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Sex-specific body mass ageing trajectories in adult Asian elephants

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Abstract

In species with marked sexual dimorphism and where one sex undergoes stronger intrasexual competition, that sex is expected to age earlier or quicker. 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 living shorter, and test the hypothesis that males show earlier and/or faster body mass ageing than females. We show 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 that sex-specific life-histories shape ageing patterns, consistent with the predictions of the classical theory of ageing.

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

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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 (Douhard et al., 2017). 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, classic theory predicts that the sex with the highest intrasexual competition has a shorter lifespan and an earlier onset and/or higher rate of ageing (Maklakov & Lummaa, 2013). 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). 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.

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Here, we used a unique long-term dataset to describe sex-specific body mass ageing trajectories in a nutritionally unsupplemented semi-captive timber population of Asian elephants (*Elephas maximus*) living in their natural 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 (Hämäläinen et al., 2014). 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, et al., 2015).

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

Material and methods

Study population

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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, pedigree details, 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 and, at night, they socialise, mate and forage freely, unsupervised in forests (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 1-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

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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 retirement around age 50. 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, omitting the phase during which elephants grow in height (Mumby, Chapman, et al., 2015). From the logbooks, we extracted 1,901 body masses of 347 elephants with known sex, year of birth ('YOB'), alive or dead status, origin (captive-born or wild-caught) and measurement season (hot: Feb-May, monsoon: Jun-Sep, cold: Oct-Jan (Mumby, Mar, et al., 2015)) from 325 working localities ('township'). Study elephants were aged 18 – 72 years (mean = 39.3) and born 1941 – 1999. Age and cohort information were comparable between sexes, with 171 males (n = 1,316) born 1954 – 1999 and aged 18 – 64 years (mean = 37.4), and 322 females (n = 2,570) born 1941 – 1999 and aged 18 – 72 years (mean = 40.2).

When body mass measurements were not available, we estimated body masses using height to the shoulder and chest girth (n = 1,985 measurements on 342 individuals, method in Supplementary Information 1). In Asian elephants, chest girth reflects changes in mass in addition to the fixed effect of structural size during adulthood (details in SI2).

Most elephants of this semi-captive population get at least occasionally measured for height and chest girth, with no selection with respect to their age, sex or condition. Body mass is measured only in camps provided with measurement scales (mainly in regions with the highest concentrations of elephants and the best accessibility). All elephants within the reach of those camps get weighed, again

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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 reason, but again without any bias or pre-selection of certain individuals.

In total, we obtained 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). Two influential observations measured at age 18 and 23 were removed for one male because of particularly low Δage (Cook's distance = 0.61 and 0.25, mean of 0.001 on all males). Other observations for this male, all after age 50, were included.

Statistical analyses

We investigated the age- and sex-specific variation in body mass in R version 4.0.5 (R Core Team, 2020), using the log-transformed body mass as a dependent variable with a normal error distribution. We first tested whether there were sex-specific ageing trajectories (table S2) and then compared the sex-specific ageing trajectories using general additive mixed models (GAMs) with cubic regression splines (but note that other spline functions gave similar conclusions to those shown here) and general linear mixed models (GLMs), with respectively the functions 'gamm' of the package 'mgcv' (Wood, 2017) and the function 'lmer' of the package 'lme4' (Bates et al., 2015). GAMs allow more flexible ageing trajectories than GLMs, but the more constrained ageing trajectories in GLMs allow a less descriptive identification of differences in ageing trajectories (figure 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

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Information Criterion (AICc) as implemented in the package 'MuMIn' (Bartoń, 2019). In brief, the best fitting model has the lowest AICc value, with other models within 4 ΔAICc being plausible and models become increasingly equivocal up to 14 ΔAICc, after which they become implausible (Burnham et al., 2011). Visual inspection of model residuals confirmed that these fulfilled all assumptions of distribution and homogeneity 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. In order to alleviate this problem to the best possible in this long-lived species, we decomposed 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-centred 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 Δage² (Bolker, 2008; Zuur et al., 2009). Our dataset included 105 individuals with one measurement after the age of 18 and we included these individuals by giving them Δage = 0 (*i.e.* mean-centred) so they do not contribute to the coefficient but do contribute to the variance along the Y axis on Δage = 0, diminishing the likelihood of a false positive,

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and ii) do 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: GAMs can have any shape and for GLMs we tested linear, quadratic, threshold and terminal models (figure S1) and we selected the ageing trajectory with the lowest AICc. For GAMs, we identified the age at which maxima occurred based on the first-order derivative (= 0) using the function 'fderiv' of the package 'gratia' (Simpson & Singmann, 2021). For threshold models (figure 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 (1 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. 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 (figure 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 (figure 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)

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measured or estimated, (ii) individuals were alive or dead, (iii) captive- or wild-born and (iv) the measurement season. To this end we used a combination of backward elimination and forward selection approaches, *i.e.* first we analysed the models including these covariates using the most complex ageing trajectory, identified that none of these factors improved the model, then we eliminated these co-variates from the model, identified the best fitting ageing trajectory, and then we repeated the final models obtained with these covariates and identified again that none of these improved the model fit or altered the previously obtained conclusions (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 (except in male GLMs which lacked power), although actually adding township worsened the model fit (male GAM: ΔAICc = +1.5; female GAM: ΔAICc = +0.6).

Results

At the measurements' starting age of 18 years, males were on average 253 kg heavier than females, weighing respectively 2,559 kg [95%CI: 2,431 – 2,694] and 2,306 kg [95%CI: 2,258 – 2,355] and this difference was statistically significant (ΔAICc = -122.6 in a GLM with vs without sex as a fixed effect).

We identified the elephants body mass ageing trajectories using general additive models (GAMs) and general linear models (GLMs) and both approaches gave consistent results. Both analyses showed that sexes have different body mass ageing trajectories (GAM: ΔAICc = -65.7, figure 1, table S2; GLM: ΔAICc = -47.0, figure 2, table S2) and hence, we identified the ageing trajectories for both sexes separately.

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For males, both GAMs and GLMs indicated a body mass gain from age 18 years until their late-forties or early fifties (GAM maximum: 54 years, 95%CI: 53 – 56, figure S2; GLM maximum: 48.3 years, 4 AICc CI: 46.6 – 52.3, figure 2A), followed by a decline until death (figure 1A, figure 2A, Table 1). In GLMs, 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 21 kg/year [95%CI: 19.1 – 23.4] or 0.9% [95%CI: 0.9 – 1.0] of males' mean body mass and then lost mass at a rate of 28 kg/year [95%CI: 14.6 – 41.3] or 1.3% [95%CI: 0.7 – 1.8] of males' mean body mass (figure 2A). Regarding the decline, neither GAMs nor GLMs showed confident statistical support that it was terminal (*i.e.* determined by time before death rather than age): in GAMs, models with and without the terminal term were almost equivalent (ΔAICc=+0.01, Table 1) and in GLMs adding a terminal term worsened the model fit (ΔAICc=+5.0, Table 1, figure S3A).

For females, both GAMs and GLMs indicated a body mass gain throughout their lives until a terminal decline during their last year of life (figure 1B, figure 2B, Table 1). GLMs indicated a mass gain of 8 kg/year [95%CI: 7.4 – 10.3] or 0.3% [95%CI: 0.3 – 0.4] of females' mean body mass (ΔAICc = -6.7, Table 1). Loss of body mass occurred in the last year of life (GAM: ΔAICc = -12.2, Table 1, figure 1B; GLM: ΔAICc = -4.9, Table 1, figure 2B, figure S3B) and consisted of 173 kg [95%CI: 80 – 263] or 6.8% [95%CI: 3.2 – 10.4] of their mean body mass. For comparison, the extent of the terminal decline in males, if any, is just over half that in females at 97 kg [95%CI: -20 – 207] or 4.3% [95%CI: -0.9 – 9.2] of males' mean body mass (quantified in the aforementioned best-fitting threshold model).

Discussion

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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 both sexes: males began to lose mass from 48.3 years old onwards. In contrast, 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 more numerous 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 theories of ageing (Williams, 1957) and of the management of Asian elephants.

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, classic theory predicts that males should show an earlier onset or accelerated ageing (Williams, 1957). Indeed, in several polygynous mammals, males display higher rates of body mass declines than females, suggested to be due to their stronger intrasexual competition (Beirne et al., 2015; Clutton-Brock & Isvaran, 2007). Our results are consistent with those studies and with the prediction of the classic theory of ageing. Moreover, our results are inconsistent with later alternatives that suggest that the prediction of the classic theory can be disrupted by high early-life condition-dependent mortality in males (Chen & Maklakov, 2014) or by canalisation (Flatt, 2005).

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Our study is subject to a number of limitations when it comes down to identifying why 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 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. 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. Although both sexes have the same molar dental anatomy, it is possible that the earlier onset of body mass declines in males may reflect sex-specific differences in tooth wear rather than sex-specific sexual selection. Indeed, in captive elephants, dental problems have been described well before the age at onset of the terminal decline found in this study (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. 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

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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 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 be to some extent sex-specific, although at this point, we can only speculate as to why these constraints may drive sex-specific ageing trajectory. Finally, we found a maximum body mass in males but not in females. This sex-specific differences could be driven by the fact that male elephants benefit more than females from being heavy during intrasexual competition (Sukumar, 2003). However, 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. 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

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European badgers (*Meles meles*), a species in which females outlive males, both sexes displayed terminal body mass declines (Beirne et al., 2015). It is possible that the sex-specific terminal declines in our study resulted from differences in power, with 5 old dead males and 18 old dead females. Indeed, for both males and females, the coefficient and effect size of the terminal terms were negative, but the effect size in males remained about half of that in females (Cohen's d_{males} = -0.045 [-0.10, 0.01], Cohen's $d_{females}$ = -0.071 [-0.11, -0.03]). 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, 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) and such terminal effects were shown for example for body mass and sexual signals in mammals and birds (Beirne et al., 2015; 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.

This manuscript is available on a preprint server (Lalande et al., 2021).

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Ethics

The study was performed with the permission from the Myanmar Ministry of Natural Resources and Environmental Conservation and following the University of Turku ethical guidelines. Note that the University of Turku does not provide project numbers.

Data accessibility

The dataset supporting the conclusions of this article will be published on a digital repository and made publicly available upon acceptance.

Authors' contributions

Lucas D. Lalande: Formal analysis, Data curation, Writing – Original draft, Writing – Review & Editing, Visualization, **Virpi Lummaa:** Conceptualization, Supervision, **Htoo H. Aung:** Investigation, Resources, **Win Htut:** Investigation, Resources, **U. Kyaw Nyein:** Investigation, Resources, **Vérane Berger:** Conceptualization, Writing – Review and Editing, Supervision, **Michael Briga:** Conceptualization, Writing – Review and Editing, Supervision.

Competing interests

None. We declare we have no competing interests.

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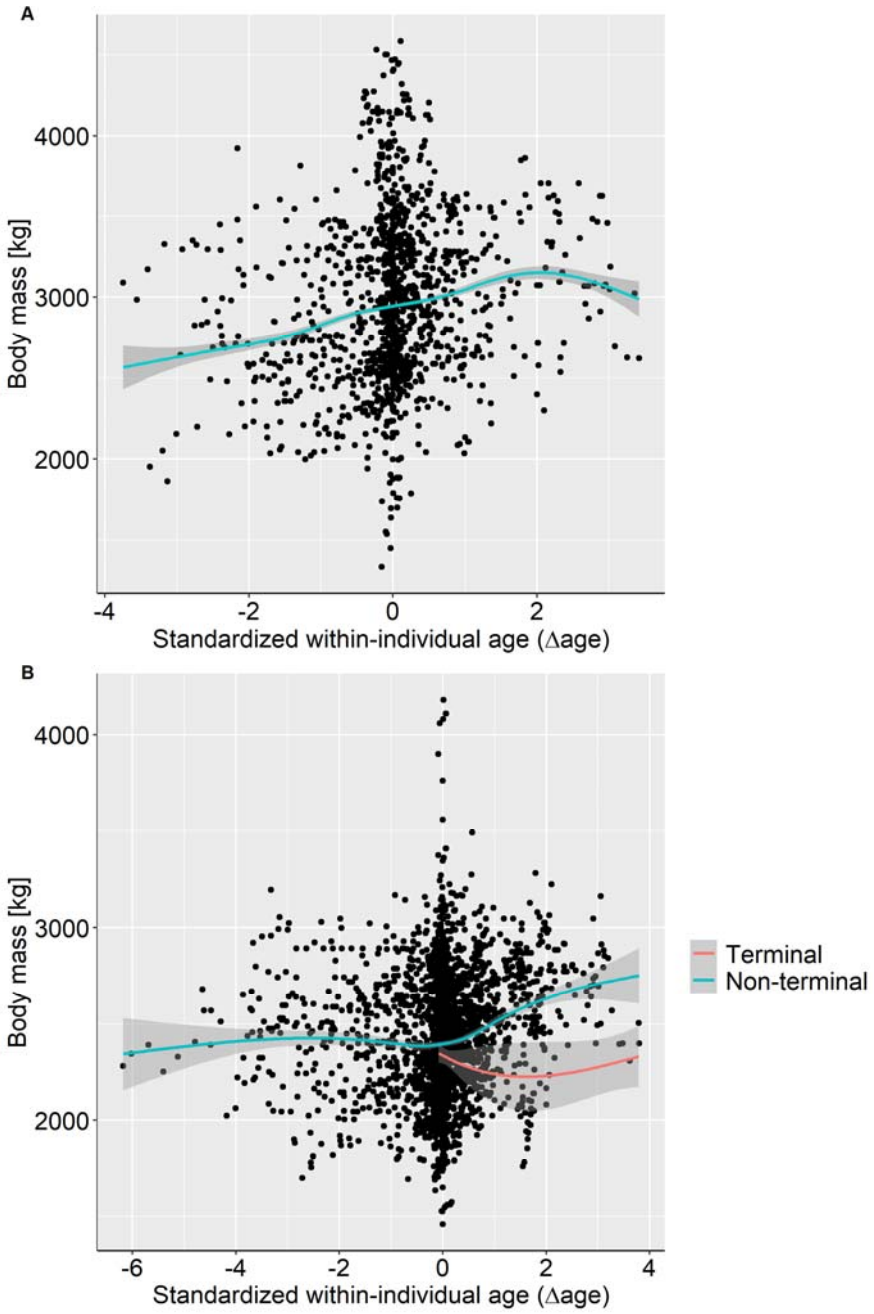

Figure 1. Body mass ageing trajectories of (A) males (n=1,316 measurements on 171 individuals) and (B) females (n=2,570 measurements on 322 individuals) with solid lines showing predictions of the best-fitting GAM models (table 1) and grey areas 95%CI. For females, measurements in the terminal year (red) 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.

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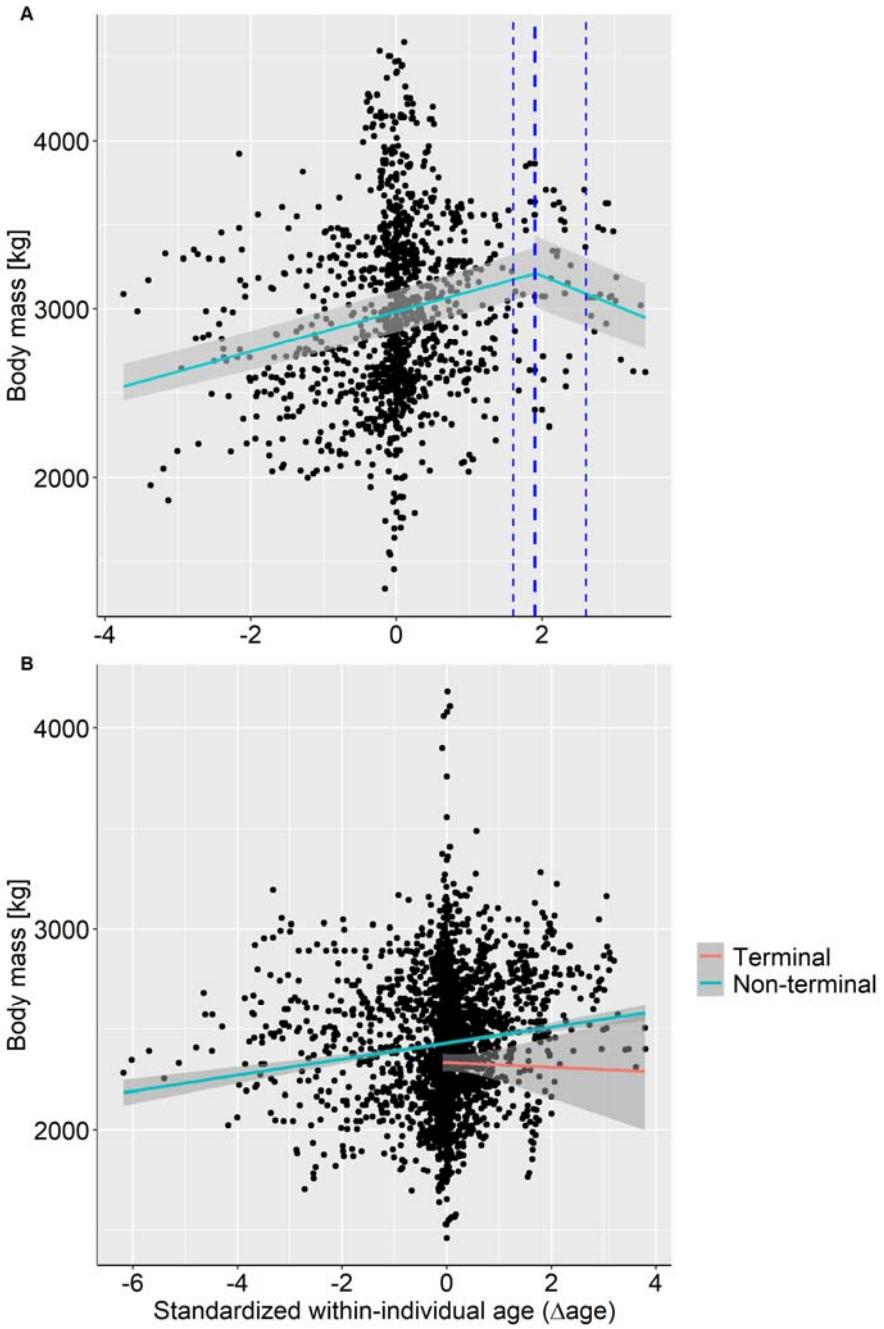

Figure 2. Body mass ageing trajectories of (A) males (n = 1,316 measurements on 171 individuals) and (B) females (n = 2,570 measurements on 322 individuals) with predictions of the best-fitting GLMs (table 1) with grey areas 95%CI. For males, the thick dashed-line shows the threshold age at onset of 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.

Table 1. Best fitting body mass ageing trajectories (bold) for males and females, using GAMs (top) and GLMs (bottom) with 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
GAM							
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**	**0.0**	8.7	-5,613.9	25.8
+terminal	log(bm) ~ terminal + s(Δage) + age-last	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) ~ terminal + s(Δage) + age-last + age-last^2**	10.1	-3,221.3	0.6	**10.9**	**-5,639.7**	**0.0**
GLM							
null	log(bm) ~ 1	3.0	-2,830.3	364.0	4.0	-5,442.9	160.7
linear	log(bm) ~ Δage + age-last	5.0	-3,163.9	30.4	6.0	-5,586.1	17.5
+terminal	log(bm) ~ terminal + Δage + age-last	6.0	-3,158.7	35.6	7.0	-5,592.3	11.3
age-last^2	log(bm) ~ Δage + age-last + age-last^2	6.0	-3,156.4	37.9	7.0	-5,598.7	4.9
+terminal	**log(bm) ~ terminal + Δage + age-last + age-last^2**	7.0	-3,151.2	43.1	**8.0**	**-5,603.6**	**0.0**
Δage^2	log(bm) ~ Δage + Δage^2 + age-last	6.0	-3,178.5	15.8	7.0	-5,571.6	32.0
+terminal	log(bm) ~ terminal + Δage + Δage^2 + age-last	7.0	-3,172.9	21.4	8.0	-5,577.9	25.7
quadratic	log(bm) ~ Δage + Δage^2 + age-last + age-last^2	7.0	-3,171.0	23.3	8.0	-5,584.3	19.3
+terminal	log(bm) ~ terminal + Δage + Δage^2 + age-last + age-last^2	8.0	-3,165.4	28.9	9.0	-5,589.3	14.3
threshold	**log(bm) ~ Δage1 + Δage2 + age-last**	**7.0**	**-3,194.3**	**0.0**	8.0	-5,580.5	23.1
+terminal	log(bm) ~ terminal + Δage1 + Δage2 + age-last	8.0	-3,189.3	5.0	9.0	-5,586.0	17.6
threshold (age-last^2)	log(bm) ~ Δage1 + Δage2 + age-last + age-last^2	8.0	-3,186.7	7.6	9.0	-5,592.6	11.0
terminal	log(bm) ~ terminal + Δage1 + Δage2 + age-last + age-last^2	9.0	-3,181.8	12.5	10.0	-5,596.9	6.7

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