Sex-specific body mass ageing trajectories in adult Asian elephants

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Sex-specific life-histories are thought to shape senescence patterns differently for males and females. In species with marked sexual dimorphism and where one sex is undergoing stronger intrasexual competition, it is expected that this sex ages earlier or quicker. Here, we utilise a unique, longitudinal dataset of a semi-captive population of Asian elephants (*Elephas maximus*) to describe the body mass ageing trajectories in this species with marked sexual dimorphism in size and lifespan, with males being larger and living shorter. Our results show sex-specific ageing trajectories: males gained weight throughout their life, at a diminishing rate until natural death. In contrast, adult female body mass did not change significantly with age until an abrupt decline during the last year of life. Our study shows that sex-specific life-histories shape ageing patterns contrary to those predicted by classical theory and expands the previously described diversity of ageing dynamics.

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

Introduction

Senescence – a gradual age-specific decline in contribution to fitness [1] – has been observed across species [2]. However, the onset and rates of senescence differ both between [2] and within species [3] and between sexes [4]. A main challenge in senescence research is to quantify and explain these differences in onset and rates [*e.g.* 5].

In species with sex-specific intrasexual competition, theory predicts that the sex with the highest intrasexual competition should have the shorter lifespan and show an earlier onset and/or higher rate of senescence [6]. 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, dye young* pace of life [6–8]. Accordingly, in polygynous species where intrasexual competition is higher for males, males often die earlier (15.7% earlier in mammals [9]) and senesce earlier or faster than females [4,8,10–12]. However, recent conceptual developments have shown that this classic association can be disrupted, for example because of condition-dependent extrinsic mortality [9] or canalisation (*i.e.* the more a trait contributes to fitness, the less it should deviate from optimal trait value, with respect to environmental variations [14]), thereby contradicting the theoretically expected earlier or faster ageing in males. The extent to which such phenomena occur in nature remains unknown.

Here, we took advantage of a unique long-term dataset to describe the sex-specific body mass ageing trajectories of an unsupplemented semi-captive population of Asian elephants (*Elephas maximus*) living in natural conditions in Myanmar. Body mass is of interest in the study of senescence because it is positively associated with key life-history traits such as reproduction and lifespan in many non-human species [15]. Accordingly, Asian elephants show seasonal variation in body mass which is positively associated with subsequent survival [16].

However, we know almost nothing on body mass ageing in this species despite the interest of studying ageing on such a long-lived, social and sexually dimorphic non-human species. While females live in kin groups, adult males roam solitary through the forest [17], undergo a more intense intrasexual competition for dominance and mating [17] and are therefore bigger, heavier [18], and shorter-lived (median lifespan: 30.8 years) than females (44.7 years) [19]. Based on this male-biased intrasexual competition and shorter lifespan, we expected males to display earlier and/or faster body mass ageing than females [6,7,20].

Material and methods

Study population

The unsupplemented study population is the world's largest semi-captive Asian elephant population, including around 3,000 individually-marked elephants owned by the government-run Myanma Timber Enterprise (MTE) [21]. These elephants are distributed across Myanmar in forest camps and used as riding, transport and drafting animals. Their birth, death and pedigree details, and morphological measurements have been recorded for almost a century by local veterinarians in elephant-specific logbooks. Elephants work during the day and socialise, mate and forage freely in forests at night (see [22,23] for further details). Consequently, their life-history and lifespan closely resemble that of wild elephants [19].

Data collection and selection

We extracted 1,975 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 [16]) from the 325 working localities ('township') monitored on average every 1.5 years between 1968-2018. When body mass measurements were not available, we estimated body masses using height to the shoulder and chest girth (n = 2,098, r = 0.89, method described in table S1). We obtained a median of 4.0 measurements/individual [2.5-97.5th percentiles: 1.0-38.7], followed for a median of 2.8 years [2.5-97.5th: 0.0-37.3] for a total of 493 elephants (n = 4,073).

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 [18]. The study elephants were aged 18-72 years (mean = 39.3) and born 1941-1999. Age and cohort information were consistent between the sexes, with 171 males (n = 1,378) born 1954-1999 and aged 18-64 years (mean = 37.2), and 322 females (n = 2,695) born 1941-1999 and aged 18-72 years (mean = 40.4).

Statistical analyses

All analyses were performed on R version 4.0.2 [24]. We investigated the age- and sex-specific variation in body mass, 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 ageing trajectories for both sexes separately using general linear mixed models with the function 'lmer' (package 'lme4' [25]) and identified the models that best fitted the data using model selection with the function 'dredge' (package 'MuMIn' [26]). Better-fitting models are indicated by their lower AICc, models <4 ΔAICc are plausible and models become increasingly equivocal up to 14 ΔAICc, after which they become implausible [27]. Visual inspection of model residuals confirmed that these fulfilled all assumptions of distribution and homogeneity without any influential data points or outliers.

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. Here we are interested in within-individual changes in body mass. Because population composition can change with age (*e.g.* selective disappearance), body mass changes at the population level can result from both between-individual and within-individual changes [28]. To capture the within-individual trajectory, we decomposed the age variable in the models into *i)* a 'mean age' term (mean age for all the measurements of the same individual) capturing the between-individual changes with age and *ii)* a 'Δage' term (age at measurement minus the individual's mean age) capturing the within-individual changes with age, following the approach developed in [28]. We mean-centered and standardized all age terms.

Testing ageing trajectories

We tested a number of within-individual ageing trajectories of increasing complexity (linear, quadratic, threshold models, figure S1). To determine whether changes in body mass started at a certain threshold age (figure S1C), we followed the approaches previously developed in [4,29]. Briefly, we tested a series of models varying the threshold in the 'Δage' term between -36 to 22 years with intervals of 1 Δage (= 3.4 years for males and 4.5 years for females). We identified the best fitting threshold model based on the AICc and its confidence intervals using ±4 ΔAIC age range. Ageing is sometimes better described using the time before death (terminal decline). A 'terminal' change (figure S1D) is captured by a binomial factor for whether an individual died during the year following the measurement. To avoid dealing with seasonally-driven terminal effects, we used a terminal decline window of one year prior to death. Note that other time windows gave consistent conclusions (Results section, figure S2). We tested the terminal decline in combination with each ageing trajectories.

Accounting for seasonal and spatial variation in body mass

As body mass variation can be influenced by seasonal, spatial and within-individual factors, we accounted for whether body mass values were measured or estimated, individuals were alive or dead, captive- or wild-born, and the measurement season in the selected models for both sexes (table S3). For females, ID and township were included as random intercepts, but YOB was removed because of insufficient power to estimate its variance [30]. For males, ID and YOB were included and 'township' excluded for the same reasons. Note that for models with only ID as random intercept, results yielded consistent conclusions. Repeating the analyses adding log(height) as a covariate to correct for the allometric relationship between height and body mass gave consistent conclusions (table S4, S5 and S6).

Results

Elephants weighed 1,334-4,582 kg (mean = 2,631.3). Males weighed 1,334-4,582 kg (mean = 3,024.3) and were on average 593.9 kg heavier than females which weighed 1,458-4,181 kg (mean = 2,430.4). This difference was statistically significant (ΔAICc = -257.0, table S2).

At the measurements' starting age of 18 years, the body mass difference between the sexes was reversed, with males weighing on average 478.5 kg less than females, respectively at 1,861.6 kg [95%CI: 1,742.3-1,989.0] and 2,330.1 kg [95%CI: 2,288.6-2,372.3]. However, sexes displayed different body mass ageing trajectories (-78.5<ΔAICc<-75.0, figure 1, table 1 and S2). Males continuously gained weight but the rate of increase diminished with age, as shown by a quadratic within-individual body mass ageing trajectory (ΔAICc = -45.6 compared to a linear trajectory, figure 1A, table 1), with a maximum at the oldest age at measurement of 64 years.

In contrast, females showed a linear within-individual increase in body mass with age (β = 0.013±0.001, ΔAICc = -2.8), followed by a terminal decline in body mass during the last year of life (β = -0.076±0.019, ΔAICc = -7.5, figure 1B and S2) of 184.8 kg [95%CI: 94.7-271.5] (7.3% [95%CI: 3.8-10.8] of the mean adult body mass). The equivalent model containing a terminal decline factor for males was not statistically significant (ΔAICc = +7.3, table 1, figure S3) as the drop in body mass was smaller and overlapped with 0: 27.8 kg [95%CI: -134.0-181.1] or 0.9% [95%CI: -4.5-6.1].

Discussion

We tested for sex differences in body mass ageing trajectories of Asian elephants in which the sexes differ in size, life-history and lifespan. We found that males gained weight at a decreasing rate throughout their lifespan, while females showed no body mass ageing until a 7.3% decline during the last year of life. In Asian elephants, males are more aggressive than females [31], fight more for dominance and show higher rates of mortality at all ages than females [19]. In species with such male-biased intrasexual selection on mortality, classic theory predicts that males should show an earlier onset or accelerated ageing [32]. Indeed, in several polygynous mammals, males had higher rates of body mass declines than females, and this difference was suggested to be due to their higher intra-sexual competition [8,11]. Our results are thus opposite to what expected from classic theory and we here discuss three possible mechanisms and implications of our study.

The lack of body mass decline in males of this highly polygynous species is unlikely to be due to a power issue. First, the median lifespan in males and females is 30.8 and 44.7 years respectively [19]. Our dataset included 114 males (n = 899) and 108 females (n = 1,051) beyond these ages. Second, the MTE retires elephants at the age of 53 years [33], when the elephant's physical condition is insufficient for timbering, and we included 15 males (n = 141) and 57 females (n = 601) beyond that age. Third, we included 5 dead males (n = 65) and 18 dead females (n = 185) to detect for a terminal decline. Although the power was lower for males, power is unlikely to be an issue here because the coefficient for the terminal decline in males was more than 8 times smaller than that of females (β_{males} = -0.009±0.027, $\beta_{females}$ = -0.076±0.019) and, including a male terminal factor resulted in a 7.3 ΔAICc increase relative to the model without decline. Hence, we do not believe the lack of body mass decline in males or the different ageing trajectories between sexes to be driven by the power of the data.

The fact that the observed sex-specific body mass ageing trajectories were opposite to the classic predictions on sexual selection and ageing [32] raises questions regarding the underlying evolutionary mechanisms. Body mass in male elephants plays a predominant role in intrasexual competition [17], and therefore in the contribution to fitness, potentially causing the canalisation of males body mass, thereby preventing its decline [14]. Alternatively, condition-dependent mortality can filter weakest individuals and alter (sex-specific) within-individual ageing trajectories [34]. The rationale is that the disappearance of weaker males that would have declining body masses at older ages can result in a selection of males without body mass declines. Such condition-dependent mortality can occur at evolutionary timescales, but also at an individual timescale. For example, in Asian elephants, males experience higher mortality than females at all ages, including development and calfhood [19], and parasite-associated mortality is higher for males than females at all ages [33]. In polygynous species, raising a male is costlier than raising a female and this could translate in a more pronounced condition-dependent mortality in males during early-life, as suggested in the wild boar (*Sus scrofa*) [35]. Although canalisation and condition-dependent mortality are possible explanations for the absence of male-biased ageing in polygynous species [6], female-biased ageing is not supported in most of the current literature. Our finding that females experienced only a terminal body mass decline is an interesting result. It emphasizes that the chronological age is rarely a perfect estimation of the biological age which can better describe the ‘true biological state’ of an organism [36]. The ‘terminal illness’ hypothesis refers to the age-independent decrease of a trait value, related to the imminent death of the individual [37] and such terminal effects were shown for example for body mass and sexual signals in mammals and birds [38]. Which traits or under which conditions to expect terminal declines remains yet unknown 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.

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.

Data accessibility

The dataset supporting the conclusions of this article will be made publicly available upon acceptance.

Authors’ contributions

HHA, WH and UKN performed field work and data collection. VL, VB and MB designed the study and LL selected, extracted and translated data. LL carried out all statistical analyses with contributions from VB and MB. LL wrote the manuscript and VL, VB and MB critically reviewed it. All authors approved the manuscript for publication and agree to be held accountable for the content therein and approve the final version of the manuscript.

Competing interests

We declare we have no competing interests.

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Table 1. Selected models for males and females (bold). Model comparison describing the population body mass (bm) ageing trajectory. Models ranked from the least to most complex. For each model type, first is presented the model and second its equivalent adding the terminal decline binary factor as a fixed variable ('+terminal'). Models within 4ΔAICc in italic. AICc: Akaike Information Criteria; ΔAICc: relative AICc to the best model; k: degrees of freedom.

Model type	Model	k	Males		Females	
			AICc	ΔAICc	AICc	ΔAICc
linear	log(bm) ~ Δage + mean age	6	-3,174.6	45.61	-5,999.8	22.21
+terminal	log(bm) ~ terminal + Δage + mean age	7	-3,167.5	52.67	-6,010.4	11.58
mean age^2	log(bm) ~ Δage + mean age + mean age^2	7	-3,169.7	50.45	-6,014.6	7.46
+terminal	**log(bm) ~ terminal + Δage + mean age + mean age^2**	**8**	-3,162.7	57.51	**-6,022.0**	**0.00**
Δage^2	**log(bm) ~ Δage + Δage^2 + mean age**	**7**	**-3,220.2**	**0.00**	-5,985.1	36.94
+terminal	log(bm) ~ terminal + Δage + Δage^2 + mean age	8	-3,212.9	7.29	-5,995.6	26.39
quadratic	log(bm) ~ Δage + Δage^2 + mean age + mean age^2	8	-3,215.9	4.32	-5,999.9	22.10
+terminal	log(bm) ~ terminal + Δage + Δage^2 + mean age + mean age^2	9	-3,208.6	11.60	-6,007.3	14.75
threshold	log(bm) ~ Δage1 + Δage2 + mean age + mean age^2	9	-3,213.4	6.75	-6,012.6	9.44
terminal	*log(bm) ~ terminal + Δage1 + Δage2 + mean age + mean age^2*	*10*	-3,206.1	14.08	*-6,019.2*	*2.80*

Figure Captions

Figure 1. Body mass ageing trajectories for *a)* males (N=171, n=1,378) and *b)* females (N=322, n=2,695). Prediction of the models selected (table 1) with 95% confidence intervals. Evidence for a terminal decline in females body mass trajectory. The figure shows significantly lighter individuals during their last year of life (red) compared to the rest of life (blue). Δage: within-individual age; Δage=0: mean age of males (37.2 years) and females (40.4 years). 1 Δage = 3.4 and 4.5 years for males and females respectively.

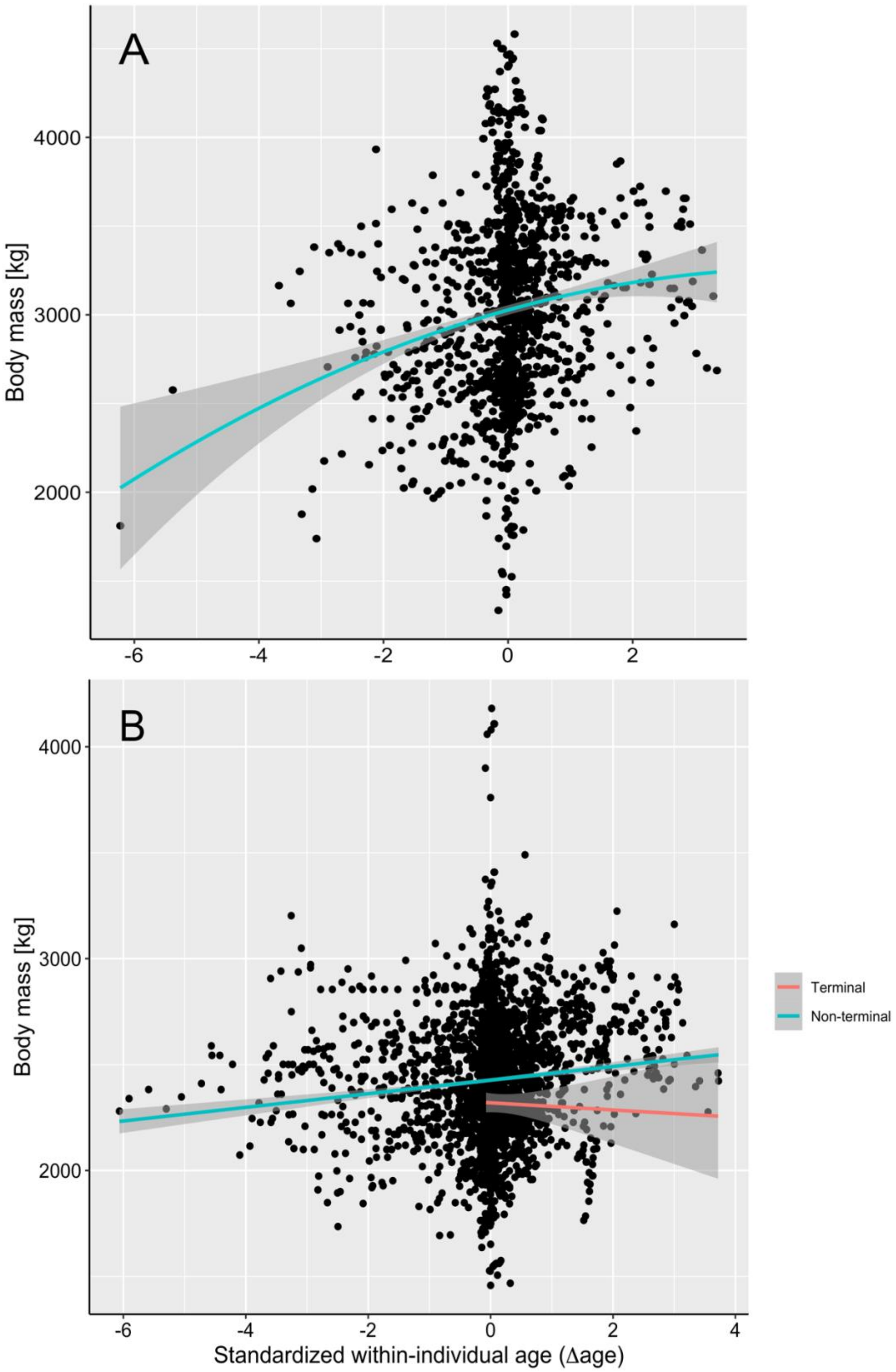
A
Body mass [kg]
4000
3000
2000
-6
-4
-2
0
2
B
Body mass [kg]
4000
3000
2000
-6
-4
-2
0
2
4
Standardized within-individual age (Δage)
Terminal
Non-terminal

Figure 1