trait contributes to fitness, the less it should deviate from optimal trait value, with respect to environmental variation (Flatt, 2005)), thereby contradicting the theoretically expected earlier or faster ageing in males. The extent to which such phenomena occur in nature remains unknown.

Here, we used a unique long-term dataset to describe sex-specific body mass ageing trajectories in a nutritionally unsupplemented semi-captive population of Asian elephants (*Elephas maximus*) employed in timber harvesting and living in their natural forest environment in Myanmar. Body mass is of interest in the study of ageing because it is positively associated with key life-history traits such as reproduction and lifespan in many non-human species (Briga et al., 2019; Gaillard et al., 2000; Hämäläinen et al., 2014; Pelletier et al., 2007). Therefore, the study of body mass ageing fits into the evolutionary framework of ageing. Accordingly, in Asian elephants, seasonal variation in body mass was positively associated with survival the following month (*e.g.* low body mass was associated with low survival during dry season) (Mumby, Mar, Thitaram, et al., 2015). Moreover, male Asian elephants benefit from being heavy during intrasexual competition for dominance and mating (Sukumar, 2003).

However, we know almost nothing about body mass ageing in elephants despite the interest in studying ageing in a long-lived, social and sexually dimorphic non-human species. While females live in kin groups, adult males often roam solitarily, undergo a more intense intrasexual competition for dominance and mating (Sukumar, 2003) and hence are bigger, heavier (Mumby, Chapman, et al., 2015), more aggressive, less sociable (Seltmann et al., 2019) and shorter-lived than females (respective median lifespans in this population: 30.8 and 44.7 years) (Lahdenperä et al., 2018). Based on this male-biased intrasexual competition and shorter lifespan, and following the classical theory of ageing (Williams, 1957), we tested the prediction that males experience an earlier and/or faster body mass loss than females (Bonduriansky et al., 2008; Maklakov & Lummaa, 2013).

Material and methods

Study population

We studied the world's largest semi-captive Asian elephant population consisting of around 3,000 individually-marked elephants owned by the government-run Myanma Timber Enterprise (MTE) (Leimgruber et al., 2008). Their birth, death, maternal-lineage pedigree, and morphological measurements have been recorded for almost a century by local veterinarians. These elephants are distributed across Myanmar in forest camps and used as riding, transport and drafting animals. Elephants work during the day but socialise, mate and forage freely and unsupervised in forests at night (Oo, 2010; Zaw, 1997). There are no husbandry procedures and timber elephants are never culled. Calves born in captivity are cared for and nursed by their biological mother and allomothers (Lahdenperä et al., 2016; Lynch et al., 2019). Therefore, breeding rates are natural with no reproductive management. Moreover, there is minimal food provisioning, but elephants benefit from veterinary care that consists of treatment of simple injuries and monitoring of working conditions.

Both males and females are used in the workforce, and each working group of six elephants is composed of both sexes. Males and females follow the same government set limitations on taming age, working and retirement age, working-days per year, hours of work per day and tonnage pulled annually apply to both sexes, although it is possible that males might be used for somewhat different working tasks at times (*e.g.* when use of tusks is required; only males can possess long tusks in Asian elephants). Pregnant females are given a rest period from mid-pregnancy (around 11 months into gestation) until the calf is one year old (Toke Gale, 1974), while they and their calf are being monitored by their mahouts (individual caretakers and riders) throughout this period. Following this break, mothers are used for light work but are kept with calves at heel and able to suckle on demand until the calf is four or five years old (Oo, 2010) at which point calves are assigned a rider, name, logbook and registration number. After the training period, elephants are used for light work duties until the age of 17, when they enter the full workforce until their retirement at the age of 50 years old. The MTE maintains their care and logbooks until death.

Data collection and selection

Our analyses focused on age- and sex-specific variation in adult body mass from age 18 onwards to omit the phase during which elephants grow in height (Mumby, Chapman, et al., 2015) and to focus only on adult body mass age-specific variations. We compiled a total of 3,886 body mass measurements on 493 individuals (2,570 body masses on 322 females, and 1,316 body masses on 171 males). These data came from two sources: (i) body masses were either measured on elephants on the field or (ii) estimated using height to the shoulder and chest girth (method in Supplementary Information 1 and following Chapman et al., 2016). For the first source, we collected 1,901 body masses of 347 elephants (1,297 measurements on 230 females, and 604 measurements on 117 males) and for the second source we estimated 1,985 body masses on 342 individuals (1,273 estimations on 226 females, and 712 estimations on 116 males - a same individual can have both measured and estimated body masses). For all elephants, we knew their working localities (‘township’), sex, year of birth (‘YOB’), alive or dead status at the moment of the study, origin (captive-born or wild-caught) and measurement season (hot: Feb-May, monsoon: Jun-Sep, cold: Oct-Jan (Mumby, Mar, Thitaram, et al., 2015)). The alive or dead status was used to test for a potential terminal decline. Of the 493 individuals considered, 5 males (63 observations) and 18 females (185 observations) died during the study period. We had measurements during the last year of life for 2 males (7 observations) and 10 females (54 observations). The elephants in our study had an age range between 18 – 72 years (mean = 39.3) and were born between 1941 – 1999. Age and cohort information were comparable between sexes, with 171 males (n = 1,316 observations) born between 1954 – 1999 and aged between 18 – 64 years (mean = 37.4), and 322 females (n = 2,570 observations) born between 1941 – 1999 and aged between 18 – 72 years (mean = 40.2).

Most elephants of this semi-captive population are at least occasionally measured for height and chest girth by local veterinarians using tape measures in inches or centimetres, depending on location, with no selection with respect to their age, sex or condition. Body mass is measured to the nearest kg only in camps provided with measurement scales such as Eziweigh 3000 used in this study. All elephants within the reach of those camps get weighed, again without any bias regarding their age, sex or condition. The logbooks containing these measurements have thus far been translated from Burmese to English mainly from the Sagaing region for logistic reasons, but again without any bias or pre-selection of certain individuals.

In total, we used a median of 4.0 measurements/individual (2.5 – 97.5th percentiles: [1.0; 36.4], followed for a median period of 2.8 years (2.5 – 97.5th: [0.0; 36.6] on 493 elephants (n = 3,886 observations). Two influential observations of one male measured at age 18 and 23 were removed because of particularly low Δage (Cook's distance = 0.61 and 0.25, relative to a mean of 0.001 for all males). Other observations for this male, all after age 50, were included and showed no particular Cook's distance.

Statistical analyses

We investigated the age- and sex-specific variation in body mass in R version 4.1.1 (R Core Team, 2021), using the body mass (log-transformed to reach normality of the variable and because of the allometric relationship between body mass and size) as a dependent variable with a normal error distribution. First, we tested in a single model, whether there were sex-specific ageing trajectories using an interaction term (Table S2). Given that this interaction was statistically significant, we compared the sex-specific ageing trajectories for both sexes separately. We did these analyses using both general linear mixed models (GLMMs) and general additive mixed models (GAMMs) with cubic regression splines (but note that other spline functions gave similar conclusions as those shown here) using the functions 'lmer' of the package 'lme4' (v. 1.1-27.1, Bates et al., 2015) and 'gamm' of the package 'mgcv' (v. 1.8-36, Wood, 2011), respectivelyt. GAMMs allow more flexible ageing trajectories than GLMMs, but the more constrained ageing trajectories in GLMMs allow a more precise identification of differences in ageing trajectories (Fig. S1) and both approaches gave consistent conclusions (see results section). We identified the best fitting models using the model selection approach based on the second order Akaike Information Criterion (AICc) as implemented in the package 'MuMIn' (v. 1.43.17, Bartoń, 2021). In brief, the best fitting model has the lowest AICc value, with other models within 7 ΔAICc being plausible and models becoming increasingly equivocal up to 14 ΔAICc, after which they become implausible (Burnham et al., 2011). Thus, we performed model averaging on ageing trajectories within 7 ΔAICc to calculate averaged model estimates with confidence intervals. Visual inspection of model residuals confirmed that all assumptions of distribution and homogeneity were fulfilled without any influential data points or outliers (see above).

Within- vs. between-individual change

In all models, we accounted for non-independence of data due to repeated measurements from the same individual by including elephant identity (‘ID’) as a random intercept. The composition of the population can change with age for example due to selective disappearance of certain (*e.g.* lighter or heavier) individuals, which can affect the age trajectory. To alleviate this problem as much as possible, we disentangled body mass changes with age into between- and within-individual changes following the approach developed by van de Pol & Verhulst, (2006) and van de Pol & Wright, (2009) using two terms: *i)* the age at last measurement for each individual, which captures the between-individual variations and *ii)* a ‘Δage’ term (age at measurement minus the individual’s mean age for all measurements) capturing the within-individual changes with age. We mean-centered and standardised ‘Δage’ so that *i)* individuals measured once all get a Δage = 0 and hence contribute to the variance of the Δage intercept but not to its slope and *ii)* to avoid collinearity and to have comparable variance for Δage and Δage^2 (Bolker, 2008; Zuur et al., 2009). Among the 493 individuals of our dataset, 105 individuals had only one measurement. We included these individuals by giving them Δage = 0 (*i.e.* mean-centered), so they do not contribute to the coefficient but contribute to the variance along the Y axis on Δage = 0, diminishing the likelihood of a false positive, and contribute to the coefficient of the age at last measurement term, thereby avoiding a bias in the dataset from selecting only the longer-lived or most monitored individuals.

Testing ageing trajectories

We tested several within-individual ageing trajectories, first using GAMMs, which can provide curvilinear relationships and allow to describe trends, and using GLMMs, able to detect breaking points if necessary, by testing linear, quadratic, threshold and terminal models (Fig. S1) and we selected the ageing trajectory with the lowest AICc. For GAMMs, we identified the age at which maxima occurred based on the first-order derivative (= 0) using the function 'fderiv' of the package 'gratia' (v. 0.6.0, Simpson & Singmann, 2021). For threshold models (Fig. S1C), we followed the approaches previously developed in Briga et al., (2019) and Douhard et al., (2017). In brief, we first identified the best-fitting threshold age in a series of models, varying the threshold in the 'Δage' term between -35 to 22 years with intervals of one Δage (a unit of the mean-centered Δage = 4.4 and 4.5 years for males and females respectively) and estimated the threshold and its confidence intervals using ± 4 ΔAIC age range. Note that threshold models give separate coefficients for the pre-peak and post-peak slopes and thus allow to discriminate between a post-peak asymptote, decline or increase in body mass. However, if a threshold ageing trajectory is retained as the best-fitting ageing trajectory, we tested the statistical significance of the post peak slope using only post-peak data, with the intercept offset to the peak. Then we compared the best-fitting threshold model with the other ageing trajectories. Sometimes, declines in trait value appear shortly before death (terminal decline). We coded a 'terminal' change (Fig. S1D) as a binomial factor for whether an individual died during the year following the measurement. We used a one-year-window to avoid a possible seasonal covariation in weight and because it was the best fitting time-window, but note that models with other time-windows gave consistent conclusions (Fig. S3).

Accounting for temporal and spatial variation in body mass

As body mass variation can be influenced by seasonal, spatial and within-individual factors, we tested whether body mass values were affected by (i) whether they were measured or estimated, (ii) whether individuals were alive or dead at the time of the analyses, (iii) whether individuals were captive- or wild-born, and (iv) the season during measurement. To this end, we used a model selection approach, using the function 'dredge' of the package 'MuMIn' (v.

1.43.17, Bartoń, 2021) on the best-fitting ageing trajectories for each sex to test for confounding factors (Table S3). In our models, we included as random intercepts individual identity to account for the repeated measurement of the same individual. We also included 'township' to account for the spatial clustering of individuals across Myanmar, although actually adding township worsened the model fit in most cases (male GLMM: ΔAICc = +1.8; male GAMM: ΔAICc = +1.5; female GLMM: ΔAICc = -21.2; female GAMM: ΔAICc = +0.6).

Results

At the measurements' starting age of 18 years, males were on average 235 kg heavier than females, weighing respectively 2,541 kg [95%CI: 2,406; 2,683] and 2,306 kg [95%CI: 2,258; 2,355] and this difference was statistically significant (ΔAICc = -122.6 in a GLMM with vs without sex as a fixed effect).

We identified the elephant's body mass ageing trajectories using general linear mixed models (GLMMs) and general additive mixed models (GAMMs) and both approaches gave consistent results. Both analyses showed that sexes have different body mass ageing trajectories (interaction term, GLMM: ΔAICc = -47.0, Fig. 1, Table S2; GAMM: ΔAICc = -65.7, Fig. S4, Table S2) and hence, we identified the ageing trajectories for both sexes separately.

For males, both GLMMs and GAMMs indicated a body mass gain from age 18 years until their late-forties or early fifties (GLMM maximum: 48.2 years [4 AICc CI: 47.1; 51.6], Fig. 1A; GAMM maximum: 54 years [95%CI: 53; 56], Fig. S5), followed by a decline until death (Fig. 1A, Fig. S4A, Table 1, Table S4). In GLMMs, this maximum was shown through the best fit of a threshold model (ΔAICc = -30.4 compared to a linear trajectory): males gained mass at a rate of 22 kg/year [95%CI: 19.4 23.7] or 1% [95%CI: 0.9; 1.1] of males' mean body mass. Following the peak, males lost mass at a rate of 29 kg/year [95%CI: 14.9; 41.9], *i.e.* 1.3% [95%CI: 0.7; 1.9] of males' mean body mass (Fig. 1A, Table 2) or an effect size (Cohen's d) of -0.59 [95%CI: -0.87; -0.30] based on 47 observations of 14 individuals. An analysis with only the post-peak data confirmed this decline with males losing mass at a rate of 22 kg/year [95%CI: 6.3; 37.1], *i.e.* 1.0% [95%CI: 0.3; 1.7] of males' mean mass or an effect size of -0.40 [95%CI: -0.68; -0.11].

For females, both GLMMs and GAMMs indicated a body mass gain throughout their lives until a terminal decline during their last year of life (Fig. 1B, Fig. S4B, Table 1, Table S4). GLMMs indicated a mass gain of 9 kg/year [95%CI: 7.5; 10.4] or 0.35% [95%CI: 0.3; 0.4] of females' mean body mass (ΔAICc = -6.7, Table 1, Table 2). Loss of body mass occurred in the last year of life (GLMM: ΔAICc = -4.9, Table 1, Fig. 1B, Fig. S3B; GAMM: ΔAICc = -12.2, Table S4, Fig. S4B) and consisted of 173 kg [95%CI: 80; 263], *i.e.* 6.8% [95%CI: 3.2; 10.4] of their mean body mass (Table 2) or an effect size of -0.071 [95%CI: -0.11; -0.03] based on 185 observations of 18 females.

In comparison to females, in males, neither GLMMs nor GAMMs showed statistical support that the decline was terminal rather than mid-age: in GLMMs replacing the mid-age decline by a terminal decline worsened the model fit (ΔAICc = +35.6, Table 1) and there was no statistical support for the same trajectory in males and females (ΔAICc = +42.1, Table 1). For males, in GLMMs, adding a terminal term on top of the mid-age decline also worsened the model fit (ΔAICc = +5.0, Table 1, Fig. S3A), but in GAMMs, models with and without the terminal term were almost equivalent (ΔAICc = -0.01, Table S4). To better understand the possibility of terminal declines in both sexes, we compared the extent and effect size of the terminal decline in both sexes. In males the terminal decline, if any, is just over half that in females at 96 kg

[95%CI: -19; 205], *i.e.* 4.3% [95%CI: -0.9; 9.2] of males' mean body mass or an effect size of -0.05 [95%CI: -0.10; 0.01] based on 1,316 observations on 171 males.

Note that for females and for both GLMMs and GAMMs, the second best model confirms the linear age trajectory, but excludes the terminal effect (GLMM: ΔAICc = +4.9, Table 1; GAMM: ΔAICc = +12.2, Table S4). For males, the second best model (for GLMMs and GAMMs) conserves the same threshold trajectory, but includes the terminal effect (GLMM: ΔAICc = +5.0, Table 1; GAMM: ΔAICc = -0.01, Table S4). Model averaging on ageing trajectories within 7 ΔAICc (Burnham et al., 2011) confirmed the ageing trajectories found, *i.e.* a threshold trajectories for males with a significant decline of body mass from 48 years old onwards (GLMM: β = -0.06 [95%CI: -0.09; -0.03]) and a non-significant terminal decline (GLMM: β = -0.04 [95%CI: -0.10; 0.01], GAMM: β = -0.04 [95%CI: -0.09; 0.01]). Similarly, model averaging performed on models within 7 ΔAICc for females confirmed the ageing trajectory found, *i.e.* a body mass gain throughout life (GLMM: β = 0.015 [95%CI: 0.01; 0.02]) with a significant decline starting in the last year of life (GLMM: β = -0.07 [95%CI: -0.11; -0.03]). Also, we found no effect of the temporal and spatial confounding variables tested (Table S3).

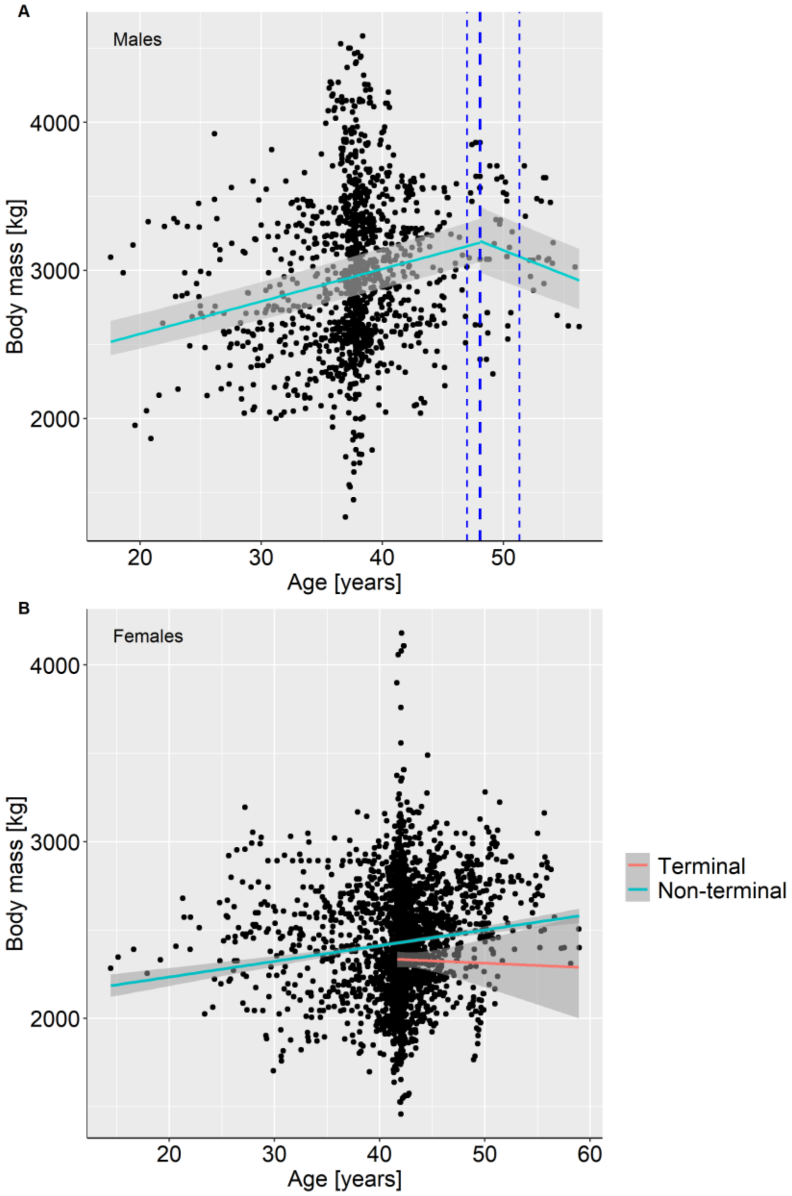

Figure 1. Body mass ageing trajectories of (A) males (n = 1,316 measurements on 171 individuals) and (B) females (n = 2,570 measurements on 322 individuals) with predictions of the best-fitting GLMMs (Table 1) with grey areas 95%CI. For males, the thick dashed-line shows the threshold age at onset of the body mass decline (1.9 or 48.3 years) with thin dashed-lines the 4 ΔAICc-CI [46.6, 52.3]. For females, measurements in the terminal year (red) are significantly lower (intercept) than measurements at other ages (blue). Note 1: the terminal slope is for illustration purposes only and was not statistically tested. Note 2: the original x-axis is Δage, but for simplicity, we presented here the x-axis as age. For the original figure, please see Fig. S2.

Table 1. Best fitting body mass ageing trajectories (bold) for males and females, using GLMMs for each model ageing trajectories ranked from the least to the most complex. AICc: second-order Akaike Information Criterion; ΔAICc: change in AICc relative to the best fitting model; k: degrees of freedom. Δage1 and Δage2 refer respectively to the pre- and post-peak changes of body mass with age in the threshold models.

Model type	Model	Males			Females		
		K	AICc	ΔAICc	k	AICc	ΔAICc
null	log(bm) ~ 1	4.0	-2,828.3	364.2	4.0	-5,442.9	160.7
linear	log(bm) ~ Δage + age-last	6.0	-3,162.0	30.4	6.0	-5,586.1	17.5
+terminal	log(bm) ~ Δage + age-last + terminal	7.0	-3,156.9	35.6	7.0	-5,592.3	11.3
age-last^2	log(bm) ~ Δage + age-last + age-last^2	7.0	-3,155.5	37.0	7.0	-5,598.7	4.9
+terminal	**log(bm) ~ Δage + age-last + age-last^2 + terminal**	8.0	-3,150.4	42.1	**8.0**	**-5,603.6**	**0.0**
Δage^2	log(bm) ~ Δage + Δage^2 + age-last	7.0	-3,176.8	15.7	7.0	-5,571.6	32.0
+terminal	log(bm) ~ Δage + Δage^2 + age-last + terminal	8.0	-3,171.2	21.3	8.0	-5,577.9	25.7
quadratic	log(bm) ~ Δage + Δage^2 + age-last + age-last^2	8.0	-3,170.1	22.3	8.0	-5,584.3	19.3
+terminal	log(bm) ~ Δage + Δage^2 + age-last + age-last^2 + terminal	9.0	-3,164.6	27.9	9.0	-5,589.3	14.3
threshold	**log(bm) ~ Δage1 + Δage2 + age-last**	**8.0**	**-3,192.5**	**0.0**	8.0	-5,580.5	23.1
+terminal	log(bm) ~ Δage1 + Δage2 + age-last + terminal	9.0	-3,187.5	5.0	9.0	-5,586.0	17.6
threshold (age-last^2)	log(bm) ~ Δage1 + Δage2 + age-last + age-last^2	9.0	-3,185.8	6.6	9.0	-5,592.6	11.0
terminal	log(bm) ~ Δage1 + Δage2 + age-last + age-last^2 + terminal	10.0	-3,180.9	11.6	10.0	-5,596.9	6.7

Table 2. Parameter estimates of linear mixed-effect models including individual body mass beyond 18 years of age as the response variable (in kg, log-transformed) for male and female Asian elephants. V: variance, SD: standard-deviation, SE: standard-error. Marginal and conditional R^2 give the variance explained by fixed effects, and both fixed and random effects, respectively. Δage1 and Δage2 refer respectively to the pre- and post-peak changes of body mass with age in the threshold models.

Males			Females		
Random effects	**V**	**SD**	**Random effects**	**V**	**SD**
Individual identity	0.019	0.137	Individual identity	0.011	0.103
Township	0.0005	0.023	Township	0.003	0.056
Fixed effects	**Estimate**	**SE**	**Fixed effects**	**Estimate**	**SE**
Intercept	7.707	0.021	Intercept	7.840	0.019
Age at last measurement	0.087	0.012	Age at last measurement	0.025	0.007
Δage1	0.041	0.002	Age at last measurement²	-0.028	0.006
Δage2	-0.057	0.014	Δage	0.016	0.001
			Terminal (1)	-0.071	0.020
Marginal R^2	0.24		**Marginal R^2**	0.10	
Conditional R^2	0.89		**Conditional R^2**	0.77	

Discussion

We tested whether in a species with marked male-biased intrasexual competition, males showed an earlier and/or faster rate of body mass ageing than females. Both sexes gained mass during early adulthood. However, the onset of body mass ageing differed between the sexes: whilst males began to lose mass from 48.3 years old onwards, females lost body mass generally at an older age, namely in their last year of life. Compared to a previous study on growth curves of this population (Mumby, Chapman, et al., 2015), we are now using a larger dataset, including older and a larger number of retired individuals. This allowed us to evidence body mass ageing in this species, which was not possible until now. Here we discuss the implications of our results in the light of the classical theory of ageing (Williams, 1957) and of the management of Asian elephants.

To the best of our knowledge, we describe for the first time a sex-specific pattern of body mass ageing in this species. Body mass ageing is often used in mammals as it may underpin actuarial and reproductive ageing (Beirne et al., 2015; Bérubé et al., 1999; Nussey et al., 2011). In our population, sex-specific actuarial senescence has already been shown (Lahdenperä et al., 2018) and males display higher mortality than females at all ages. However, reproductive ageing has only been described for females of this population, which is in part due to the difficulty of recording paternity in male elephants (Hayward et al., 2014; Mumby, Mar, Hayward, et al., 2015; Robinson et al., 2012). Our results in this long-lived and highly social species provide valuable insights on how body condition declines with age and offer a broader perspective on the multifaceted ageing, often referred to as a mosaic ageing (Walker & Herndon, 2010).

Asian elephants show male-biased intra-sexual competition, with males being more aggressive (Seltmann et al., 2019), fighting more for dominance and showing higher rates of mortality at all ages than females, including during early development, as calves and during adulthood (Lahdenperä et al., 2018). In such species, the classical theory of ageing predicts that males should show an earlier onset or accelerated ageing (Williams, 1957). Indeed, in several polygynous mammals, males display an earlier onset or higher rates of ageing than females, suggested to be due to their stronger intrasexual competition (Clutton-Brock & Isvaran, 2007 but see also Camus et al., 2012; Tower, 2006). For example, in European badgers (*Meles meles*, Beirne et al., 2015) and Soay sheep (*Ovis aries*, Hayward et al., 2015), males systematically showed stronger or earlier body mass ageing compared to females. Conversely, in monogamous species, the onsets and rates of ageing tend to be similar in males and females

(Bronikowski et al., 2011; Clutton-Brock & Isvaran, 2007; Thorley et al., 2020). Our results are consistent with those studies and with the prediction of the classical theory of ageing, but the agree less with later alternatives proposing that the prediction of the classical theory of ageing can be disrupted by high early-life condition-dependent mortality in males (Chen & Maklakov, 2014) or by canalisation (Flatt, 2005).

Previous work on this population showed age-related declines in the survival and reproduction of females (Hayward et al., 2014; Robinson et al., 2012). Hence, the ageing trajectories do not synchronise between traits in females. Empirically, this heterogeneity of ageing patterns is more the rule than the exception as found in other species (Briga & Verhulst, 2021; Hayward et al., 2015; Walker & Herndon, 2010). In our population, this mismatch can be explained by the fact that body mass is a poor predictor of reproductive success, number of offspring produced or raised up to independence (5 years old), and that no relationship between height and survival has been found in females (Crawley et al., 2017). Our results that females do not show age-dependent body mass decline combined with previous results are at odds those on other vertebrates. Asian elephants reproduce all year around (Brown, 2014), despite living in a seasonal environment, meaning that females finance reproduction through energy stored before reproduction. This is contrary to, say roe deer (*Capreolus capreolus*), an income breeder energetically financing reproduction concurrently to gestation as this ungulate does not store reserves (Andersen et al., 2000). In the latter case, reproductive success therefore depends on body condition and available resources, while in the former case, elephants reproduce when they have stored sufficient resources to finance gestation. This might in part explain the absence of relation between female body mass ageing and reproductive senescence, contrary to males, which benefit more than females from being heavy during intrasexual competition (Sukumar, 2003).

Our study is subject to a number of limitations when it comes down to identifying why the sexes may differ in their ageing trajectories. First, it is possible that male elephants in our timber elephant population are used more for tasks requiring strength or tusks, thereby causing an earlier onset of body mass declines in males than in females. However, both sexes fall under the same government-set workload, care and retirement regulation, except for females' maternity leave. One substantial difference between the sexes is that parental care is concentrated on females, with for example only females being given 'parental leave' following reproduction (Toke Gale, 1974). However, since maternity is energetically expensive and no more favourable than timber working, this is unlikely to lead to the delayed onset of body mass declines in females. An ideal test would be to analyse the effect of timber work and maternity leave on body mass dynamics, but it has not been conducted to-date.

Second, elephants have a specific dentition that consists of molar teeth that eventually wear down at the end of their lives, and pathologic malocclusions or lack of molars can lead to weight loss and death by starvation. In sexually dimorphic species of ungulates, males generally display smaller molar teeth size compared to females, relative to body size. This results in teeth wearing down faster and depleting earlier in males than in females (Carranza & Pérez-Barbería, 2007), with potential consequences for sex-specific senescence. In Asian elephants, although both sexes have the same molar dental anatomy, it is possible that the earlier onset of body mass declines in males reflects sex-specific differences in tooth wear. Indeed, in captive species, dental problems have been described well before the last year of life (Gaillard et al., 2015) and, if there is sex-specific tooth wear, this could be associated with the earlier onset of body mass ageing in males.

Third, male elephants have recurring periods of physiological “musth” throughout their adult lives, which can temporarily but profoundly impact the body mass of individual males (Eisenberg et al., 1971) thereby affecting the body mass ageing trajectory. Although accounting for musth would improve future analyses, recording morphological measurements is unfortunately difficult during the musth period when males display highly aggressive behaviours.

Fourth, in our study, we did not find any evidence for body mass-based selective disappearance, but, as it is often the case in long-lived species, the average longitudinal individual monitoring is short relative to the lifespan of this species (*e.g.* Global BMI Mortality Collaboration et al., 2016; Prospective Studies Collaboration, 2009), and hence we only have limited power to detect such an association. It is possible that there are sex-specific dynamics of selective disappearance, but whether that is the case in Asian elephants remains to be shown. An analysis with more longitudinal data would be useful to tackle this question.

Fifth, for both sexes, it is possible that maximum body mass is set by physiological and ecological constraints as indicated by the weight growth curves found earlier in this population (Mumby, Chapman, et al., 2015). These constraints could to some extent be sex-specific, although at this point, we can only speculate as to why these constraints may drive sex-specific ageing trajectories. Finally, we found a maximum body mass in males but not in females. This sex-specific difference could be driven by the fact that male elephants benefit more than females from being heavy during intrasexual competition (Sukumar, 2003).

Another factor to take into account is that retirement occurs at around 50 years in both sexes, which likely diminishes physical exercise and allows more time for foraging, thereby continuing the weight gain. The reduced intrasexual competition in females relative to males, together with this retirement, could lead to the continued mass gain of females. One way of disentangling the effect of senescence and retirement on body mass trajectories would be to know whether muscle is lost over fat. Unfortunately, we do not have such data. However, a recent study in this semi-captive population did not detect declines in muscle function with age in either sex, as measured by the activity of the creatinine kinase (Reichert et al., 2022). On the contrary, fat storage as measured by levels of circulating triglycerides remained constant up to adulthood, decreasing from retirement onwards in both sexes (Reichert et al., 2022). Also, all elephants officially retire at age 55, but most elephants enter a form of pre-retirement, or reduced labour around the age of 50. These points, taken together with the onset of body mass decline we found in males (*i.e.* 48 years old), suggest that retired individuals lose fat in both sexes rather than muscle and that body mass ageing is a cause rather than a consequence of retirement in males. Nevertheless, given that elephants in the wild do not experience timber labour and retirement, we cannot exclude that the sex-specific body mass ageing trajectories could be different in a wild (non-working) population of Asian elephants compared to those found in our study.

We found that females experienced a terminal body mass decline in the last year of life. Our data contain both males and females among the oldest ages (>50), hence sex-specific terminal decline is unlikely to emerge from differences in lifespan. In European badgers, a species in which females outlive males, both sexes displayed terminal body mass declines (Beirne et al., 2015). We evaluated the possibility that sex-specific ageing trajectories result from differences in sample sizes. For males, our post-peak data (starting at Δage = 1.9, equivalent to an age of 48 years old) contain 47 observations on 14 individuals. For females, the dataset after a peak at the same age (Δage = 1.4) contains 191 observations on 35 individuals. Thus, as is often the case in ageing studies, the sample sizes at older ages are relatively small, which is a limitation. Note however that the three best ageing trajectories for males include a mid-age decline in body mass and that we found a medium effect size (Cohen, 1988) of -0.59 [95%CI: -0.87; -0.30] for the post-peak decline, which makes, we believe, our results trustworthy. For the terminal decline, our data contain only 5 dead males (63 observations) and 18 dead females (185 observations), and among them, we had measurements during the last year of life for 2 males (7 observations) and 10 females (54 observations). Hence, sample sizes are small and it is possible that the sex-specific declines in our study resulted from differences in power. Indeed, for both males and females, the coefficient and effect size of the terminal terms were negative, although the effect size in males remained about half of that in females (Cohen's d_{males} = -0.045 [95%CI: -0.10; 0.01] = a decline of 96 kg [95%CI: -19; 205], Cohen's $d_{females}$ = -0.071 [95%CI: -0.11; -0.03] = a decline of 173 kg [95%CI: 80; 263]). Noteworthy, these effect sizes are below 0.20 and hence remain small following the conventional benchmarks (Cohen, 1988; Nakagawa & Cuthill, 2007). Hence, it is possible that the sex-specific terminal effect is driven by power issues and we look forward to testing that with several more years of monitoring.

Terminal declines emphasise that the chronological age is rarely a perfect estimation of the biological age which can better describe the 'true biological state' of an organism (Klemera & Doubal, 2006). In that sense, a terminal decline is a biomarker of health and remaining lifespan. The 'terminal illness' hypothesis refers to the age-independent decrease of a trait value, related to the imminent death of the individual (Coulson & Fairweather, 2001). Such terminal effects were shown for example for body mass in European badgers, with larger effects in males than females (Beirne et al., 2015), in both sexes in Soay sheep (Hayward et al., 2015) and in male but not female Alpine marmots (Tafani et al., 2013) and for sexual signals in birds (Simons et al., 2016). For which traits or under which conditions to expect terminal declines remains yet poorly understood but our study highlights the importance of studying sex-specific differences in ageing and illustrates the need to improve our understanding of the mechanisms driving the diversity of ageing patterns in the wild.

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Supplementary information to:

Sex-specific body mass ageing trajectories in adult Asian elephants

Table of content

Supplementary Information 1. Body mass estimation

Because of the high correlation of chest girth (CG) with body mass, compared to other morphological metrics (Chapman et al., 2016), we performed a model selection according to AICc values (Akaike Information Criteria corrected) to choose the best way of estimating body masses from CG for males and females separately, as they have different weight growth curves (Chapman et al., 2016; Mumby, Chapman, et al., 2015). In addition to CG being a good predictor of body mass, we also included height to shoulders (H) in the models as indicative of structural size in Asian elephants. Our data indicate a robust correlation between CG and body mass for individuals with both measurements (r_{males}=0.80; $r_{females}$=0.71). The correlation between CG and body mass is higher than the correlation between CG and H (*i.e.* structural size (r_{males}=0.64; $r_{females}$=0.51). Body mass estimations and equations were estimated comparing n = 1,470 (n_{male} = 491, n_{female} = 979) known body mass measurements to the same number of both CG and H measurements.

For females, the full model, including both CG and H and their quadratic effects, showed lower AICc and the best correlation between estimations and measurements, while it was the model including the linear and quadratic effect of CG, and the linear effect of H which was retained for males (table S1). We would rather use the most accurate equations to predict body mass from other metrics, although CG and H were correlated for both sexes (r_{males} = 0.65, t = 18.7, $p < 0.0001$; $r_{females}$ = 0.51, t = 18.5, $p < 0.0001$). From the coefficients of the selected model, we formulated equations (1) and (2) for males and females respectively. The last term of both equations was added to correct for the tendency of the equations to overestimate body masses. Correlations between estimated body masses from equations (1) and (2) and known body masses was r = 0.90 [95%CI: 0.89; 0.91].

Males

$$BM = 2{,}829 - 32.17 \times CG + 0.06 \times CG^2 + 17.57 \times H - 63.26 \tag{1}$$

Females

$$BM = 7{,}697 - 16.40 \times CG + 0.04 \times CG^2 - 48.77 \times H + 0.14 \times H^2 - 21.26 \tag{2}$$

Table S1. Best predictors (in bold) of body mass estimation based on morphometric measures based on the second-order Akaike information criterion (AICc). CG: chest girth, H: height, r: spearman correlation coefficient, k: degrees of freedom.

Response	Model	r	Male			Female		
			AICc	k	r	AICc	k	r
Body mass	CG	0.851	7,116.7	3	0.800	13,596.5	3	0.711
	CG + CG^2	0.858	7,096.8	4	0.810	13,559.0	4	0.725
	CG + H	0.895	6,849.4	4	0.890	13,434.9	4	0.763
	CG + CG^2 + H	**0.902**	**6,802.2**	**5**	**0.901**	13,404.2	5	0.772
	CG + H + H^2	0.898	6,841.5	5	0.892	13,406.0	5	0.771
	CG + CG^2 + H + H^2	-0.461	6,803.4	6	0.496	**13,389.8**	**6**	**0.776**

Supplementary Information 2. Illustration of body mass ageing trajectories using GLMMs

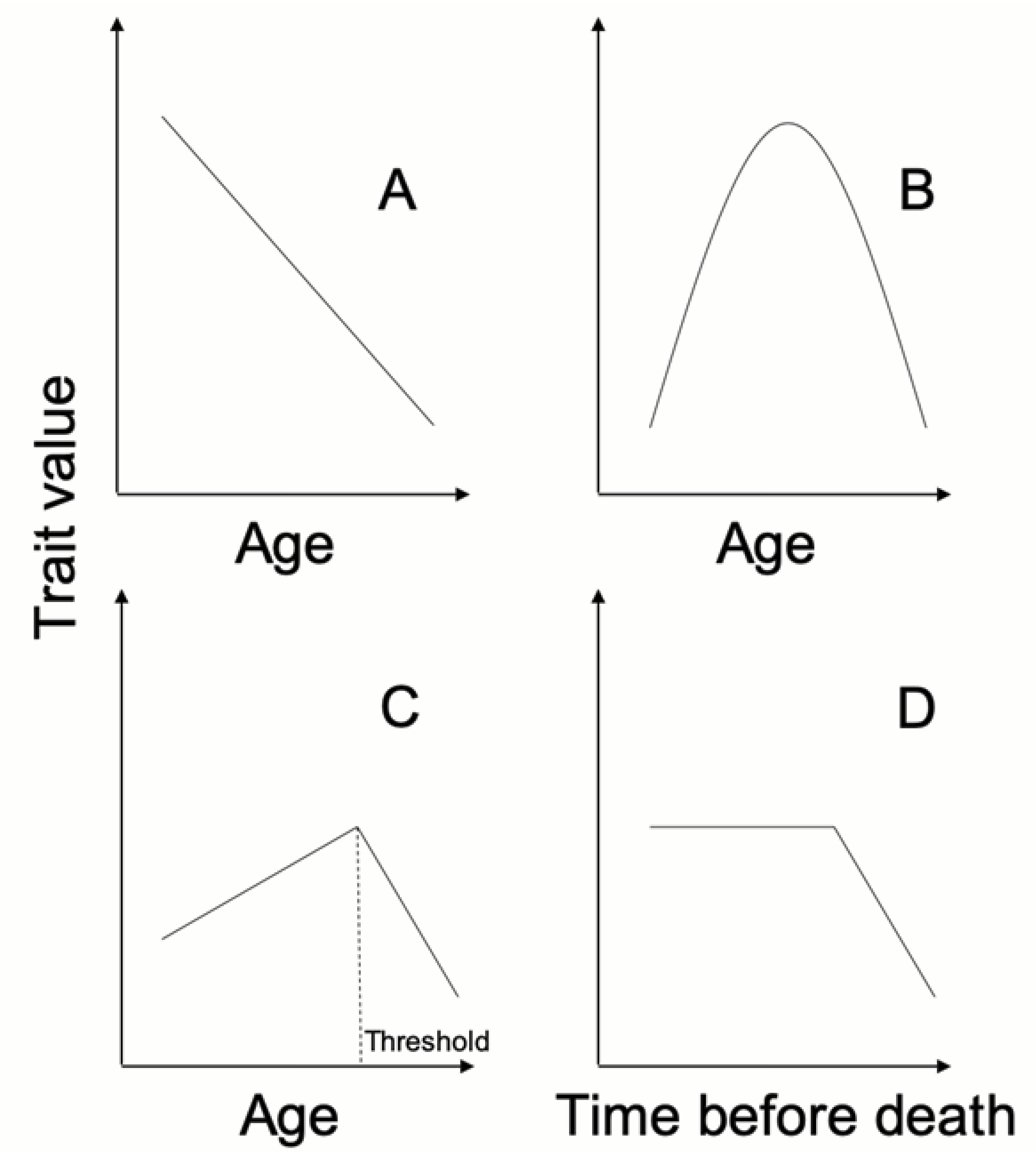

Figure S1. Schematic representation of the four ageing trajectories tested. Using the individual's chronological age, ageing trajectory can be (A) linear, (B) quadratic, or (C) with a threshold. However, using the time before death, ageing can correspond to (D) a terminal decline. The slopes here are illustrative only and can, in practice, take any value. Figure adapted from Briga et al., 2019.

Supplementary Information 3. Sex-specific age trajectories

Table S2. Evidence for sex-specific body mass ageing trajectories both in GAM and GLM models based on model selection approaches. The models are ranked from the best-fitting (lowest AICc, on the top) to poorer-fitting ones (higher AICc, at the bottom). Best-fitting in bold. AICc: second-order Akaike Information Criteria, ΔAICc: difference in AICc relative to the best model, k: degrees of freedom, w: model weight, s=smooth. All models contain the random intercepts individual identity *(1|ID)* and township *(1|township).*

Model	Model	k	AICc	ΔAICc	w
GAMM	**log(bm) ~ terminal + sex + s(Δage) + age-last + age-last^2 + s(Δage, by=sex)**	**17.9**	**-8,809.1**	**0.0**	**1.0**
	log(bm) ~ terminal + sex + s(Δage) + Δage^2 + age-last + age-last^2	10.3	-8,743.4	65.7	0.0
GLMM	**log(bm) ~ terminal + sex + Δage + age-last + age-last^2 + sex:Δage**	**10.0**	**-8,730.6**	**0.0**	**1.0**
	log(bm) ~ terminal + sex + Δage + age-last + age-last^2	9.0	-8,683.6	47.0	0.0

Supplementary Information 4. Seasonal and spatial confounding variables

Table S3. Model selection of covariates based on the best fitting models in Table 1 describing body mass ageing trajectories for both sexes. The column 'Model' refers to the model names as given in Table 1. AICc: Akaike Information Criteria (corrected) of the selected models, k: degrees of freedom, 'season': ΔAICc (*i.e.* AICc differential compared to the selected model) when including the season of the body mass measurement, 'alive': ΔAICc when including whether individuals were dead or alive at the moment of the analysis, 'cw': ΔAICc when including whether the individuals were captive-born or wild-caught, 'measure': ΔAICc when including whether the body masses were estimated or measured.

Sex	Model selected	AICc	ΔAICc	k	w
Males GAMMs	log(bm) ~ s(Δage) + age-last + cw	-3,222.8	0.0	9.1	0.234
	log(bm) ~ s(Δage) + age-last	**-3,221.9**	**0.9**	**8.1**	**0.148**
	log(bm) ~ s(Δage) + age-last + cw + season	-3,221.2	1.6	11.1	0.104
	log(bm) ~ s(Δage) + age-last + cw + measure	-3,220.8	2.0	10.1	0.085
	log(bm) ~ s(Δage) + age-last + cw + alive	-3,220.4	2.4	11.1	0.071
	log(bm) ~ s(Δage) + age-last + season	-3,220.2	2.6	10.1	0.066
	log(bm) ~ s(Δage) + age-last + alive	-3,219.9	2.9	10.1	0.055
	log(bm) ~ s(Δage) + age-last + measure	-3,219.8	2.9	9.1	0.054
	log(bm) ~ s(Δage) + age-last + cw + measure + season	-3,219.1	3.6	12.1	0.038
	log(bm) ~ s(Δage) + age-last + alive + measure + season	-3,218.7	4.1	13.1	0.031
Females GAMMs	log(bm) ~ terminal + s(Δage) + age-last + age-last^2 + season	-5,641.5	0.0	12.8	0.316
	log(bm) ~ terminal + s(Δage) + age-last + age-last^2 + season + measure	-5,640.2	1.4	13.7	0.160
	log(bm) ~ terminal + s(Δage) + age-last + age-last^2	**-5,639.7**	**1.8**	**10.9**	**0.127**
	log(bm) ~ terminal + s(Δage) + age-last + age-last^2 + season + cw	-5,638.8	2.7	14.8	0.082
	log(bm) ~ terminal + s(Δage) + age-last + age-last^2 + measure	-5,638.4	3.1	11.7	0.066
	log(bm) ~ terminal + s(Δage) + age-last + age-last^2 + season + alive	-5,638.1	3.4	14.8	0.057
	log(bm) ~ terminal + s(Δage) + age-last + age-last^2 + season + measure + cw	-5,637.5	4.1	15.9	0.042
	log(bm) ~ terminal + s(Δage) + age-last + age-last^2 + cw	-5,637.0	4.5	12.9	0.033
Males GLMMs	**log(bm) ~ Δage1 + Δage2 + age-last**	**-3,192.5**	**0.0**	**8.0**	**0.889**
	log(bm) ~ Δage1 + Δage2 + age-last + cw	-3,187.9	4.6	9.0	0.089
	log(bm) ~ Δage1 + Δage2 + age-last + alive	-3,184.4	8.1	10.0	0.016
Females GLMMs	**log(bm) ~ terminal + Δage + age-last + age-last^2**	**-5,603.6**	**0.0**	**8.0**	**0.983**
	log(bm) ~ terminal + Δage + age-last + age-last^2 + measure	-5,594.6	9.0	9.0	0.011

Supplementary Information 5. Body mass ageing trajectories using GLMMs

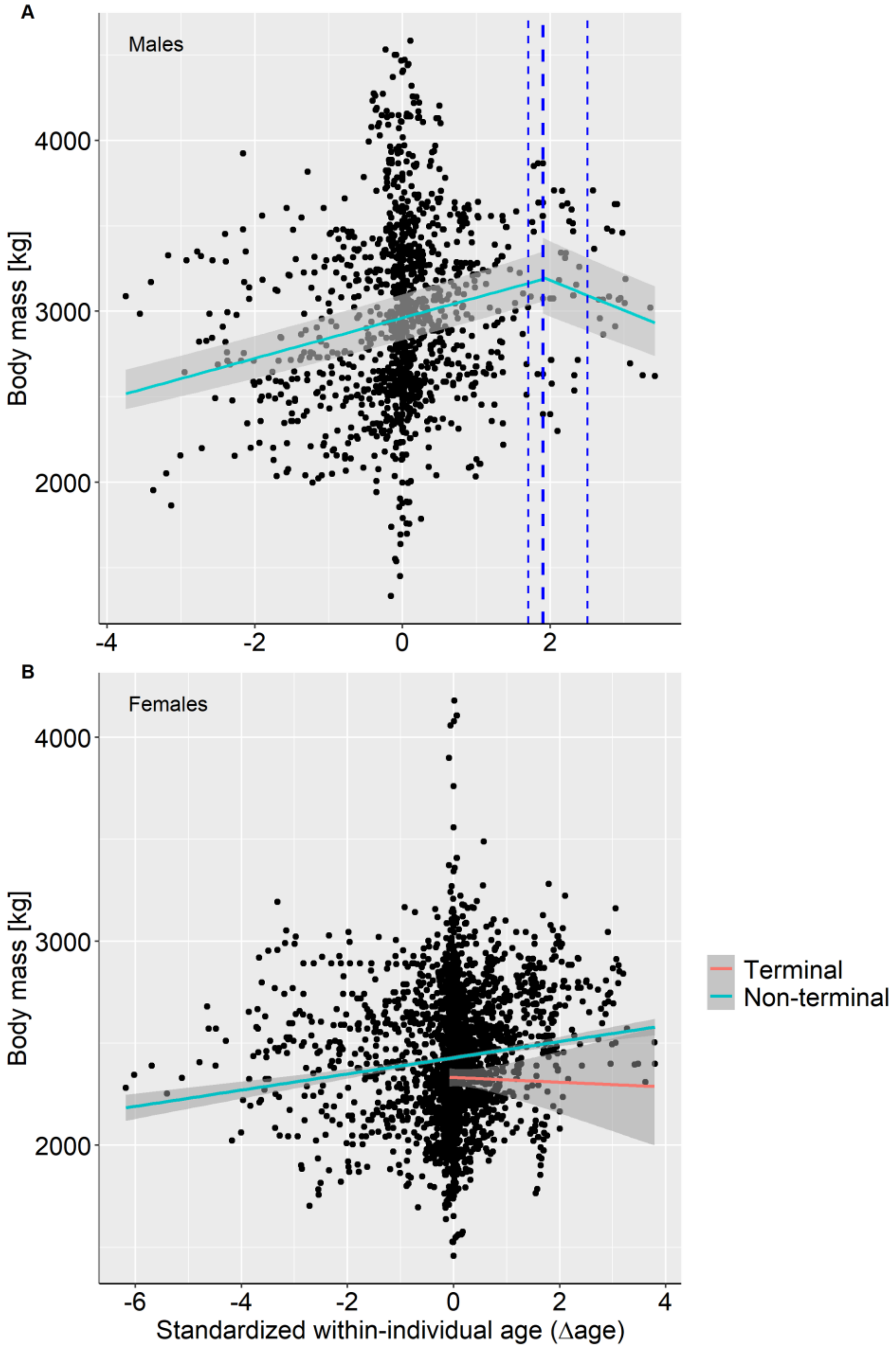

Figure S2. Body mass ageing trajectories of (A) males (n = 1,316 measurements on 171 individuals) and (B) females (n = 2,570 measurements on 322 individuals) with predictions of the best-fitting GLMMs (Table 1) with grey areas 95%CI. For males, the thick dashed-line shows the threshold age at onset of the body mass decline (1.9 or 48.3 years) with thin dashed-lines the 4 ΔAICc-CI [46.6, 52.3]. For females, measurements in the terminal year (red) are significantly lower (intercept) than measurements at other ages (blue). Note that the terminal slope is for illustration purposes only and was not statistically tested.

Supplementary Information 6. Testing terminal decline windows

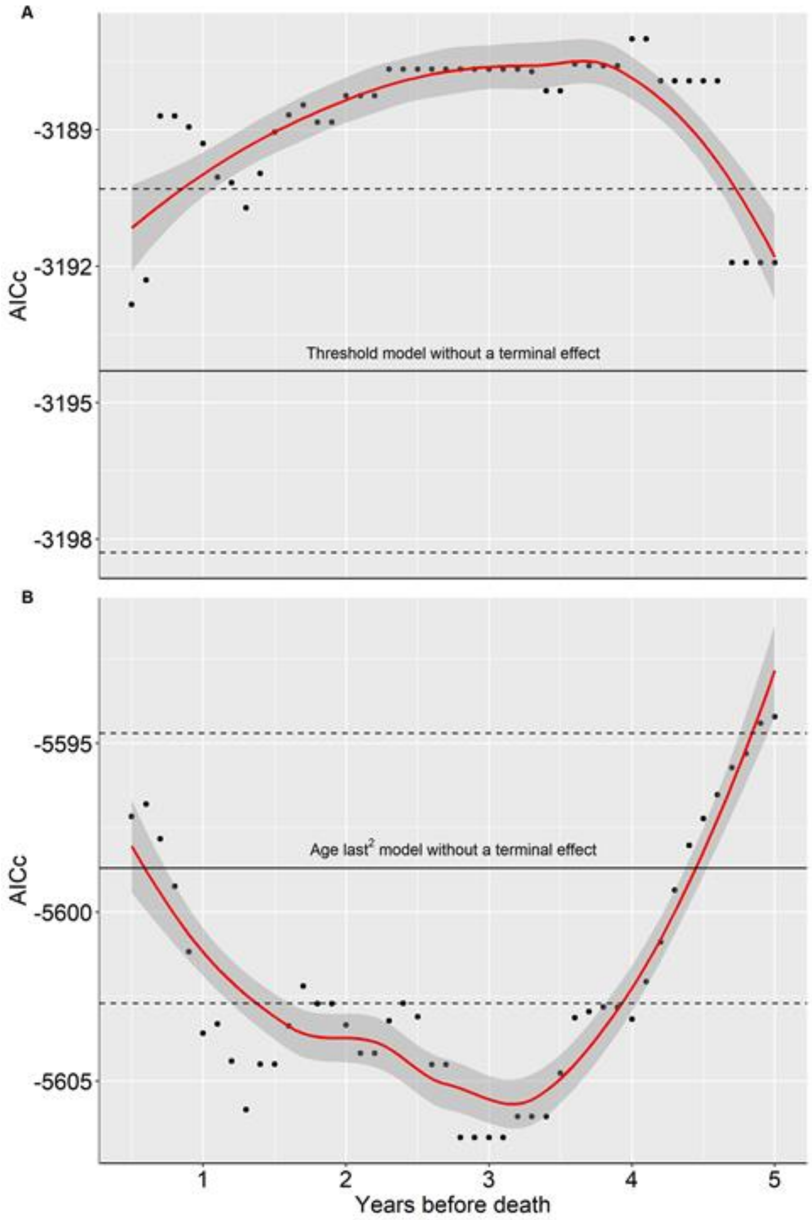

Figure S3. Testing variation in windows for the age at onset of the terminal decline for A) males and B) females. The black solid line represents the fit of the model selected without a terminal effect, and the dashed lines represent the confidence interval of this model (±4AICc). A) In males, terminal declines were not statistically supported (best fitting model in table 1), irrespective of the window used. B) In females, a statistically significant terminal decline occurs between 1 and 4 years before death and the statistical support through this windows is equivalent. Hence, we chose to illustrate models with terminal windows of one year.

Supplementary Information 7. Body mass ageing trajectories using GAMMs

Table S4. Model selection of body mass ageing trajectories (bold) for males and females, using GAMMs for each model ageing trajectories ranked from the least to the most complex. AICc: second-order Akaike Information Criterion; ΔAICc: change in AICc relative to the best fitting model; k: degrees of freedom.

Model type	Model	Males			Females		
		k	AICc	ΔAICc	k	AICc	ΔAICc
null	log(bm) ~ 1	4.0	-2,835.8	386.1	4.0	-5,422.6	217.1
smooth1	**log(bm) ~ s(Δage) + age-last**	**8.1**	**-3,221.9**	**0.01**	8.7	-5,613.9	25.8
+terminal	log(bm) ~ s(Δage) + age-last + terminal	9.1	-3,221.9	0.0	10.0	-5,627.3	12.4
smooth2	log(bm) ~ s(Δage) + age-last + age-last^2	9.1	-3,221.2	0.7	9.7	-5,627.5	12.2
+terminal	**log(bm) ~ s(Δage) + age-last + age-last^2 + terminal**	10.1	-3,221.3	0.6	**10.9**	**-5,639.7**	**0.0**

Table S5. Estimates of general additive mixed models (GAMMs) including individual body mass beyond 18 years of age as the response variable (in kg, log-transformed) for male and female Asian elephants. V: variance, SD: standard deviation, SE: standard-error, Df: degrees of freedom, F: Fisher value. Marginal and conditional R^2 give the variance explained by fixed effects, and both fixed and random effects, respectively.

Males			Females		
Random effects	V	SD	**Random effects**	V	SD
Individual identity	0.018	0.136	Individual identity	0.009	0.095
Township	0.0004	0.021	Township	0.004	0.060
Fixed effects	**Estimate**	**SE**	**Fixed effects**	**Estimate**	**SE**
Intercept	7.997	0.013	Intercept	7.832	0.009
Age at last measurement	0.089	0.012	Age at last measurement	0.034	0.007
			Age at last measurement^2	-0.023	0.006
			Terminal (1)	-0.075	0.020
Smooth term	Df	F	Smooth term	Df	F
Δage	6.096	70.4	Δage	6.899	27.9
Marginal R^2	0.23		**Marginal R^2**	0.10	
Conditional R^2	0.89		**Conditional R^2**	0.80	

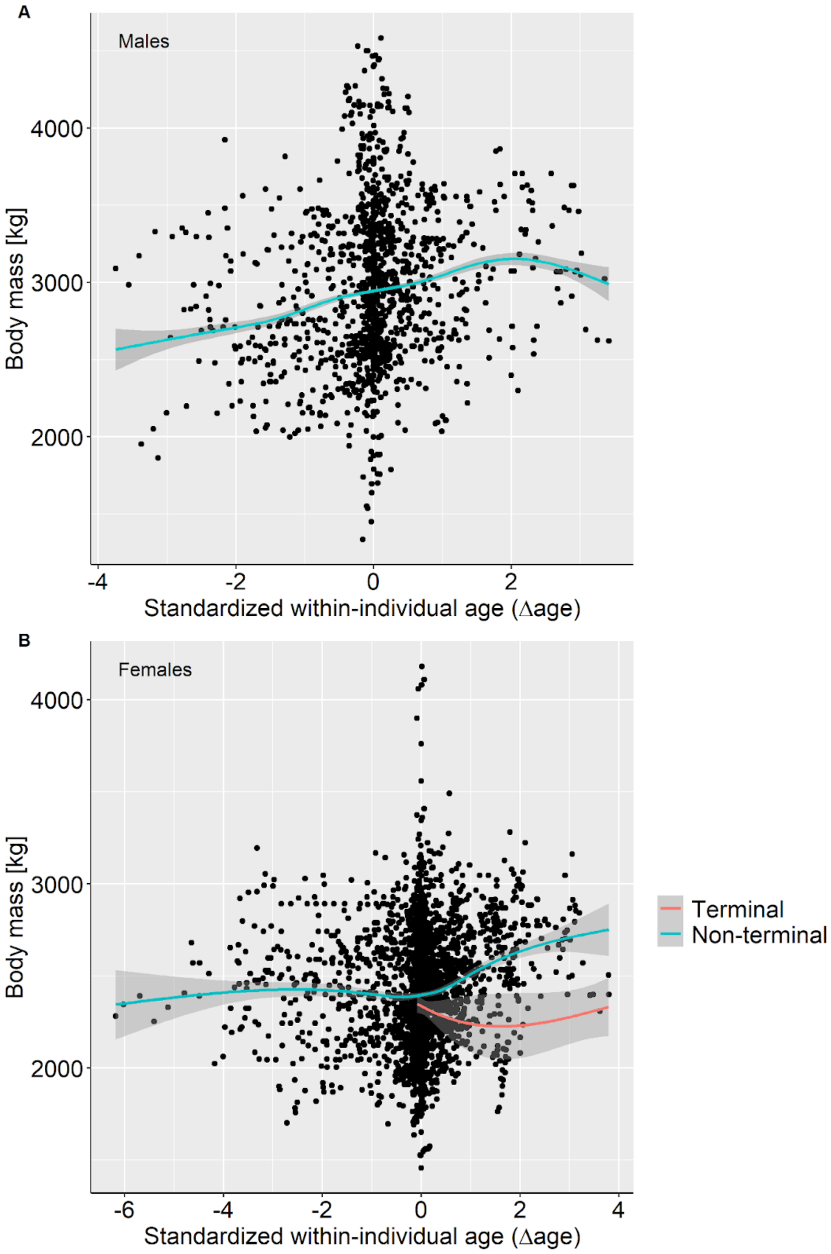

Figure S4. Body mass ageing trajectories of (A) males (n=1,316 measurements on 171 individuals) and (B) females (n=2,570 measurements on 322 individuals) with solid lines showing predictions of the best-fitting GAM models (Table S4) and grey areas 95%CI. For females, measurements in the terminal year (red) are significantly lower than measurements at other ages (grey), but note that the association (slope) with Δage is for illustration purposes only and was not statistically tested.

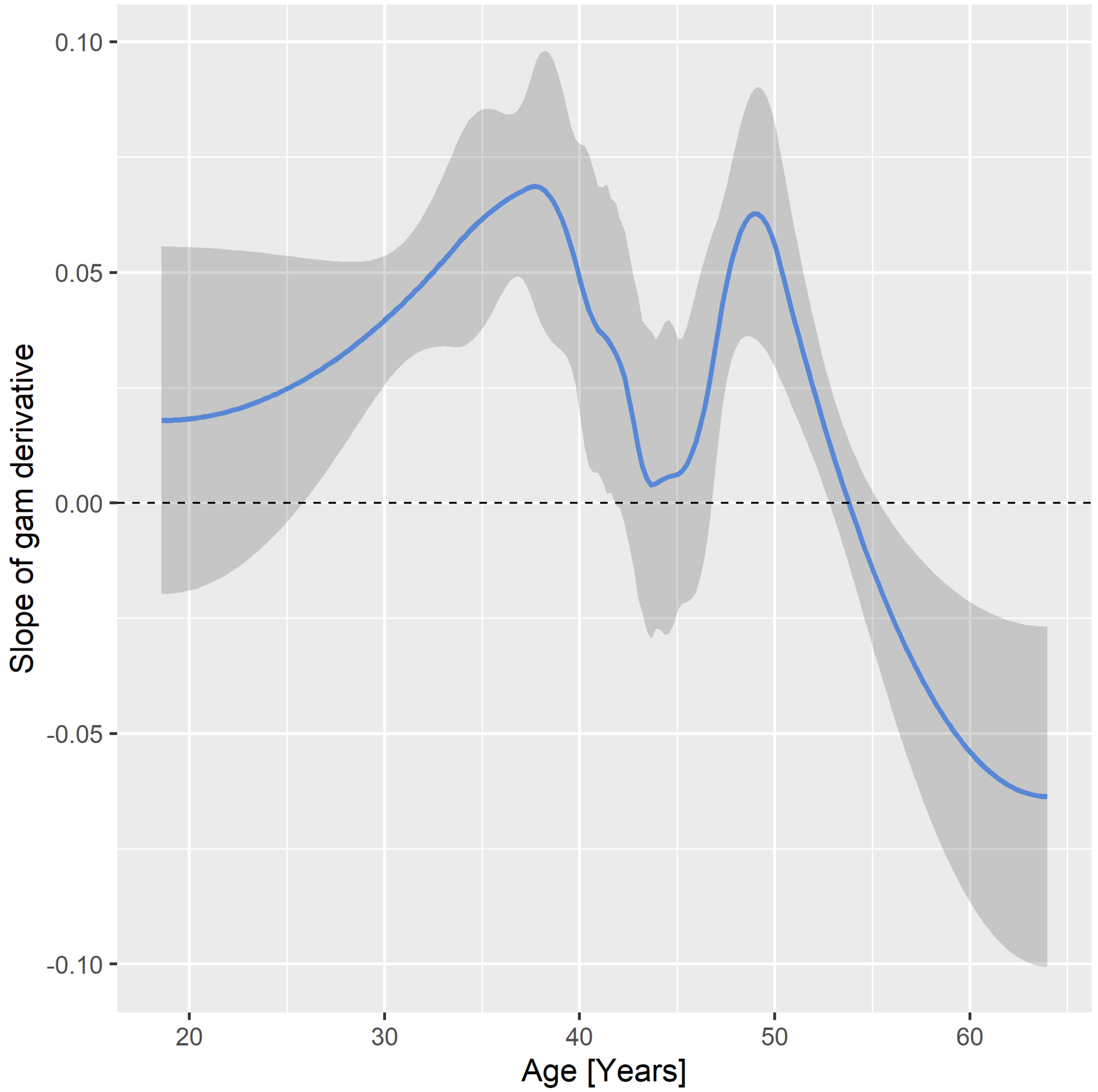

Figure S5. Derivative of the best fitting GAM model in males (Table S4, smooth 1) to identify the age at which maximum body mass is reached, *i.e.* when the derivative (blue line) is zero. Grey zones indicate the 95% confidence interval around the age at maximum.

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